



Environmental correlates of wild bee assemblages in pastoral landscapes in Ireland (Hymenoptera, Apidae)

Veronica M. Santorum Crespo

Publication date

01-01-2013

Licence

This work is made available under the [CC BY-NC-SA 1.0](#) licence and should only be used in accordance with that licence. For more information on the specific terms, consult the repository record for this item.

Document Version

1

Citation for this work (HarvardUL)

Santorum Crespo, V.M. (2013) 'Environmental correlates of wild bee assemblages in pastoral landscapes in Ireland (Hymenoptera, Apidae)', available: <https://hdl.handle.net/10344/6520> [accessed 9 Feb 2023].

This work was downloaded from the University of Limerick research repository.

For more information on this work, the University of Limerick research repository or to report an issue, you can contact the repository administrators at ir@ul.ie. If you feel that this work breaches copyright, please provide details and we will remove access to the work immediately while we investigate your claim.



UNIVERSITY *of* LIMERICK

O L L S C O I L L U I M N I G H

ENVIRONMENTAL CORRELATES
OF WILD BEE ASSEMBLAGES
IN PASTORAL LANDSCAPES IN
IRELAND (HYMENOPTERA, APIDAE)

Submitted by

Veronica M. Santorum Crespo

Supervisor: Professor John Breen

Submitted in accordance with the academic requirements for
the Degree of Doctor of Philosophy to the Department of Life
Sciences, Faculty of Science and Engineering, University of
Limerick

June, 2013

DECLARATION

I hereby declare that I am the sole author of this thesis and that it has not been submitted for any other academic award. References and acknowledgements have been made where necessary to the work of others.

Signature: _____ Date: _____

Veronica Santorum Crespo

Department of Life Sciences

Faculty of Science and Engineering

University of Limerick

ACKNOWLEDGEMENTS

I wish to thank:

The Environmental Protection Agency for funding my studies as part of Ag-Biota: Monitoring, Functional Significance and Management for the Maintenance and Economic Utilisation of Biodiversity in the Intensively Farmed Landscape.

Dr. John Breen for his patience, encouragement, support and supervision throughout this study.

Dr. Kevin Hayes for introducing me to and guiding me through the Bayesian analyses of Chapter 10. Dr. Tim Carnus for introducing me to Information theoretic methods. Dr. Jennifer Donlan for getting me started with Geographical Information Systems. Dr. Tomás Murray for his assistance with and validation of bee identifications. Liam Dundon, Glenn Light, Michael Hayes, Katrin Wagner, Elaine Keegan, Jennifer Culloty and others who assisted with fieldwork and the preparation of specimens and data. Diarmuid Mc’Intyre, Gearoid Mc’Intyre, David Santorum and Mairead O’Connor who helped with proof-reading. NPWS and Teagasc staff who helped in contacting landowners. Landowners, who gave access, shared information and provided welcome cups of tea. Colleagues in the Life Sciences department and Ag-biota and AGRI-BASELINE project team members who through their feedback, discussions and encouragement facilitated the development and completion of this project.

And especially my family who gave me the time and support that I required to complete this study.

ABSTRACT

Declines in wild bees have been reported internationally and attributed to habitat loss associated with agriculture. Recent research has led to a better understanding of the responses of bumblebees, especially within mixed, arable or fruit-growing agricultural landscapes. However gaps remain in scientific understanding of the responses of bees, particularly of solitary bees, to agricultural intensification in pastoral landscapes. In general, studies of bee declines have focussed on measures such as total abundance, species richness and diversity indices and there is a need for studies of changes in assemblages' species composition in order to identify resilient and vulnerable species.

The aim of this study is to examine the responses of solitary bees and bumblebees to grassland intensification in lowland, pastoral landscapes. The study identifies factors that influence wild bee diversity, abundance and assemblage composition. The relative importance of landscape composition; agricultural management (considered at the field, farm and landscape level); habitat structure and quality and more immutable environmental conditions such as latitude and longitude, altitude and edaphic factors on bee responses are studied. Based on differences in foraging distances and social behaviour, it is likely that solitary bees and bumblebees respond to anthropogenic change occurring at different scales. This hypothesis is tested.

A field survey of bees across fifty agricultural sites, together with a survey of the environmental conditions at these sites was undertaken. Correlations were investigated using Mantel's tests and Mantel correlograms, Procrustean rotations and indirect gradient analyses with ordinations. The relative importance of environmental variables was evaluated using a combination of methods. The variance in species composition of bee assemblages was decomposed between environmental predictors using distance-based Redundancy Analysis (RDA). Bayesian and Information theoretic methods were used to evaluate the relative importance of predictors of bee diversity and abundance.

The abundance and species richness of bees in pastoral landscapes in Ireland are impacted by intensifying grassland management, with solitary bees showing a response to intensification at the field scale and bumblebees to intensification at the landscape scale. A shift in bee assemblage composition from assemblages dominated by diverse solitary bees to assemblages dominated by a few common bumblebees and a small number of solitary bee species was observed as field management became more intense. This gradient was also associated with a calcicole-calcifuge vegetation gradient and it is not possible to distinguish between the effects of the two factors on bee assemblage. Solitary bees showed greater sensitivity to site management than bumblebees, possibly due to previous local extinctions of more sensitive bumblebee species from the majority of farm sites. A model of extinction order from wild bee assemblages in the face of intensifying grassland management is proposed.

There is high natural variability of bee assemblage composition, associated with solitary bees. Biogeographical influences were more influential in shaping assemblage composition than agricultural management. Spatial effects upon bees were significant for distances up to approximately 10km. Associations with vegetation contributed to this spatial pattern. Autogenic factors were also influential in spatial patterning of solitary bees.

The mechanisms by which intensification of grassland management impacts on bees remain to be identified. To date, agri-environmental schemes have focused on the conservation of hedgerows. The conservation of bees in pastoral landscapes requires initiatives focused on grassland management at both the field and landscape scale. This will aid the conservation of common bee species and the maintenance of pollination services across regions. Rarer bees require conservation initiatives targeted at the locations where they survive. This study has suggested characteristics of such locations which may aid in their identification. The proposed 'order of extinction' model requires validation. It has potential to be used in quantifying the level of impact on bee assemblages and in monitoring the effects of environmental degradation and restoration on wild bees.

THESIS OVERVIEW

Chapter 1: Introduction

This chapter introduces the questions addressed by this thesis and the approach taken to answering them. A literature review introduces the main topics. This is expanded upon in later chapters when further review of the literature places each particular chapter in its scientific context.

Chapter 2: Bumblebee declines in Ireland

Two published papers provide evidence that bumblebees have declined in Ireland.

Chapter 3: Study design and bee sampling methods

The study design is described. Methods used to sample and identify bees are explained. The preparation of the bee data for subsequent analyses is described.

Chapter 4: Measuring landscape composition

Details of the methods used to describe landscape composition, for later bee analyses, are provided. Descriptive statistics provide an overview of the landscape composition of the study region. Landscape variables are reduced to a small number of representative variables. The strongest gradient in landscape composition was in the relative areas of semi-natural or semi-improved grasslands to improved grasslands and was therefore also a measure of agricultural intensity at the landscape scale.

Chapter 5: Measuring field boundary structure and composition

The methods used to measure and summarise field boundary structure and composition are presented. Preliminary analyses show the structural complexity of hedgerows to be correlated with the species composition of solitary bee assemblages.

Chapter 6: Measuring the botanical composition of grasslands

This chapter provides an overview of the dominant gradients in the composition of grassland vegetation within the studied fields. Plant species abundances were reduced from 134 variables to a small number of variables that described these gradients. Preliminary analyses suggested bee species richness but not abundance was correlated with grassland composition.

Chapter 7: Measuring agricultural management intensity

Interviews with farmers were used to quantify the intensity of agricultural management at field and farm level. Analyses explored how this management information could best be reduced to a small number of explanatory variables for analyses of bee responses. Preliminary analyses suggested that the intensity of field and farm management is correlated with bee species richness.

Chapter 8: Bee-vegetation linkages and spatial pattern in pastoral agri-ecosystems

Correlations between the composition of bee and plant assemblages are tested. Methods such as Mantel tests and Procrustes tests allow assemblage composition to be considered as species abundances. The composition of plant assemblages is also used to integrate information on environmental conditions, on vegetation structure and on site history and the associations of bees with such factors tested indirectly.

Spatial patterning in bee and plant assemblages is studied using correlograms and the contribution of plants to the spatial patterning in bees is determined.

Key findings include significant correlations between bee and vegetation assemblages; species-rich hedgerows are associated with species rich assemblages of solitary bees but not bumblebees; spatial pattern is significant at distances less than 10km.

Chapter 9: Environmental conditions associated with the species composition of bee assemblages.

Variance partitioning is used to identify major influences shaping bee assemblages. The relative importance of geographical location, farm management, landscape composition and habitat composition and structure on the composition of bee assemblages in lowland grasslands in southern Ireland is determined.

A North-east to South-west gradient was identified as the primary environmental gradient shaping wild bee assemblages, predominantly via the responses of solitary bee species. A shift in bee assemblage composition from assemblages dominated by diverse solitary bees to assemblages dominated by a few common bumblebees and a small number of solitary bee species was noted as field management became more intense.

Chapter 10: Environmental conditions associated with the abundance and diversity of bees in pastoral landscapes

Frequentist methods, information-theoretic methods and Bayesian methods are used to rank the relative importance of landscape composition, agricultural management intensity, habitat composition and structure and location on the abundance and diversity of bees. Each statistical approach provides different outputs, which together enhance understanding of the problem. Bumblebees and solitary bees are predicted to differ in their relative vulnerabilities to environmental factors and are analysed separately.

Impacts on bees are detected more readily as reductions in diversity and abundance rather than shifts in species abundance composition of assemblages. Intensifying pastoral management has a strong depressing influence on the abundances and diversity of both solitary bee and bumblebee guilds. The level at which agricultural intensification was measured was important in detecting impacts: field level intensification was associated with solitary bee responses and landscape level intensification associated with bumblebee responses.

Chapter 11: Conclusions

The main findings of this thesis are integrated. Their contribution to scientific understanding of the responses of wild bees to environmental factors in pastoral agri-ecosystems is presented. Implications for the conservation of wild bee populations and assemblages in grassland-dominated landscapes are discussed.

A model of ‘order of extinction’ from bee assemblages in Ireland and the UK is proposed. The potential of bees as indicators of change in the environment is evaluated.

TABLE OF CONTENTS

CHAPTER 1: Introduction	41
Introduction	43
Concerns about declines in wild bee populations	44
How does pastoral agriculture impact on bees?	45
Variability in species responses	46
Bees as bio-indicators	48
Purpose of the study.....	48
CHAPTER 2: Bumblebee declines in Ireland	51
CHAPTER 3: Study design and bee sampling methods	75
3. 1. Sampling Design.....	77
Randomised block design	78
3. 2. Bee Data.....	81
3. 3. Environmental Data.....	86
Assumptions and Limitations.....	86
Assumptions associated with these methods	86
Limitations of the methods used	87
Species names: convention used	88
CHAPTER 4: Measuring landscape composition.....	89
4. 1. Introduction	91
4.1.1. Describing landscape composition	91
4.1.2. The need to consider scale	93
4. 2. Methods.....	95
4.2.1. Data collection to describe landscape composition.....	95
4.2.2. Methods of Analysis	98
Descriptive statistics to describe landscape composition within the study region	98
Analysis methods to reduce landscape variables to a few summary variables.....	99
Using PCA axes scores.....	99

Using landscape types	99
Using one or more habitat areas measured to summarise landscape composition	101
Analysis methods to select the best variables to summarise landscape composition for bee analyses.....	101
Univariate analyses.....	101
Multivariate analyses.....	103
4. 3. Results.....	104
4.3.1. Overview of landscape composition	104
4.3.2. Data reduction of landscape composition set of variables	107
Habitat availability	107
Using PCA axes scores	107
Using landscape types.....	107
Using one or more habitat areas measured to summarise landscape composition	108
4.3.3. best variables to describe landscape composition for bee analyses.	113
Univariate analyses.....	113
Multivariate analyses	114
4. 4. Discussion and conclusions	117
CHAPTER 5: Measuring field boundary structure and botanical composition	119
5. 1. Introduction	121
5. 2. Methods.....	122
5.2.1. Data collection methods.....	122
Structural survey	122
Botanical survey	122
Methods used to measure supplementary environmental data.....	123
5.2.2. Methods of Analysis	124
Descriptive analyses to provide an overview of field boundaries within the study region.....	124
Field boundary structure	124

Field boundary botanical composition	124
Analysis methods to summarise field boundary structure and composition to a few variables	125
Summarising field boundary structure	126
Summarising botanical composition of wooded field boundaries	127
Summarising structure and composition of field boundaries with one measure	128
Analysis methods to select the best variables to summarise field boundary composition and structure for bee analyses.	128
5. 3. Results.....	130
5.3.1. an overview of field boundary structure and composition within the study region.....	130
Structure of field boundaries in the study region.....	130
Botanical composition of field boundaries in study region	131
Relationship between indicator species abundances, composition indices and NMDS of field boundary woody vegetation.....	135
5.3.2. data reduction of field boundary structure and composition to a few variables	136
PCO of field boundary woody vegetation.....	141
5.3.3. best variables to describe field boundaries for bee analyses	145
5. 4. Discussion and conclusions	146
CHAPTER 6: Measuring the botanical composition of grasslands.....	149
6. 1. Introduction	151
6. 2. Methods.....	151
6.2.1. Data collection methods.....	151
Botanical survey method	151
Methods used to measure supplementary environmental data.....	152
6.2.2. Analysis methods to describe grassland composition within the study region	152
6.2.3. Analysis methods to reduce grassland botanical composition to a few summary variables	153
6.2.4. Analysis methods to select the best variables to summarise grassland botanical composition for bee analyses.....	155

6. 3. Results.....	156
6.3.1. Overview of grassland botanical composition	156
6.3.2. Data reduction of grassland botanical composition to a few variables.	162
6.3.3. Best variables to describe grassland botanical composition for bee analyses.....	167
6. 4. Discussion and conclusions	167
CHAPTER 7: Measuring agricultural management intensity.....	169
7. 1. Introduction	171
7. 2. Methods.....	174
7.2.1. Data collection methods.....	174
7.2.2. Analysis methods to describe farm management within the study region	175
7.2.3. Analysis methods to reduce farm management set of variables to a few summary variables.....	176
Principal co-ordinates analysis to summarise field management	177
Checking if farm types could be used to summarise field management	178
Checking if a natural typology of farms emerged from their field management	178
Checking if one field management variable could summarise overall field management data.....	178
7.2.4. Analysis methods to select the best variables to describe farm management for bee analyses	179
7. 3. Results.....	180
7.3.1. Overview of agricultural management within the study region	180
7.3.2. Reduction of farm and field management data to a few summary variables	198
7.3.3. Best variables to describe farm management for bee analyses.....	202
7. 4. Discussion and conclusions	203

CHAPTER 8: Bee-Vegetation linkages and spatial pattern in pastoral agri-ecosystems.....	207
8. 1. Introduction	209
Vegetation – bee associations	209
Spatial Pattern	211
8. 2. Methods.....	213
8.2.1. Data preparation.....	213
8.2.2. Reduction of dimensionality	214
NMDS solutions	214
Indices summarising vegetation composition	215
8.2.3. Analysis methods	215
Mantel correlograms to examine spatial effects on bees and vegetation composition.	216
Mantel Test.....	218
Procrustes Test	219
8.2.4. Partial Mantel Analysis.....	219
Partialling out the spatial effect from bee-vegetation correlations	219
Partialling out the effects of vegetation from bee-space correlations.....	220
Partial Mantel correlograms.....	220
Partialling out the effects of vegetation from bee-space correlations.....	221
Partialling out the effects of sampling location from bee-space correlations.....	221
Rotational vector fitting	221
Correlations between vegetation indices and bee composition	221
Identification of species influential in bee - plant correlations	222
8. 3. Results.....	223
8.3.1. Preliminary Exploration.....	223
8.3.2. Mantel correlograms to examine spatial effects on bees and vegetation composition.	223
8.3.3. Correlations between composition of bee assemblages and grassland and hedgerow vegetation.....	227
Solitary bees and vegetation, given sampling location and space	228
Bumblebees and vegetation, given sampling location and space	228

8.3.4. Partial Mantel correlograms	229
8.3.5. Rotational vector fitting: correlations between vegetation indices and bee composition	231
8.3.6. Rotational vector fitting: identification of species which were particularly influential in the correlations between bee and plant assemblages.....	235
Grassland plant species correlations with bee composition	235
Hedgerow tree and shrub species correlations with bee composition	237
Solitary bee species correlations with vegetation	242
Bumblebee species correlations with vegetation.....	243
8. 4. Discussion	247
8.4.1. Plant and bee assemblage associations	247
Plant assemblage qualities driving the association with bee assemblages	248
Associations with grassland vegetation	248
Soil moisture	248
Grassland ‘semi-naturalness’ gradient	249
Grassland succession gradient.....	250
Calcifuge-Calcicole grassland gradient	250
Associations with hedgerow vegetation	251
Hedgerow diversity gradient	251
Insights into causes of vulnerability among bumblebee species	252
To what extent are the correlations between bees and plants driven by spatial dependence?.....	254
Spatial Pattern	255
Summary.....	257
CHAPTER 9: Environmental conditions associated with bee species composition	259
9. 1. Introduction	261
Geographical location and bee assemblage composition	262
The importance of habitat quality in determining bee assemblage composition.....	265

The importance of agricultural management intensity in determining bee assemblage composition	267
The importance of landscape in determining bee assemblage composition	270
Summary.....	271
9. 2. Methods.....	272
Survey methods	272
Methods of statistical analyses.....	276
Selection of distance measure and constrained ordination method	276
Stepwise model selection using all variables to develop a model to explain the variance in composition of wild bee assemblages	278
Decomposing the variance in composition of wild bee assemblages	278
Decomposing the variance in composition of solitary bee assemblages and bumblebee assemblages.....	281
Permutational MANOVA testing for differences between bee assemblages of farms managed intensely and extensively and between landscapes.....	281
9. 3. Results.....	282
9.3.1. Model derived for all wild bees by automatic backwards stepwise selection	282
9.3.2. Partitioning of variance in bee assemblages	283
First tier of decompositions: quantifying the relative importance of spatial and environmental influences' pure and shared effects.	283
Decomposition of variance, between spatial and environmental influences, for all wild bees	283
Decomposition of variance, between spatial and environmental influences, for solitary bees	283
Decomposition of variance, between spatial and environmental influences, for bumblebees	284
9.3.3. Importance of Geographical Location	286
Second tier of decompositions: quantifying the relative importance of environmental influences' pure and shared effects.	287
9.3.4. Importance of environmental factors in influencing bee assemblage structure	288

9.3.5. Species trends	291
Species responses to spatial model for all wild bees (M3).....	291
Species responses to environmental model for all wild bees (M2).....	291
Species responses to environmental model for solitary bees (M1)	294
9.3.6. Permutational MANOVA testing for differences between bee assemblages of farms managed intensely and extensively and between landscapes.	296
Agricultural intensity at the field level.....	296
Agricultural intensity at the farm level	296
Agricultural intensity at the landscape level	296
9. 4. Discussion	297
9.4.1. Spatial effects on bee assemblage composition in lowland pastoral landscapes	297
Relative importance of spatial influences	297
Spatial gradients influencing bee assemblage composition.....	298
9.4.2. Environmental influences on bee assemblage composition in lowland pastoral landscapes.....	299
Effects of landscape composition on bee assemblage composition.....	300
Effects of habitat quality on bee assemblage composition	301
Effects of agricultural management on bee assemblage composition ...	302
Summary.....	304
CHAPTER 10: Environmental conditions associated with bee abundance and diversity	307
10. 1. Introduction	309
10.1.1. Literature review	309
10. 2. Methods.....	314
10.2.1. Preparation and preliminary exploration of data	314
10.2.2. Identification of major environmental predictors using stepwise multiple regression	317

10.2.3. Ranking of predictor variables using Bayesian methods	318
10.2.4. Ranking of predictor variables using Information-theoretic methods	319
10.2.5. Post-hoc model checks	320
10.2.6. Predicting abundance and diversity of bees in three scenarios using averaged models.....	320
10.2.7. Examining the extent to which the effects of influential environmental variables were shared with location	322
10. 3. Results.....	324
10.3.1. Correlations between response and explanatory variables	324
10.3.2. Modelling using three different statistical paradigms to identify the most important environmental influences on bees	325
10.3.3. Using stepwise model selection to identify the most important influences.....	326
10.3.4. Ranking the relative importance of predictor variables using Bayesian methods	329
10.3.5. Ranking the relative importance of predictor variables using Information Criterion methods and evidence ratios	331
10.3.6. Post-hoc checks on residuals of averaged models	341
Predictions of bee abundances and diversity, based on averaged models, in three scenarios	341
10.3.7. Effects of influential environmental variables shared with location	345
10.3.8. Bringing together the main findings from the three statistical approaches.....	346
10. 4. Discussion	348
CHAPTER 11: Overall discussion and conclusions	363
11. 1. A review of study goals.....	365
11. 2. The main findings.....	366

Natural environmental gradients shape bee assemblages in lowland pastoral landscapes of Southern Ireland	366
North-South and East-West gradients.....	366
Vegetation linkages	367
Spatial effects	369
Anthropogenic Impacts	369
Grassland management impacts	369
Other landscape associations with bees.....	373
11.2.1. Bees as indicators?.....	373
Number of genera as indicators of species diversity and functional diversity	373
Bee species as indicators of response to climatic change	373
Species and guilds as indicators of the impacts of agricultural intensification on bee assemblages.....	374
Spatial variability as an indicator	375
Difficulties associated with using bees as indicators	375
11. 3. Recommendations.....	377
11.3.1. Suggestions for further research.....	377
Spatial pattern in bee assemblages	377
Rare bumblebees indicate HNV.....	377
Order of extinction model	377
Bumblebee diversity hotspots.....	378
Disentangling the effects associated with area of woodland, scrub and young forestry	378
Habitat value of calcareous grasslands for bees.....	378
Diversity at the level of genera as a measure of functional diversity of bees	379
Processes by which intensive field management impacts on bees	379
Climate change	380
Dairy farms and hedgerows.....	380
Methodological issues.....	380
11.3.2. Recommendations for conservation	381
REFERENCES	386
APPENDICES	416
RAW DATA	on CD

LIST OF ABBREVIATIONS

ACE	abundance-based coverage estimator
ag.	species aggregate
AIC	Akaike information criterion
ANOVA	Analysis of variance
Ball	Ballylanders
Barr	Barrigone
BIC	Bayesian Information Criterion
CBD	Convention on Biological Diversity
CCA	Canonical Correspondence Analysis
Co.	County
Corine	Corine Land Cover 2000 database, part of the European Commission programme to COoRdinate INformation on the Environment
CV	Coefficient of variation
dbPCA	distance based Principal Component Analysis
DCA	Detrended Correspondence Analysis
e.g.	exempli gratia
EC	European Commission
EPA	Environmental Protection Agency
EV	posterior distribution mean
FBEGS	The Field Boundary Evaluation and Grading System (FBEGS) Index
FIPS	Forest Inventory and Planning System
FTB	Full <i>Taraxacum officinale</i> ag. bloom
GCV	Generalized Cross-Validation
GIS	Geographical Information System
GPS	Global Positioning System
ha	hectare
IMS	Industrial Methylated Spirit
IUCN	International Union for Conservation of Nature
Jack1	first-order Jackknife estimate
kg	kilogram
Ln	Natural logarithm
log	logarithm
MANOVA	Multivariate analysis of variance
NHA	Natural Heritage Area
NMDS	Non-metric Multidimensional Scaling

NRC	National Research Council (United States)
NPWS	National Parks and Wildlife Service
OSI	Ordnance Survey Ireland
p	probability
p!	posterior probability
PCA	Principal Component Analysis
PCO	Principal Coordinates Analysis
pers. comm.	personal communication
QQ plot	plot of the quantiles of two distributions against each other
RDA	Redundancy Analysis
REPS	Rural Environment Protection Scheme
SAC	Special Area of Conservation
SD	standard deviation
Sobs	Species observed
SS	Sum of squares
Tipp	Tipperary
TSR	Total Species Richness
UK	United Kingdom of Great Britain and Northern Ireland
USDA-ARS	United States Department of Agriculture, Agricultural Research Service
wAIC	Akaike weight
ε	Term in linear regression models for unexplained information captured by residuals.

LIST OF FIGURES AND PLATES

CHAPTER 3: Study design and bee sampling methods	75
Figure 3.1. Sampling design showing how study farms were to be stratified along a gradient of agricultural management intensity and sampled in blocks of increasing semi-natural habitat area (A-E)	77
Figure 3.2. Map of study region showing location of sampling sites in Counties Tipperary and Limerick in the Republic of Ireland	80
Figure 3.3. Randomised species accumulation curves for three local areas: Ball=Ballylanders, Barr= Barrigone, Tipp = Tipperary. X axis as follows: (i) x= samples on linear scale. (ii) x= individuals observed on linear scale. (iii) x= samples on log2 scale. (iv) x= individuals observed on log2 scale. Y axis = number of species observed.....	84
Figure 3.4. Nonparametric estimator curves (ACE, Chao1, Chao2 and Jack1) for three local areas: Ballylanders, Barrigone, Tipperary. X = number of sampling units. Y = estimated number of species. Mean= estimated total species richness calculated as mean of nonparametric estimates.	85
CHAPTER 4: Measuring landscape composition.....	89
Figure 4.1. Example of a habitat map , here for a 500m radius circle around the sampling point. Legend explains abbreviations used for habitat types throughout chapter.....	97
Figure 4.2. PCA of habitat composition (within 100m radius of each sampling point) showing major landscape gradients distinguishing study farms.....	109
Figure 4.3. PCA correlation biplot of landscape composition showing areas of habitats and landuse at each site: (i) intensively managed grassland, (ii) boundary habitat, (iii) semi-natural / semi-improved grassland and (iv) semi-natural woodland, scrub and young forestry. Size of bubble represents relative area of habitat component around that site. Red contour lines show a smooth fitted surface of estimated area for each habitat type, fitted using a generalized additive model using the R function <i>ordisurf</i>	110

Figure 4.4. PCA correlation biplot of sites' habitat composition showing sampling location: blue=West Limerick; red =East Limerick; black = Central Limerick and green= Tipperary	111
Figure 4.5. Three dimensional graphs showing areas of semi-natural habitats in three landscape types. Intensive landscapes (Type 1) were defined as >1.5ha intensive grassland area, intermediate landscapes (Type 2) as >1ha & <1.5ha intensive grassland, semi-natural landscapes (Type 3) as <1ha intensive grassland. Colours show location: blue=West Limerick; red =East Limerick; black = Central Limerick and green= Tipperary.	112
Figure 4.6. Boxplots showing area of semi-natural habitat present in each landscape type: Type 1= Intensive landscape (mean=21.1% semi-natural habitat, std.dev=11.8, n=26) Type 2=Intermediate landscape (mean =60.3% semi-natural habitat, std.dev=3.7, n=10) Type 3=Semi-natural landscape (mean =87.1% semi-natural habitat, std.dev=9.2, n=20)	113
Figure 4.7. Solitary bee NMDS (Jaccard distances for presence-absence data) showing significant correlations with landscape composition at a scale of 100m radius (permutation testing across entire dataset). Length and direction of arrows show correlations with: ForestA = area of coniferous forestry; NatwoodA= area of semi-natural woodland, scrub and very young forestry plantations. Size of symbol reflects area of habitat around that site. Sites with no nearby woodland or forestry are shown as black crosses. Green= Sites with nearby woodland. Red (2 only)= Sites with mature coniferous forestry nearby.....	116
Figure 4.8. Bumblebee NMDS (Jaccard distances for presence-absence data) showing significant correlations with landscape composition at a scale of 100m radius (red = significant at $p=0.05$ with permutation testing across entire dataset, green= significant at $p=0.05$ with permutation testing in blocks defined by sampling location). Length and direction of arrow show correlations with: (a) Axis 2 = site scores on 2nd axis of landscape composition PCA which reflected a gradient from historically unenclosed and now wooded landscape to historically enclosed landscape; (b) WoodA= area of semi-natural woodland, scrub and very young forestry plantations; (c) BuiltA = area of buildings, roads, car-parks and active quarries.....	117

CHAPTER 5: Measuring field boundary structure and botanical composition	119
Figure 5.1. Cluster dendrogram of sites based upon their field boundary's woody vegetation (hierarchical cluster analysis using average agglomeration on Bray Curtis dissimilarity matrix).....	132
Figure 5.2. Biplot of NMDS of woody vegetation of field boundaries showing species and sites associated with the two hedge groups identified by cluster analysis together with correlations with altitude, location and soil pH. (POINT_X= Easting coordinate, POINT_Y= Northing coordinate, pH= soil pH, ALT=altitude.)	133
Figure 5.3. NMDS graphs showing the observed and modeled abundance of Indval Indicator Species (i) <i>Crataegus monogyna</i> , (ii) <i>Fraxinus excelsior</i> , (iii) <i>Hedera helix</i> , (iv) <i>Rosa canina</i> , (v) <i>Rosa pimpinellifolia</i> at sites in the two hedgerow groups identified by cluster analysis. The size of symbol is proportional to observed abundance of indicator species. The two hedge groups described are delineated in black. Red arrows indicate the strength and direction of significant linear correlations between species abundance and the ordination. Red contour lines show a smooth fitted surface of estimated abundance of each indicator species, fitted using a generalized additive model using the R function <i>ordisurf</i>	135
Figure 5.4. Scatterplots (3d) of variables describing field boundary structure. Jitter has been applied to keep all datapoints visible. Boundaries are coloured by [i] earthen bank height and [ii] presence of drain. Group A hedges were wider than tall and structurally complex. Group B hedges were tall, wide and complex, and generally also had a high bank and a drain present. Group C hedges were low, narrow and simple in structure. Group D hedges were tall, narrow and of low structural complexity.	137
Figure 5.5. Correlations and dotplots showing how the Structural Index is associated with variables describing field boundary structure:.....	138
Figure 5.6. NMDS graphs of hedgerow composition showing (i) species number, S and (ii) Inverse Simpson's Index, InvSimp, at each site for the two main hedgerow groups. Arrows indicate the strength and direction of linear correlations between species number ($p < 0.05$) and Inverse Simpson's index	

($p < 0.05$) and the ordination. Red contour lines show estimated values of S and InvSimp fitted using a generalized additive model using the *vegan* function, *ordisurf*..... 140

Figure 5.7. Biplots of hedgerow composition PCO, (i) first 2 axes of PCO, (ii) axes 2 and 3 of PCO..... 141

Figure 5.8. NMDS biplots of field boundary botanical composition showing how structural characteristics of field boundaries are correlated with woody vegetation (i) hedgerow height, *envfit* $r^2 = 0.15$, $p = 0.002$, (ii) hedgerow width, *envfit* $r^2 = 0.10$, $p = 0.043$ (iii) bank height, *envfit* $r^2 = 0.31$, $p = 0.001$ and (iv) Structural Index, *envfit* $r^2 = 0.30$, $p = 0.069$. The two main hedgerow groups described are delineated in black. 144

Figure 5.9. Indirect gradient analysis of correlation between physical structure of field boundaries and NMDS of solitary bee species (using Jaccard distances for presence/absence data (stress=0.19)) Arrow indicates the strength and direction of linear correlation between Structural Index and solitary bee composition, *envfit* $r^2 = 0.31$, $p = 0.002$. Red contour lines show estimated values of Structural Index fitted using a generalized additive model using the R function *ordisurf*..... 146

CHAPTER 6: Measuring the botanical composition of grasslands..... 149

Figure 6.1. Level of stress associated with different numbers of axes in NMDS ordination of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization)..... 153

Figure 6.2. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21) showing correlations of soil conditions with botanical composition, [i] shows strength and direction of correlations with soil conditions, significant at $p = 0.05$. Red contour lines in [ii]-[iv] represent a smooth fitted surface for each edaphic variable: soil phosphate (P), soil organic matter (OM) and soil pH (pH) respectively, fitted using generalized additive models using the R function *ordisurf*. Open circles = species, a selection of which are labelled. Solid circles = sites..... 158

Figure 6.3. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species

composition and cover (stress = 0.21) showing correlations of field management with botanical composition. Open circles = species, a selection of which are labelled. Solid circles = sites. [i] Correlation with nitrogen fertiliser application. [ii] Correlation with reseeded (red = reseeded, black = not reseeded in previous 15 years). [iii] Correlation with grazing and cutting regime. Sites coloured by management, see legend..... 160

Figure 6.4. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21) showing correlations of geographical location with botanical composition. Open circles = species, a selection of which are labelled. Solid circles = sites, coloured by local area: blue=West Limerick, red =East Limerick , green =Tipperary and black= other areas of County Limerick. [i] Correlation with location summarised by Easting and Northing coordinates. [ii] Correlation with altitude in metres..... 161

Figure 6.5. Three dimensional ordination plot of PCO of grassland vegetation (Bray Curtis distance) sampled by species composition and cover. 3 axes explained 35.6% total variance. Red= reseeded fields, Black = not reseeded within previous 15 years. 163

Figure 6.6. Biplot showing strength and direction of correlations of grassland vegetation indices with NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21). All correlations are significant at $p < 0.05$. Ellen_Water = mean Ellenberg score for soil moisture, Ellen_N = mean Ellenberg score for soil Nitrogen, Ellen_pH = mean Ellenberg score for soil pH, SpNo = species number, Simpsons = 1-Simpson's Index..... 166

CHAPTER 7: Measuring agricultural management intensity..... 169

Figure 7.1. Frequency histograms showing farm size, stocking levels and stocking density, participation in environmental scheme and farming activity within sample, $n=49$. (NB sample was stratified to capture a range of intensities of farm management and therefore has more small and 'less intensive' farms than would have been captured by a random sample.) 180

Figure 7.2. Frequency of fertiliser use upon sampled fields. (Note: fields that received a fraction of an annual application of fertiliser e.g. 0.3 or 0.5, received one application per 3 years or 2 years respectively.) (NB stratification of sample means that more small and ‘less intensive’ farms are included than would have been captured by a random sample.)	182
Figure 7.3. Frequency of different grazing and cutting regimes among sampled fields. Key: 1= rotation grazing + cut; 2= two cuts; 3 = one cut early summer and grazing; 4= one cut late summer and grazing; 5= continuous grazing, no cut.	183
Figure 7.4. Frequency of chemical use, reseeding and hedgerow management in sampled fields. Key: 1= absence of management activity, 2 = active management	184
Figure 7.5. Graphs showing fertiliser applications, farming activity and stocking density (Livestock units per hectare, LU/ha) in relation to farm size.	186
Figure 7.6. Boxplots showing stocking density (Livestock units per hectare, LU/ha) in relation to farming activity and participation in environmental scheme. Key: dairying activity: 1= nondairying, 2 = dairying; participation in environmental scheme: 1=conventional farm, 2= participant.	187
Figure 7.7. Three dimensional graph showing total nitrogen applied to sampled field [kg/ha] on (i) non-dairy farms and (ii) dairy farms showing participation in agri-environmental scheme and farm size. Key: Black = conventional farm; Red = REPS and Green = Organic.....	188
Figure 7.8. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to dairying activity. <i>Farm type:</i> 1 = nondairying; 2 = dairying farms. <i>Grassland management:</i> 1 =short rotation grazing; 2= 2 cuts of silage; 3= 1 cut in early summer + grazing; 4= 1 cut in mid-late summer + grazing; 5= not cut and extensively grazed. <i>Reseed:</i> 1= Not reseeded, 2= reseeded. <i>Spray:</i> 1= Not sprayed, 2= sprayed. <i>Hedge cut:</i> 1= Not cut, 2= Cut)	190
Figure 7.9. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to participation in agri-environmental scheme. Farm	

type: 1 = conventional; 2 = farms in REPS scheme. *Grassland management*: 1 =short rotation grazing; 2= 2 cuts of silage; 3= 1 cut in early summer + grazing; 4= 1 cut in mid-late summer +- grazing; 5= not cut and extensively grazed. *Reseed*: 1= Not reseeded, 2= reseeded. *Spray*: 1= Not sprayed, 2= sprayed. *Hedge cut*: 1= Not cut, 2= Cut) 191

Figure 7.10. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to farm type classified by participation in environmental scheme and dairying activity. *Grassland management*: 1 =short rotation grazing; 2= 2 cuts of silage; 3= 1 cut in early summer + grazing; 4= 1 cut in mid-late summer +- grazing; 5= not cut and extensively grazed. *Reseed*: 1= Not reseeded, 2= reseeded. *Spray*: 1= Not sprayed, 2= sprayed. *Hedge cut*: 1= Not cut, 2= Cut) 193

Figure 7.11. Dotplots showing levels of annual Nitrogenous fertiliser applied, broken down by type of grassland management, farm activity and participation in an environmental scheme. 195

Figure 7.12. Correlation matrix and graphs visualising associations between field management practices. Farm symbols and grassland management categories as in Figure 7.11. *Reseed*: 1= Not reseeded, 2= reseeded. *Spray*: 1= Not sprayed, 2= sprayed. *Hedge cut*: 1= Not cut, 2= Cut. 196

Figure 7.13. Conditional plot showing total nitrogenous fertiliser applied to fields that were reseeded and not reseeded under different grazing and harvesting regimes. (Symbols as in Figure 7.11.)..... 197

Figure 7.14. Indirect gradient analyses showing correlations of fertiliser use with PCO of field management data (using Gower's distances). Symbol size represents the value, for that site, of the fertiliser variable being illustrated. Arrows show strength and direction of correlations with fertiliser variables (all significant at $p=0.05$). Red contour lines show a smooth fitted surface for each fertiliser variable: total Nitrogenous fertiliser (Tot_N), total Phosphate fertiliser (Tot_P) and number of fertiliser applications (Tot_apps), fitted using generalized additive models using the R function *ordisurf*..... 200

Figure 7.15. Indirect gradient analyses showing correlations between use of chemical sprays, reseedling and hedgerow management and PCO of field

management data (using Gower's distances). Symbol colour represents the value, for that site, of the variable being illustrated: Black =1 (low intensity management) and Red =2 (high intensity management). Centroids (mean score of the variable on each axis) are shown by position of label. 201

Figure 7.16. Boxplots showing number of bee genera on fields that have been reseeded and fields that have not been reseeded within previous 15 years. (Note: only 14 sites of 55 had been reseeded). 203

CHAPTER 8: Bee-Vegetation linkages and spatial pattern in pastoral agri-ecosystems..... 207

Figure 8.1. Series of analyses used in this chapter. 216

Figure 8.2. Plots showing ecological distances against geographical distance (m) for solitary bees, bumblebees, grassland and hedgerow vegetation. Smaller values of Jaccard and Bray distances indicate higher similarity between species assemblages at two sites. Blue dashed line shows simple linear regression and red line shows Loess smoother. 224

Figure 8.3. Mantel correlograms for (a) grassland vegetation, (b) hedgerow vegetation, (c) solitary bee assemblages and (d) bumblebee assemblages. Positive values of the Mantel correlation coefficient indicate that assemblages are more similar (positive autocorrelation) than expected for randomly associated pairs of observations and negative values mean that assemblages are less similar than expected for randomly associated pairs of observations (negative autocorrelation). Solid symbols indicate significant correlations between changing bee composition and geographical distance at $p=0.05$. See Table 8.3 for more detail. 225

Table 8. 3 Mantel coefficients and p-values for species similarity of solitary bees, bumblebees, grassland vegetation and hedgerow vegetation regressed upon geographic distance in intervals in the correlograms of Figure 8.3. P-values 226

Figure 8.4. Partial Mantel Correlograms for solitary bees and bumblebees given vegetation and sampling location. Solid symbols indicate significant correlations between changing bee composition and geographical distance at $p=0.05$. See Table 8.5 for more detail. 229

Table 8. 5 Mantel coefficients and p-values for species similarity of (i) solitary bees and (ii) bumblebees regressed upon geographic distance, given grassland and hedgerow vegetation as in the correlograms of Figure 8.4. P-values 230

Figure 8.5. Significantly correlated vegetation indices projected onto NMDS ordinations (Jaccard distances for presence-absence data) of [A] solitary bee species (stress=0.19) and [B] bumblebee species (stress= 0.22) (See Appendix 15 for list of species abbreviations) . Arrows show direction and magnitude of significantly correlated vegetation indices (red = $p_{\text{entire}} < 0.05$, grey = $p_{\text{entire}} = 0.05$)..... 234

Figure 8.6. [A]-[G]. NMDS ordinations of bee species using Jaccard distances for presence-absence data (stress=0.19 for solitary bees and 0.18 for bumblebees). Arrows show direction and magnitude of correlations of plant species ($\log_{10} (\% \text{cover} + 1)$) with the bee ordinations. Grey = $p < 0.09$, red = $p < 0.05$. [A]-[D]= grassland plant correlations and [E]-[G] =hedgerow plant correlations. Graph labels show significance testing method as p_{entire} for permutation testing across entire datasets and p_{blocks} for testing within blocks defined by location..... 242

Figure 8.7. Indirect gradient analyses examining correlations of frequent bee species with vegetation composition. Arrows show direction and magnitude of correlations of frequent bee species ($\log_{10} (\text{abundance} + 1)$) with the plant ordinations. NMDS ordinations of hedgerow vegetation [A], [B], [D] and grassland vegetation [C] used Bray Curtis distances with square root transformed data and Wisconsin double standardization. Stress=0.20 for hedgerow and grassland vegetation ordinations. Solitary bee correlations with hedgerow vegetation with permutation tests across entire dataset [A] and within blocks defined by location [B]. Bumblebee correlations with grassland vegetation =[C] and with hedgerow vegetation =[D], both with permutation tests across entire datasets. Grey arrows = $p < 0.09$, red arrows = $p < 0.05$ 246

CHAPTER 9: Environmental conditions associated with bee species composition 259

Figure 9.1. Dotplot showing abundance of each bee species across samples. The vertical axis shows samples in the same order. See Appendix 15 for species names.....	273
Figure 9.2. Distance-based RDA (Hellinger distance) model for all wild bees derived by stepwise selection from an initial model with all 16 explanatory variables.....	285
Figure 9.3. Percentages of variation of bee species abundance data matrix explained by environment and by space. The sums of canonical eigenvalues and significance of models from which these proportions of variance were derived are presented in Appendix 17.....	286
Figure 9.4. Correlation biplot (RDA scaling 2) of distance-based RDA (Hellinger distance) spatial model (M3) of wild bee assemblage composition, conditioned on environmental variables. Species shown in red are those for which the analysis explained more than 20% of the species variance.	287
Figure 9.5. Correlation biplot (RDA scaling 2) of distance-based RDA (Hellinger distance) environmental model composition of all wild bees conditioned on spatial variables (M2). Species shown in red are those for which the analysis explained more than 20% of the species variance. High positive values on FieldVegAx3.sc indicate grassland botanical composition typical of more acid soils. A high positive value of FarmManAx1.sc reflects low intensity of agricultural inputs.	290
Figure 9.6. Hellinger distance-based RDA Model M1 (Environmental variables explanatory; no covariables) for solitary bees only. Only axis 1 is significant at $p=0.05$. Species shown in red are those for which the ordination explained $>20\%$ of their variance.	295
CHAPTER 10: Environmental conditions associated with bee abundance and diversity	307
Figure 10.1. Overview of three statistical paradigms used in analyses.....	310
Figure 10.2. Partitioning of the variance of the response variable between location and V_x , another influential variable under consideration, in partial linear regression. The length of the horizontal line corresponds to 100% of the variance in the response variable. Fraction [b] is the shared effect or intersection of linear effects of location and V_x on the response variable.	

Fractions [a] and [c] are the pure effects of location and V_x respectively.
Adapted from (Legendre 1993; Legendre & Legendre 1998). 323

Figure 10.3. Conditional plot showing that more complex hedgerows may be associated with higher abundances of bumblebees on dairy farms but not on non-dairy farms. 327

Figure 10.4. Relative importance of environmental influences on bee abundances and diversity, shown by the frequency of their inclusion in the best explanatory models, ranked using BIC. 334

Figure 10.5. Graphs showing distributions of posterior probabilities of coefficients of environmental variables for each set of models: [A] bumblebee abundance, [B] solitary bee abundance, [C] bumblebee species richness, [D] solitary bee species richness, [E] number of genera of wild bees. The maximum height of the distribution is scaled to be equal to the probability that the coefficient is not zero. The height of the solid line gives the posterior probability that the coefficient is zero. 336

Figure 10.6. Observed and predicted bee abundances and diversities using averaged models, in Scenario 1: along North-South gradient with all other factors constant and Scenario 3: along a landscape composition gradient with all other factors constant. Key: black = bumblebees, blue = solitary bees, red = wild bee genera. Observed values are shown as open circles and predicted numbers as lines. 343

Figure 10.7. Decomposition of variance in bumblebee abundance, bumblebee species number, solitary bee abundance, solitary bee species number and number of wild bee genera between location and the most important predictors for each, showing pure and shared effects. 346

Figure 10.8. Schematic diagram summarising (i) A priori model that reseeded and an intensification of field management would be associated with altered field vegetation and reductions in bee abundance and diversity. (ii) Study findings that field vegetation responded to reseeded and field management and bee abundance and diversity responded to reseeded and field management but no association between field vegetation and bee abundance and diversity was observed. (iii) New model: mechanisms by which reseeded and field management impact on bee abundance and

diversity are other than field vegetation composition and remain to be identified.	355
CHAPTER 11: Overall discussion and conclusions	363
Figure 11.1. Model of extinction order within wild bee assemblages in response to intensifying grassland management in Ireland	371
Plate 11.1. Photograph showing density of tree cover in hedgerows associated with the bocage or enclosed landscape in part of the study region.....	379
Plate 11.2. Potential amelioration measures to offset the negative effects of reseeded and intensive grassland management on a dairy farm. An unfertilised grassland strip composed of traditional meadow grasses and flowers is maintained alongside a reseeded, fertilised pasture. Note that the verge has grazed and ungrazed components increasing structural diversity, microclimate and flowering potential.....	382

LIST OF TABLES

CHAPTER 4: Measuring landscape composition.....	89
Table 4.1. Habitat areas (hectares) and proportion (%) within study region (based upon 59 samples of 100m radius circles).	104
Table 4.2. Principal component loadings for habitat variables on the first three axes of landscape composition PCA. Loadings are rotated and normed. Highlighted values indicate the variables which loaded most heavily on each axis.	106
Table 4.3. Results of indirect analyses examining correlations between location parameters and PCA of landscape composition.....	106
Table 4.4. AICc values for models of bee abundance and diversity that use different methods to summarise landscape composition in the models	114
Table 4.5. Results of indirect analyses examining correlations between landscape variables and bee assemblage composition, with significance testing across entire dataset (p_{entire}) and within blocks defined by sampling location (p_{blocks}).	115
CHAPTER 5: Measuring field boundary structure and botanical composition	119
Table 5.1. Supplementary environmental variables used in analyses of composition of hedgerow and grassland vegetation	123
Table 5.2. Correlation matrix between variables describing structure of wooded field boundaries	131
Table 5.3. Indicator values (IndVal percentage) for plant species in the two major groupings of hedgerows identified in cluster analysis. (An IndVal of zero does not mean that the species was absent from that hedgerow group, but that it has no indicator value in comparisons of the two hedgerow groups.) p-value is based on 1000 permutations and tests the statistical significance of the species associations with each group.....	134
Table 5.4. Correlations between structural characteristics and botanical composition of wooded field boundaries	142

Table 5.5. Spearman's correlations between variables describing physical structure and botanical composition of field boundaries and bee abundances and diversity.	145
CHAPTER 6: Measuring the botanical composition of grasslands.....	149
Table 6.1. Results of indirect analyses examining correlations between supplementary environmental variables and grassland vegetation composition, summarized using NMDS and PCO.	156
Table 6.2. Results of indirect analyses examining correlations between edaphic variables and grassland vegetation PCO axes 1-3.....	164
Table 6.3. Correlations of vegetation indices with grassland vegetation PCO axes 1-3.	164
Table 6.4. Spearman's correlations between grassland vegetation indices and other measures of botanical composition and bee diversity and abundance	165
CHAPTER 7: Measuring agricultural management intensity.....	169
Table 7. 1. Variables used in analyses of agricultural management at farm and field level.....	174
Table 7. 2. Correlations of field management variables with PCO of field management	198
Table 7. 3. Correlations between farm management variables and PCO of field management.....	199
Table 7. 4. Correlations between agricultural management variables and bee abundance and diversity.	202
CHAPTER 8: Bee-Vegetation linkages and spatial pattern in pastoral agri-ecosystems.....	207
Table 8. 1 Overview of datasets used in this chapter and the transformations and distance measures used with each.	214
Table 8. 2 Interpretation of p-values derived from significance testing across entire dataset and within blocks defined by spatial location in Mantel, Procrustes and envfit tests.....	218
Table 8. 3 Mantel coefficients and p-values for species similarity of solitary bees, bumblebees, grassland vegetation and hedgerow vegetation regressed	

upon geographic distance in intervals in the correlograms of Figure 8.3. P-values that were significant at $\alpha=0.05$ are highlighted in bold and those that were also significant using Holm's test are highlighted in grey. 226

Table 8. 4 Multivariate correlations of solitary bee and bumblebee composition with the botanical composition of grassland (solitary bees, n=53; bumblebees, n=55) and hedgerow (solitary bees, n=48; bumblebees, n=50) vegetation, given sampling location and space between sampling sites, examined using Procrustes rotations and Mantel tests. Permutation tests were across the entire dataset giving **p_{entire}** and within blocks determined by sampling location giving **p_{blocks}**. 227

Table 8. 5 Mantel coefficients and p-values for species similarity of (i) solitary bees and (ii) bumblebees regressed upon geographic distance, given grassland and hedgerow vegetation as in the correlograms of Figure 8.4. P-values that are significant at $\alpha=0.05$ are highlighted in bold and those that are also significant using Holm's test are highlighted in grey..... 230

Table 8. 6 Envfit correlations between vegetation indices and bee composition, with significance testing across entire dataset (**p_{entire}**) and within spatially defined blocks (**p_{blocks}**). 233

Table 8. 7 Hedgerow plant species correlations with bumblebee NMDS ordination (stress = 0.18). 238

Table 8. 8 Correlations of frequent bumblebee species ($\log_{10}(\text{abundance}+1)$) with grassland and hedgerow vegetation, with permutation tests across the entire datasets and within blocks defined by sampling location. (NA = insufficient data)..... 247

CHAPTER 9: Environmental conditions associated with bee species composition 259

Table 9.1. The set of explanatory variables used to describe the influence of geographical location on wild bee assemblages. ✓ indicates inclusion of the geographic variable in models for all bees, solitary bees or bumblebees..... 274

Table 9.2. The set of explanatory variables used to describe the influence of landscape composition on wild bee assemblages. ✓ indicates inclusion of landscape variable in models for all bees, solitary bees or bumblebees. 275

Table 9.3. The set of explanatory variables used to describe the influence of habitat structure and botanical composition on wild bee assemblages. ✓ indicates inclusion of habitat quality variable in models for all bees, solitary bees or bumblebees.....	275
Table 9.4. The set of explanatory variables used to describe the influence of agricultural management on wild bee assemblages. ✓ indicates inclusion of agricultural management variable in models for all bees, solitary bees or bumblebees.....	276
Table 9.5. Models and calculations used in the first tier of decomposition of variance in all bees, solitary bees and bumblebees.	280
Table 9.6. Loadings of environmental variables onto axes of distance-based RDA (Hellinger distance) environmental model (M2) of wild bee assemblage composition, conditioned on spatial variables.....	289
Table 9.7. Proportion of variance in abundance of each species explained by spatial (M3) and environmental (M2) models.....	293
Table 9.8. Loadings of environmental variables onto axes of distance-based RDA (Hellinger distance) environmental model, with no constraints (M1), for solitary bee composition.	294
CHAPTER 10: Environmental conditions associated with bee abundance and diversity	307
Table 10.1 Explanatory variables used in analyses of bee abundances and diversity. See Chapters 4-7 for methods.	316
Table 10.2 Level of model uncertainty shown as cumulative posterior probability of the best five models ranked using BIC, together with the number of models in Occam's window over which model averaging was conducted.	319
Table 10.3 Models and calculations used to decompose the variance explained by influential variable V_x and location.....	323
Table 10.4 Relative importance of environmental influences on bee abundances and diversity, shown by their averaged model coefficients and their posterior probability models. $p!=0$ = posterior probability that the	

variable's $\beta \neq 0$; EV= posterior distribution mean calculated over all models;
SD = standard deviation of EV. 335

Table 10.5 Relative importance of environmental influences on bee abundances and diversity, shown by the sum of their Akaike weights for each response variable, [A] Bumblebee abundance, [B] Solitary bee abundance, [C] Number of bumblebee species, [D] Number of solitary bee species, [E] Number of bee genera. The three most influential environmental variables are highlighted for each bee response variable..... 341

Table 10.6 Predicted bee abundances and diversity at high and low extremes of farm management intensity (Scenario 2) when all other factors are constant..... 344

LIST OF APPENDICES

APPENDIX 1. Comparing the efficacy of pan traps and transects for bee sampling.....	416
APPENDIX 2. Definition of habitat categories for landscape mapping.	417
APPENDIX 3. Automatic digitisation of hedgerows	420
APPENDIX 4. Rescoring of FBEGS categories.....	421
APPENDIX 5. Field-proofing of Grassland classification in habitat maps..	422
APPENDIX 6. Landscape composition – shepard diagrams for selection of appropriate ordination method.....	423
APPENDIX 7. Correlations between habitat areas within 100m radius of each sampling point.	424
APPENDIX 8. Shepard plot for PCO of grassland vegetation.....	425
APPENDIX 9. Grassland vegetation PCO showing the position of species projected into the ordination.....	425
APPENDIX 10. Grassland vegetation PCO showing correlations with management	426
APPENDIX 11. Grassland vegetation PCO showing correlations with sampling location and soil factors	427
APPENDIX 12. Results of Procrustes analysis comparing NMDS and PCO of sward vegetation.....	428
APPENDIX 13. Farm management Interview Schedule	429
APPENDIX 14. Treatment of interview responses and preparation of data	432
APPENDIX 15. Bee species and abbreviations.....	436
APPENDIX 16. Grassland plant species and abbreviations.....	438
APPENDIX 17. Variance explained and significance on permutation testing of models used in the decomposition of variance of assemblages of all wild bees.....	440
APPENDIX 18. Checking the distribution of response variables using QQ Plots.....	441

APPENDIX 19. Preliminary data exploration, checking distributions and correlations of explanatory variables	442
APPENDIX 20. Variance Inflation Factors of explanatory variables	443
APPENDIX 21. Preliminary data exploration: Associations between bee response variables and environmental variables	443
APPENDIX 22. Preliminary data exploration: Conditional plots examining potential interactions	446
APPENDIX 23. Residuals of stepwise regressions	447
APPENDIX 24. Post Hoc residual analyses of Bayesian averaged models..	453
APPENDIX 25. Calculating the pure and shared effects of important variables with geographical location	458

CHAPTER 1: INTRODUCTION

INTRODUCTION

Wild bees are regarded as under threat from human activities globally, particularly from land-use changes associated with agricultural intensification.

My original contribution to knowledge is that I determine the relative importance of natural and anthropogenic factors that influence wild bee diversity, abundance and assemblage composition in lowland, grassland-dominated landscapes and assess their shared effects.

National targets in Ireland are to increase the output value of the beef sector by 20% and the dairy sector by 50% by 2020 (using average of years 2007-2009 as a baseline) (Department of Food, Agriculture and the Marine (Ireland) 2010).

If agricultural intensification to date is associated with bee declines in Ireland, which there is good reason to believe is the case, then this escalation of agricultural management intensity represents a threat to bees.

I will determine whether there are correlations between bee abundances and diversity and the level of agricultural intensification and use this information to predict bee responses to scenarios of further intensification.

Measures to offset negative effects will be required if bee diversity and a pollination service are to be maintained. In order to develop such measures, the influences on bee populations, natural and associated with pastoral agriculture, need to be understood. This research aims to provide this information. It provides new insights regarding the ecology of wild bees and information to assist in the development of targeted bee conservation measures.

The findings of this study have international application, given that pasture comprises 26% of the planet's land cover or 69% of global farmland (FAO 2006). Furthermore a strong expansion in global demand for dairy products (Department of Agriculture and Food (Ireland). 2006) is likely to stimulate agricultural intensification internationally.

The Environmental Protection Agency of Ireland have funded this work as part of the project *Ag-Biota: Monitoring, Functional Significance and Management for the Maintenance and Economic Utilisation of Biodiversity in the Intensively Farmed Landscape* (Purvis *et al.* 2008).

CONCERNS ABOUT DECLINES IN WILD BEE POPULATIONS

Declines in wild bee abundances and diversity have been documented across Europe, with the red listing of up to 65% of bee species in some countries (Patiny, Rasmont *et al.* 2009). Negative trends in wild bee abundances and species richness have also been confirmed in the Americas (Aizen & Feinsinger 1994; National Research Council 2007; Colla & Packer 2008; Grixti *et al.* 2009; Cameron *et al.* 2011).

Concerns about pollinator declines and the implications for food security and local economies, on “every continent, except Antarctica” (Kearns *et al.* 1998; FAO 2008) have led to international cooperation in the study and conservation of pollinators in agriculture and related ecosystems as part of the Convention on Biological Diversity (CBD 2005) .

The main driver of bee declines is considered to be land use change, driven chiefly by agricultural intensification, resulting in habitat loss and degradation (Ricketts *et al.* 2008; Winfree *et al.* 2009; Potts *et al.* 2010). Given the universality of landuse change (75% of the earth's land surface is converted to human use (Ellis & Ramankutty 2008) and it is estimated that people have degraded between 39 to 50% of Earth's terrestrial habitats (Vitousek *et al.* 1997)), threats to bees have been inferred in many countries and continents, for example Australia, Sub-Saharan Africa and Madagascar and the Neotropics (Batley & Hogendoorn 2009; Eardley *et al.* 2009; Freitas *et al.* 2009).

However, Winfree *et al.* (2009) recommends caution in assuming that the effects of habitat loss on bees are universal. In her meta-analysis of fifty four studies of bee responses to anthropogenic impacts, she suggests that in

regions where habitat loss is already extreme, further habitat loss is likely to result in a decline in bee abundance and diversity (Winfree *et al.* 2009).

My preliminary studies (see Chapter 2) confirmed declines in *densities* and *diversity* of bumblebees in Ireland (Santorum & Breen 2005a). Subsequently it was shown that a decline in the *range* of some Irish bumblebee species has occurred since the 1980s (Fitzpatrick *et al.* 2007). The main cause of bumblebee declines was considered to be intensifying grassland management (Santorum & Breen 2005a; Fitzpatrick *et al.* 2007) though further evidence to support this view is required.

The situation for solitary bees in Ireland is less well studied. It was the opinion of an expert panel that within Ireland, 44% of solitary bee species (of 82 species) were at risk of decline (Fitzpatrick *et al.* 2006a). Studies indicate that they may be more vulnerable than bumblebees due to different biological traits (Le Feon *et al.* 2010) (Holzschuh *et al.* 2008) (Steffan-Dewenter *et al.* 2002). There is therefore an urgent need for information regarding the responses of solitary bees to agricultural intensification.

HOW DOES PASTORAL AGRICULTURE IMPACT ON BEES?

Some of the threats faced by bees in other agri-environments, such as direct poisoning by pesticides (Brittain *et al.* 2010b; Blacquiere *et al.* 2012) are less of a risk in pastoral agri-ecosystems as less bio-cides are used (Herzog *et al.* 2006).

The threats to bees in the pastoral systems of the study area are more likely to be indirect. For example, by grassland management reducing flowers at critical times (Gathmann *et al.* 1994; Soderstrom *et al.* 2001; Carvell 2002; Franzen & Nilsson 2008; Noordijk *et al.* 2009; Weiner *et al.* 2011) and disturbing nesting sites (Sladen 1912; Vulliamy *et al.* 2006).

As well as a degradation of habitat quality, intensification of farming activity is also associated with the removal or modification of habitat patches and a simplification of the landscape (Roschewitz *et al.* 2005; Persson *et al.* 2010). Loss of habitat is one of the main cause of bee declines (Ricketts *et al.* 2008; Winfree *et al.* 2009).

Studies of bees' responses to agricultural intensification have tended to compare organic and conventional crop-producing farms (Holzschuh *et al.* 2007; Williams & Kremen 2007; Holzschuh *et al.* 2008; Rundlof *et al.* 2008; Brittain *et al.* 2010a). An exception is (Power & Stout 2011) which studied grassland production systems. Organic dairy farms were found to support higher abundances of bees than conventionally managed dairy farms (Power & Stout 2011). But uptake of organic production methods is low (1.2% of total utilisable agricultural land area (UAA) in Ireland at the end of 2010 (Department of Agriculture, Food and the Marine (Ireland). 2011)). Therefore it is important to understand how bees respond along a continuum of agricultural management. This will allow the development of more sustainable farming practices which can take other forms as well as organic production (Cobb *et al.* 1999).

Of Ireland's total land area of 6.9 million hectares, roughly half is grassland. Prior to the 1950s, Irish farms engaged in a mix of small-scale arable and livestock production (Bell & Watson 2008). Specialisation had occurred by the 1980s with the majority of farmers focusing on grassland production (3.34 million hectares are grassland pastures, hay and silage meadows and 0.45 million hectares of rough grazing (Department of Agriculture, Food and the Marine (Ireland). 2012)) and arable farming becoming concentrated in a few areas (Commins *et al.* 1999). Such changes have resulted in only 1.26% of Ireland's land area persisting as natural grassland (Environmental Protection Agency. *et al.* 2009). Ireland therefore presents a microcosm in which to study the effects of intensification of pastoral agriculture on biodiversity.

VARIABILITY IN SPECIES RESPONSES

Bee species show different vulnerabilities to anthropogenic impacts. In California larger bees were identified as more vulnerable to extinction (Larsen *et al.* 2005). There is a large body of literature showing the vulnerability of bumblebees (e.g. Williams 1982; Santorum & Breen 2005a; Biesmeijer *et al.* 2006; Fitzpatrick *et al.* 2007; Gixti *et al.* 2009; Cameron *et al.* 2011; Dupont *et al.* 2011; Bommarco *et al.* 2012). Reasons for the vulnerability of particular species have been debated intensely for

bumblebees (Goulson & Darvill 2004; Goulson *et al.* 2005; Williams 2005a; Williams 2005b; Fitzpatrick *et al.* 2007; Williams *et al.* 2007; Williams *et al.* 2009).

However solitary bees have shown greater declines in response to agricultural intensification (Steffan-Dewenter *et al.* 2002; Le Feon *et al.* 2010) resulting in bee assemblages in which bumblebees come to occupy a larger part (Le Feon *et al.* 2010).

Traits other than body size, such as nesting location, sociability and dietary breadth, have been found to be predictors of response to agricultural intensification and habitat loss (Williams *et al.* 2010) (Cane *et al.* 2006; Bommarco *et al.* 2010).

Differences in species' responses to intensification of management in agri-ecosystems are likely to lead to changes in bee community composition, with resilient species coming to dominate (Carré *et al.* 2009). A homogenisation of bee communities with generalist species coming to dominate has been observed in response to habitat loss (Dormann *et al.* 2007b; Taki & Kevan 2007).

Based upon differences in bee sizes and behaviour (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2003; Albrecht *et al.* 2007; Krauss *et al.* 2009; Williams *et al.* 2010), it was hypothesised that solitary bees and bumblebees would differ in the scale of farm intensification with which they would be most strongly correlated. Different conservation approaches may be required if bumblebees and solitary bees are sensitive to different influences. The hypotheses being investigated were:

Solitary bees will be more strongly correlated with field and farm management at the study site rather than landscape composition. They will also be sensitive to habitat structure and botanical composition at the sampling point.

Bumblebees will be more sensitive to farming intensity measured at the landscape scale as landscape composition rather than to field and farm management or habitat qualities within the immediate vicinity of the sampling point.

To test these ideas, solitary bees and bumblebees were studied separately and together. Their responses along the same environmental gradients are compared and bee assemblages typical of the extremes of environmental gradients are described.

BEES AS BIO-INDICATORS

A number of studies suggest bees may have potential as bio-indicators. Bumblebee assemblages have been recommended as indicators of human impact at the landscape scale (Sepp *et al.* 2004). Species number of all aculeate Hymenoptera (bees, wasps and ants) has been shown to be an excellent indicator of the overall arthropod species diversity at a site (Duelli & Obrist 1998) and the diversity of solitary bees was highly correlated with that of butterflies on farms in Sweden (Franzen & Nilsson 2008).

This study is a preliminary exploration of opportunities for bioindication by bees. It aims to identify environmental conditions and scale for which bees, whether individual species, guilds or the entire assemblage, may be appropriate ecological indicators. Interesting leads revealed by this exploration will then require testing to determine whether they genuinely indicate these conditions (McGeoch 1998; Duelli & Obrist 2003).

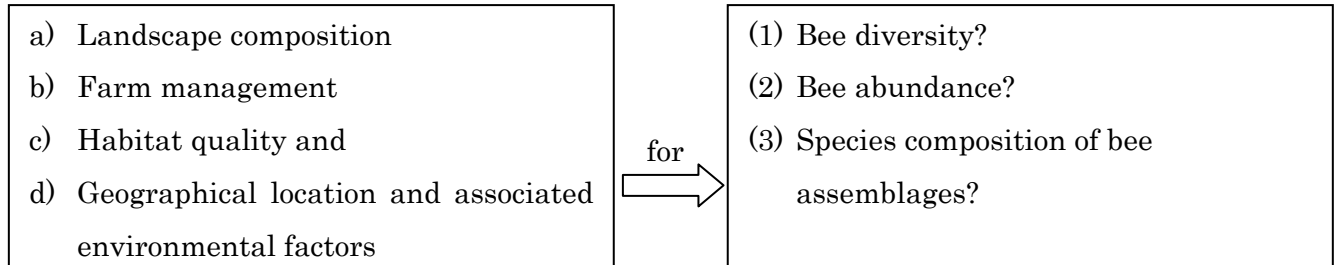
PURPOSE OF THE STUDY

The purpose of this study was to consider the entire wild bee fauna, that is solitary bees and bumblebees, in pastoral landscapes and to identify their responses to natural and anthropogenic influences. Bee responses, in terms of assemblage composition as well as species richness and abundance, were studied.

PRIMARY RESEARCH QUESTIONS

The research questions that this study aims to answer are:

1. What are the relative importance and shared effects of



2. How useful are wild bees as indicators of environmental degradation due to agricultural intensification?
3. At what level, farm or landscape or both, should conservation efforts be directed for bumblebees and solitary bees?

CHAPTER 2: BUMBLEBEE DECLINES IN IRELAND

Bumblebee diversity on Irish farmland

Veronica Santorum and John Breen

Department of Life Sciences, University of Limerick, Limerick

e-mail: veronica.santorum@ul.ie

Abstract

Bumblebee decline has been documented in several European countries but the situation in Ireland has not been investigated until now. Bumblebees are an important part of the fauna, particularly as pollinators. They also have potential as indicators of change at the landscape level. Agricultural intensification is considered a major driving factor in bumblebee decline. A survey of 28 farms in Ireland, representing a range of typical managements in the southern and eastern parts of the country, was carried out in 2003-04 as part of the Ag-Biota project. Transects and pan trapping were used. Although ten species were observed in total, of these only the *Bombus terrestris* group and *B. pascuorum* were observed on most farms. The mean density of bumblebees, in optimum weather conditions, was 3 per 100m of hedgerow (95% confidence limits 1.9 - 4.9). Since this is the first of such studies quantifying bumblebee abundance and species diversity on Irish farmland, it is not possible to compare definitively our current observations with historical data collected over the last 50 years of changing agriculture. Tentative comparisons are made with a 2004 survey in the Burren area, a region considered ideal for bumblebees, and a historical collection of bees mainly from the 1970s. The findings suggest an impoverishment of species diversity. Bumblebees that would be naturally rare, especially the parasitic 'cuckoo' bumblebees, are now apparently very scarce or absent from the typical agricultural landscapes surveyed. This study provides a baseline for bumblebees against which agri-environmental conservation measures can be evaluated in future farmland surveys.

Key index words: biodiversity, bumblebees, *Bombus*, agricultural landscapes, Ireland.

Introduction

Bumblebees (Apidae: Bombinae) can be considered a keystone species group due to their role as pollinators in natural ecosystems (Kremen and Ricketts, 2000; Larsen *et al.*, 2005; Mills *et al.*, 1993). Bumblebees are also essential pollinators of many field crops in managed ecosystems, e.g. clover, beans, blueberries, as well as glasshouse crops, e.g. tomatoes. Bumblebees are far more reliable pollinators than honeybees, flying in poorer weather conditions and pollinating flowers that are not visited by honeybees (Corbet, 1990; Thomson and Goodell 2001; Willmer *et al.*, 1994). They are not susceptible to infestation by the

honeybee mite, *Varroa*. Decreases in pollinator abundance have been related to reduced seed set and fruit yields in both crop and wild plants, with implications for both agricultural production and the conservation of wild plants (Corbet *et al.*, 1991; Kearns *et al.*, 1998; Kevan and Phillips, 2001; Memmott *et al.*, 2004). A decline in bumblebees is therefore likely to have far reaching impacts. Ignoring briefly the effects on wildflower populations and focusing solely on the economic implications of pollinator services, the value to the UK economy was recently valued at £200 million per year (Carreck and Williams, 1998).

Given Ireland's present agricultural activities, dominated chiefly by grass production, it would be easy to dismiss the importance of the pollinator service provided by bees. However, continuing change in agriculture is inevitable. Even if a grass-based agricultural economy continues to dominate, the maintenance of clover in the sward may become more important if nitrogen applications are reduced in pollution control measures. In the longer term, given climate change, changing markets and innovation by Irish farmers, it is important that we conserve bumblebees as an insurance policy for Irish agriculture into the future. For fruit growers, artificial nests of bumblebees are already being recommended for use in Ireland to pollinate field crops (Teagasc, 2004).

For bumblebees to fully serve the needs of Irish farming, they must be able to persist and thrive within the wider farmed landscape. A reliance on designated conservation areas cannot achieve this widespread protection, as there are too few such areas and these are unevenly distributed. The case of bumblebees illustrates the very important role of agri-environmental schemes in the conservation of beneficial species that are currently widespread and wide ranging in the landscape.

The large-scale movements of at least some bumblebee species enables them to meet their nesting, foraging and over-wintering requirements within the mosaic of fragmented habitats across the farmed landscape. Mark and recapture studies have shown bumblebees to travel between 350-600m, with occasional individuals travelling up to 1750m (Dramstad, 1996; Saville *et al.* 1997; Walther-Hellwig and Frankl, 2000). In homing studies, *Bombus terrestris* (L.) has been found capable of finding its way to back to the nest from 9.8km away (Goulson and Stout, 2001). Harmonic radar studies have monitored bumblebees regularly foraging between 0.70 and 6.31km from their nest (Osborne *et al.*, 1999) and genetic studies have revealed a foraging

range of the order of <300 to 750m (Darvill *et al.*, 2004; Knight *et al.*, 2005). Data on bumblebee incidence can therefore potentially capture environmental information at the landscape scale regarding habitat area, quality and possibly interconnectivity. Studies into the potential of bumblebees as indicators of change at the landscape level have found a correlation between the size of various landscape elements and the distribution of bumblebee species (Sepp *et al.*, 2004).

Lastly, bumblebees are also considered insects of 'aesthetic' value. They are one of the few insects that most people can instantly recognise. They feature in poetry, art, literature and other media. They are evocative of sunshine and summer and are generally regarded very favourably. They may therefore act as a vehicle for engaging and informing the wider public on conservation issues and generating enthusiasm, support and involvement for conservation measures. In this sense they may be regarded as a flagship group (Caro and O'Doherty, 1999), and it was in this context that they were included within the study brief of the Ag-Biota project.

International Context

Within Europe, local extinctions of bumblebee populations have been reported in the UK (Williams, 1986), and parts of France, Belgium and Germany (Peters, 1972, Rasmont, 1988). Agricultural intensification, resulting in the loss of habitat, loss of plant diversity and increased use of pesticides etc, is regarded as the major driver of these declines (Banaszak, 1983, 1992; Gathmann *et al.*, 1994; Mand *et al.*, 2002; Osborne *et al.*, 1991).

In the most intensively farmed regions of central England, local extinctions have resulted in only six species remaining ubiquitous. These still widespread and common species are *Bombus terrestris* (L.), *B. lucorum*, *B. pascuorum* (Scopoli), *B. pratorum* (L.), *B. hortorum* (L.) and *B. lapidarius* (L.). In more north-

ern and southern parts of the UK, where the impacts of agriculture appear to have been less severe, other species are still relatively frequent; however, their local distributions have contracted markedly (Williams, 1982, 1989). Five bumblebee species have been specifically designated in the UK Biodiversity Action Plan (UK Biodiversity Partnership, 2005).

There is an ongoing debate as to why certain species appear more vulnerable than others. Various hypotheses have been proposed: such as the suggestion that species with narrow dietary ranges are most at risk (Goulson and Darvill, 2004; Goulson *et al.*, 2005); or alternatively, that species closer to the edge of their geographical range are more vulnerable to the environmental pressures caused by changing agriculture (Williams, 2005).

Irish Context

Eighteen bumblebee species have been recorded consistently in Ireland (Appendix 1). Of these, thirteen species are regarded as 'true' bumblebees and five as 'cuckoo' bumblebees, parasitic on the 'true' bumblebees. As would be expected, this is a smaller total complement of species compared to Britain, and even fewer compared with mainland Europe. Nevertheless, Ireland seems to have been colonised only relatively recently by some species, such as *Bombus pratorum* (L) in the late 1940s (Faris, 1949) and *B. monticola* (Smith) in the early 1970s (Speight, 1974).

Three species – *Bombus terrestris*, *B. lucorum* and *B. magnus* Vogt – are very similar, with only the queens being distinguishable. We follow the widespread convention of recording all field observations of the workers and males of these species as '*B. terrestris* group' (Løken, 1972). A fourth species, *B. cryptarum* (Fabricius), has only recently been identified in a genetic analysis of the *B. terrestris* group (Bertsch *et al.*, 2005) and added to the bumblebee fauna of Scotland. This species has not yet been looked for in Ireland using the appropriate methodology.

There has been no prior survey describing the distribution of bumblebees in Ireland, nor are published data available on relative species abundance or typical population fluctuations. This dearth of information is currently being tackled by a number of researchers, including cross-border studies of the distribution of wild bees, including bumblebees, involving Dr. Mark Brown, Trinity College, Dublin and Dr. Robert Paxton, Queen's University, Belfast and their co-workers. A major aim of the current studies within the Ag-Biota project is the provision of baseline information for the monitoring of bumblebee diversity and abundance on Irish farmland.

With so little information about the abundance and diversity of bumblebees in Ireland prior to agricultural intensification, it is difficult to determine how past changes in farming practices have affected bees. In the absence of detailed historical data, cautious comparisons are made between our current observations from intensively managed farm sites and:

- a) parallel observations made in the Burren in Co. Clare – an agricultural landscape of relatively low farming intensity that has remained relatively unchanged and is likely to represent an optimum Irish farming environment for bumblebees;
- b) a bumblebee collection made in the 1970s and 1980s (Breen, unpublished).

Methods

Study sites

Eighteen farms were surveyed in 2003 and nineteen in 2004; as some farms were surveyed in both years, this gave us observations from a total of 28 farms located in the eastern and southern regions of Ireland (Figure 1). A range of farming systems typical of lowland Ireland (tillage, dairy, beef, sheep and mixed farming) was included. Average farm size (for a random sub-sample of twelve farms) is 64 hectares (SD=29 ha). The median stocking level is 2.15 LU/ha (lower quartile = 2.10

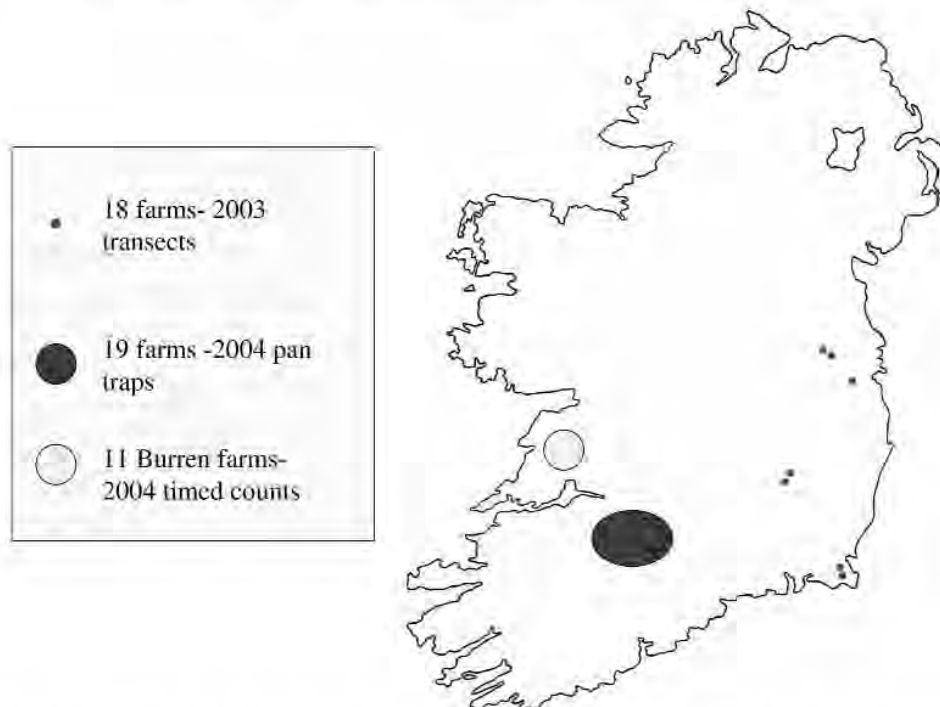


Figure 1: Location of study sites on typical modern farmland and in the more extensively managed Burren region

LU/ha and upper quartile = 2.26 L,U/ha). Nitrogen application ranged from zero to 300 kg/ha with the majority of farms in the 150-250 kg/ha range. On the farms surveyed, transects were used in 2003 and pan traps were utilised in 2004.

Transect survey in 2003

Forty-eight line transects, 200m long, were established at eighteen farms through swards and along hedgerows. On sites where there were no hedgerows, woodland edges were substituted. Bumblebees that were within 5m of the line transect were identified in the field and recorded. Each transect was visited between two and four times between June and September 2003. Transects were surveyed at a walking pace of less than 10m per second and the time spent on each transect was also recorded. All surveys took place in weather favourable to bumblebee activity; wind speed

<3 on the Beaufort Scale, temperature >16° degrees Celsius, light intensity > 10,000 lux and a minimum of 1h after rain.

Pan trapping survey in 2004

Additionally, small yellow pan traps with windows (Calabuig, 2000), containing water and detergent (Figure 2), were established along hedgerows at nineteen commercial farms in the Tipperary study region for three weeks during the month of August 2004. These were emptied weekly and the catch washed and stored in 99% industrial methylated spirits. Identification of bees was in the laboratory and followed Alford (1975) and Prys-Jones and Corbet (1987).

Burren and historical data

Comparative data were obtained from timed counts carried out at eleven locations in the Burren region, Co. Clare, during the summer



Figure 2: Yellow pan trap with windows as used on modern commercial farms in Co. Tipperary

of 2004 (funded by the Heritage Council), and from historical records derived from a collection of bumblebees caught in fields and along roadsides through mainly agricultural areas and in habitats favourable to bees between 1972 and 1988 (Breen, unpublished data). This historical collection was partially biased in the sense that sites considered attractive to bees were visited preferentially. In addition, specimens of the commonest bees, such as the *Bombus terrestris* group and *B. pascuorum* were not always collected in this previous work. These historical records were available for 119 sites across the country.

Data analysis

To remove the influence of uneven sampling effort in field observations, sample rarefaction was used to compare the species diversity of bumblebees observed in our surveys of typical farmland and farms in the Burren region. Rarefaction is a statistical method used to estimate the number of species *expected* in a ran-

dom sample of individuals taken from a larger collection (Colwell and Coddington, 1994). Only our field transect datasets were analysed in this manner in order to satisfy the ecological restrictions on the use of this method; namely that the samples compared should be 1) taxonomically similar, 2) collected by similar methods and 3) be collected from the same or similar habitats (Krebs, 1989).

Results

Species diversity using sample rarefaction

Amongst the 1,088 individual bees observed on transects and in the pan traps used to survey farms in 2003 and 2004, a total of ten bumblebee species were recorded. Thirteen species were recorded amongst 709 individuals sighted in the timed counts made in the Burren region in 2004.

Rarefaction analysis (with 95% confidence limits) suggested that between 4.4 and 7 bumblebee species could be expected in a sample of 120 bumblebee individuals sighted

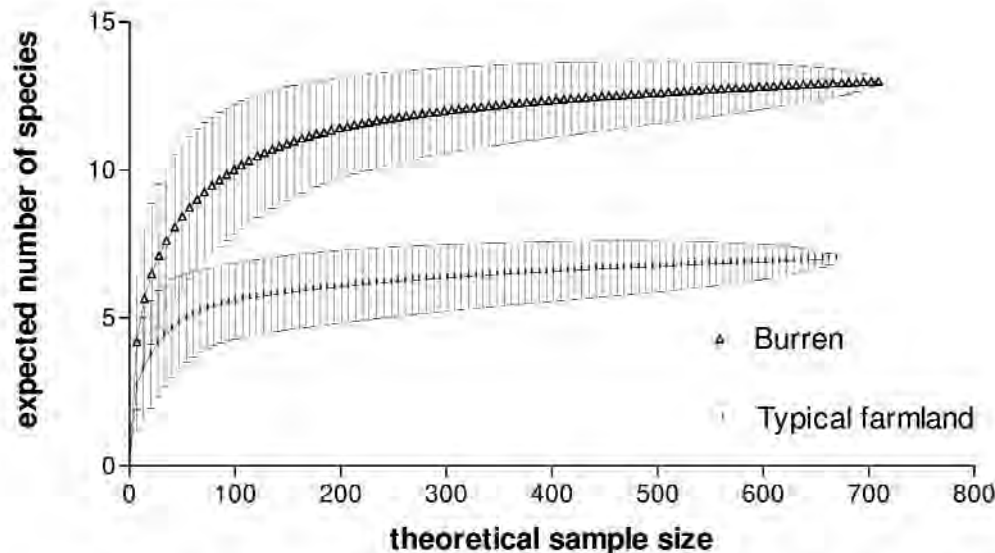


Figure 3: Sample rarefaction curves for farmland in the extensively farmed Burren region and 'typical' intensive farmland in the south-east of Ireland showing 95% confidence limits

on typical farmland (Figure 3). In contrast, between 8.4 and 12.5 species could be expected from a similar sized sample made in the Burren region (Figure 3).

Community structure

An alternative way to consider the bee diversity of the two types of farmland is by looking at the distribution (evenness) of abundance amongst species. Rank abundance curves were plotted for both typical agricultural landscapes and the Burren using the field observations made in 2004 (Figure 4), and these curves used to estimate the expected species diversity in equal sized samples of 400 bees from each type of farmland. In both farming types, the resulting rank-abundance curves fitted the log series and truncated lognormal models of species distribution (χ^2 goodness of fit test: in both cases $P > 0.05$). Although our data from both farm types fit the same models, the curve fitted for typical farmland is markedly steeper and shifted to the left of that for the Burren data, showing a decreased species

diversity in terms of both number of species and evenness of species abundance within the community.

On typical farmland, the *B. terrestris* group made up more than 60% of all bumblebee observations and *B. pascuorum* makes up a further third. The remaining six bumblebee species between them accounted for only 10% of all bumblebee observations (Figure 5a). In the Burren region, however, the community structure differs markedly with three pre-dominant species (*B. terrestris* group, *B. pascuorum* and *B. lapidarius*), each making up approximately a quarter of the bumblebees observed, and seven other species comprising the remaining 25% of observations (Figure 5b).

Distribution of bumblebees

Another way to assess rarity is to consider how frequently a species is recorded across sampled sites: for example, a 'common' species would be expected to be found at a majority of sites, but a species that occurred at only one or a

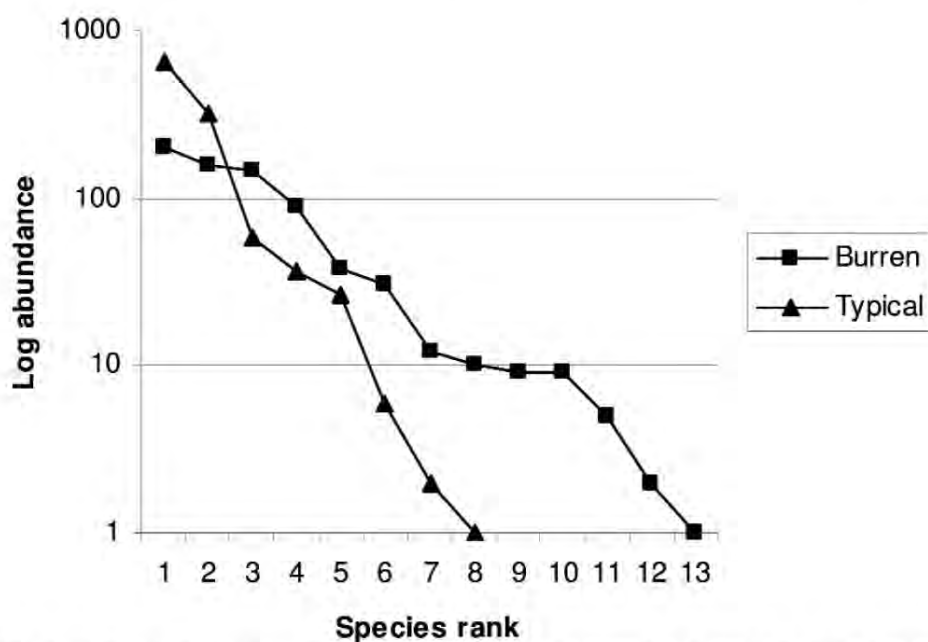


Figure 4: Rank abundance curves for bumblebee species in typical intensive agricultural farmland and in the more extensively farmed Burren region

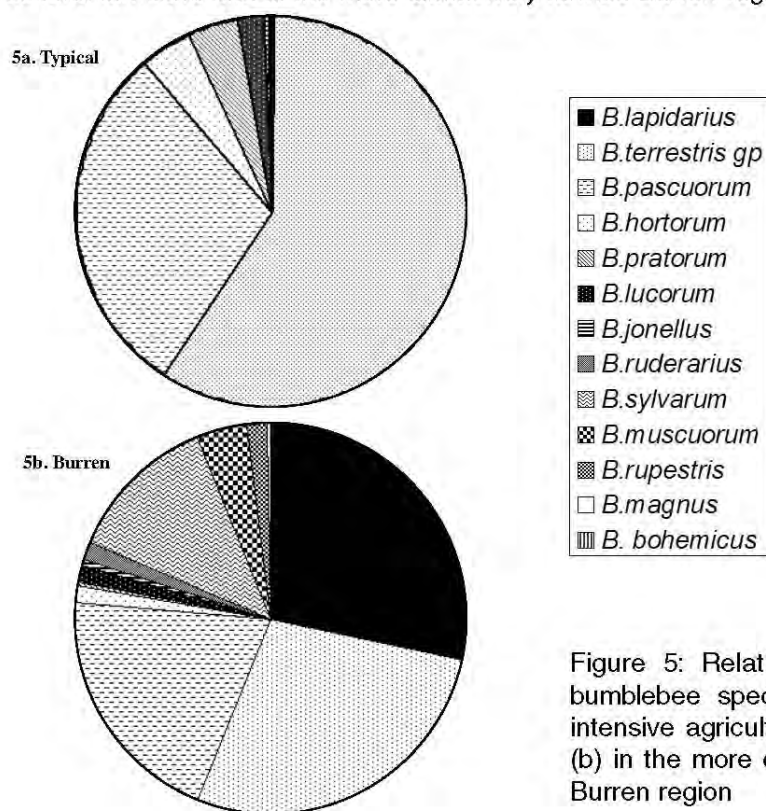


Figure 5: Relative abundance of bumblebee species in (a) typical intensive agricultural farmland and (b) in the more extensively farmed Burren region

very restricted number of sites (even if abundant at these sites) could be considered scarce and possibly endangered.

B. pascuorum and the *B. terrestris* group were the most numerous species recorded and also the most widespread, being found at near-

infrequently found on typical farmland and not seen at all in the 2004 survey. Elsewhere, this species is considered fairly widespread, in the UK being one of the relatively few species found even within the 'Central Impoverished Region' of England (Williams, 1986).

Table 1: The frequency of incidence of bumblebee species across sites surveyed in typical farmland, extensive Burren farms and recorded in historical data collected during the period 1972-1988 (* indicates species that are considered to have been under-recorded in the historical survey).

Survey	Typical farmland	Burren	1972-1988
Number of sites	28	11	119
'Free-living' bumblebees			
<i>B. distinguendus</i>	No observation	0.18	0.1
<i>B. hortorum</i>	0.54	0.55	0.34*
<i>B. jonellus</i>	0.04	0.36	0.1
<i>B. lapidarius</i>	0.11	0.82	0.22
<i>B. muscorum</i>	No observation	0.73	0.26
<i>B. pascuorum</i>	0.89	1	0.45*
<i>B. pratorum</i>	0.57	0.18	0.24
<i>B. ruderarius</i>	0.04	0.45	0.13
<i>B. sylvarum</i>	No observation	0.82	0.06
<i>B. terrestris</i>	1	1	0.39*
'Parasitic' bumblebees			
<i>B. barbutellus</i>	No observation	No observation	0.17
<i>B. bohemicus</i>	0.07	No observation	0.20
<i>B. campestris</i>	No observation	No observation	0.13
<i>B. rupestris</i>	No observation	0.45	0.06
<i>B. sylvestris</i>	No observation	No observation	0.07

ly all of the typical farms surveyed (Table 1). Although not as abundant relative to other species, these species also occurred at all sites in the Burren region and can be regarded as ubiquitous. *B. lapidarius* was both widespread and abundant in the Burren region but was

B. hortorum was found at just over 50% of sites in both the Burren and typical farmland sites, despite making up only 5% of all bumblebee observations on typical farmland and only 1% of observations in the Burren. *B. hortorum* colonies tend to be small, with a

peak size of 30-80 workers (Prys-Jones and Corbet, 1987). One would not expect therefore to observe large numbers of bees even where it is relatively common.

Bombus pratorum, a relatively recent colonist in Ireland (Faris 1949), was more widespread on typical farmland in the south and east where it was found in low numbers at over half of the sites surveyed, whereas it was found at only 18% of sites surveyed in the Burren region.

The species that one might expect now to be relatively rare are those that were previously recorded at only 10% or fewer of the sites included in the historical collections made during the 1970s and 1980s. These species were *B. sylvarum*, *B. distinguendus*, *B. ruderarius*, *B. jonellus* and of the 'cuckoo' bumblebees, *B. campestris*, *B. rupestris*, and *B. sylvestris*. These species were missing altogether from typical farmland (except for a single *B. jonellus* and a single *B. ruderarius* seen in 2004). Also absent from typical farm sites were *B. muscorum* and the 'cuckoo' bees *B. bohemicus* (one was seen in 2004) and *B. barbutellus* which in the historical dataset were present at approximately 20% of sites.

Most of these bees were relatively widespread across the Burren sites: *Bombus sylvarum*, *B. distinguendus*, *B. ruderarius*, *B. jonellus*, *B. muscorum* and *B. rupestris* were found at more than 20% of sites. However the 'cuckoo' bees *B. bohemicus*, *B. barbutellus*, *B. campestris* and *B. sylvestris* were not observed or had a very restricted distribution across Burren sites in 2004.

Density of bumblebees

Our observations suggest that on typical farmland, one would expect to see an average of 18.5 bumblebees per hour (calculated on the basis of having seen 669 bumblebees in 36.2h of observation time). Along hedgerows on typical farmland, the optimum farm habitat for bumblebees surveyed, a mean density of 3.0 bumblebees per 100m of 3m wide hedgerow was estimated (95% confidence

limits 1.9-4.9).

Discussion

The common bees

Irish agricultural landscapes do support bumblebee communities. *Bombus pascuorum* and the *B. terrestris* group, comprising *B. lucorum*, *B. magnus* and *B. terrestris*, were found to occur in all areas surveyed. These species are also considered ubiquitous in the most intensively farmed regions of the UK. Two further ubiquitous species in the UK, *B. hortorum* and *B. pratorum*, were found at over half of the farms surveyed in typical agricultural landscapes. The scarcity of *B. lapidarius* in 2003, and its absence from the 2004 sample are surprising given that this species was abundant in the Burren in the same period in 2004. This is also regarded as a ubiquitous species in the UK. While acknowledging the incompleteness and biases in the historical dataset, this data source suggests that *B. lapidarius* was not as widespread in Ireland as the *B. terrestris* group and *B. pascuorum* in the 1970-80s and this may be a species that has always had a more patchy distribution, or perhaps it is prone to population fluctuations. For example, Stelfox (1927) commented that *B. lapidarius* was not as abundant as it had been in previous years and ascribed the decline to bad weather in late spring.

The rarer bees

Based on our analyses of historical records, species that would probably always have been regarded as naturally rare in Irish bumblebee communities were missing from our surveys of typical modern agricultural landscapes. If the species we observed in the Burren region are regarded as more representative of Irish bee communities less affected by intensive agriculture, then the latter are substantially more diverse, and possess a more even community structure than we presently observe in intensively farmed landscapes. Compared to our observations in the Burren region, the bumblebee communities recorded at our modern

farming sites are dominated by a relatively reduced range of ubiquitous species with the rarer species having become even rarer or absent. In particular, the parasitic 'cuckoo' bumblebees appear to be almost entirely absent. Unfortunately, without an established historical baseline for the Irish fauna, it is not possible to confirm such a community shift.

The parasitic 'cuckoo' bumblebee species usurp a typical *Bombus* nest and trick the host species' workers into rearing their young. With their parasitic lifestyle and lack of their own workers, the abundance of parasitic 'cuckoo' species is likely to be naturally less than that of the self-supporting species and also to strongly reflect the abundance of their host species. Their incidence (or otherwise) may therefore provide a good indication of the changing status of 'conventional' bumblebee species. The parasitic species observed in our studies differed markedly between the typical farmland and Burren sites: *B. rupestris*, parasitic on *B. lapidarius*, was quite frequently seen at the Burren sites, but was not observed on modern farmland where *B. bohemicus* (parasitic on *B. lucorum*, a member of the *B. terrestris* group), was the only parasitic species seen, albeit very rarely. Whilst the Burren region might be regarded as one of the best surviving areas for bumblebees, apart from *B. rupestris* other parasitic species were found to be scarce and were not recorded on transects. It is possible that the apparent absence of parasitic species in the Burren is an early warning that bumblebee populations are under pressure even here. The historical dataset, with its implicit bias towards collecting from 'good' bee sites, recorded the incidence of all five parasitic species, with *B. barbutellus* and *B. campestris* found at approximately 10% of the sites covered and other parasitic species observed with less frequency. Further research to document the levels of natural population fluctuations in both typical and parasitic bumblebee species would allow a more informed interpretation of these findings.

Implications for conservation and further research

The ability of bumblebees to tolerate a landscape with patchy resources may offer some encouragement for their conservation. Networks of relatively small reserves may be able to sustain at least some species (Cane, 2001). Our survey of the Burren region suggests that Ireland may provide population strongholds for bumblebee species that are considered threatened elsewhere in the British Isles, e.g. species such as *B. sylvarum* and *B. distinguendus* that are specifically targeted in the UK BAP. This warrants further investigation. Banaszak (1992) recommends that a minimum of 25% of land cover should be semi-natural habitat in order to conserve a region's bee diversity. The Rural Environmental Protection Scheme (Department of Agriculture and Food, 2004) could provide a mechanism for the establishment of such a network of small semi-natural habitat patches, scattered throughout the Irish agricultural landscape. Research regarding the effects of landscape composition and farm management on bumblebee diversity is ongoing within the Ag-biota project.

Information on the distribution and natural relative abundance of parasitic bumblebee species, even in other countries, is very limited. Further work is necessary to determine whether, as our data suggest, changes in the abundance of parasitic 'cuckoo' bumblebees may provide a useful early indication of detrimental change in wider bumblebee community structure.

Acknowledgements

We thank the Environmental Protection Agency for funding this research as part of the Ag-Biota project, the Heritage Council for funding the 2004 survey of bumblebees in the Burren and landowners for granting access to their property.

References

- Alford, D.V. (1975). *Bumblebees*. London, Davis and Poynter.
- Banaszak, J. (1983). Ecology of bees (Apoidea) of agricultural landscape. *Polish Ecological Studies* 9, 421-505.
- Banaszak, J. (1992). Strategy for conserving wild bees in an agricultural landscape. *Agriculture, Ecosystems and Environment* 40, 179-192.
- Bertsch, A., Schweer, H., Titze, A. and Tanaka, H. (2005). Male labial gland secretions and mitochondrial DNA markers support species status of *Bombus cryptarum* and *B. magnus* (Hymenoptera, Apidae). *Insectes Sociaux* 52, 45-54.
- Calabuig, I. (2000). Solitary bees and Bumblebees in a Danish Agricultural Landscape. Unpublished PhD, Department of Population Ecology, University of Copenhagen.
- Cane, J.H. (2001). Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5, art. no. 3.
- Caro, T.M. and O'Doherty, G. (1999). On the use of surrogate species in conservation biology *Conservation Biology* 13, 805-814.
- Carreck, N. and Williams, I. (1998). The economic value of bees in the UK. *Bee World* 79, 115-123.
- Colwell, R.K. and Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation, *Philosophical Transactions of the Royal Society of London (Series B – Biological Sciences)* 345, 101-118.
- Corbet, S.A. (1990). Pollination and the Weather, *Israel Journal of Botany* 39, 13-30.
- Corbet, S.A., Williams, I.H. and Osborne, J.L. (1991). Bees and the pollination of crops and wild flowers in the European Community. *Bee World* 72, 47-59.
- Darvill, B., Knight, M.E. and Goulson, D. (2004). Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* 107, 471-478.
- Department of Agriculture and Food (2004). *Farmer's Handbook for REPS 3* (http://www.agriculture.gov.ie/areasof/reps3/reps3_farmershandbook.pdf).
- Dramstad, W.E. (1996). Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behavior* 9, 163-182.
- Faris, R.C. (1949). *Bombus pratorum* in Ireland. *The Irish Naturalists' Journal* IX, 245-246.
- Gathmann, A., Greiler, H.J. and Tschamtkke, T. (1994). Trap-nesting bees and wasps colonizing set-aside fields – succession and body-size, management by cutting and sowing. *Oecologia* 98, 8-14.
- Goulson, D. and Darvill, B. (2004). Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? *Apidologie* 35, 55-63.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. and Knight, M.E. (2005). Causes of rarity in bumblebees. *Biological Conservation* 122, 1-8.
- Goulson, D. and Stout, J.C. (2001). Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera : Apidae). *Apidologie* 32, 105-111.
- Kearns, C.A., Inouye, D.W. and Waser, N.M. (1998). Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29, 83-112.
- Kevan, P.G. and Phillips, T.P. (2001). The economic impacts of pollinator declines: an approach to assessing the consequences. *Conservation Ecology* 5. (online: <http://www.consecol.org/vol5/iss1/art8/>).
- Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A. and Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14, 1811-1820.
- Krebs, C. (1989). *Ecological Methodology*. Harper Collins Publishers, University of Columbia.
- Kremen, C. and Ricketts, T. (2000). Global perspectives on pollination disruptions. *Conservation Biology* 14, 1226-1228.
- Larsen, T. H., Williams, N. M. and Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8, 538-547.
- Løken, A. (1972). Studies on Scandinavian bumblebees (Hymenoptera, Apidae). *Norsk Entomologisk Tidsskrift* 20(1), 1-218.
- Mand, M., Mand, R. and Williams, I. H. (2002). Bumblebees in the agricultural landscape of Estonia. *Agriculture Ecosystems and Environment* 89, 69-76.
- Memmott, J., Waser, N.M. and Price, M.V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London (Series B – Biological Sciences)* 271, 2605-2611.
- Mills, L.S., Soule, M.E. and Doak, D.F. (1993) The key-

- stone-species concept in ecology and conservation. *Bioscience* 43, 219-224.
- Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R. and Edwards, A.S. (1999). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36, 519-533.
- Osborne, J.L., Williams, I.H. and Corbet, S.A. (1991). Bees, pollination and habitat change in the European Community. *Bee World* 72, 99-116.
- Peters, G. (1972). Ursachen für den Rückgang der seltenen heimischen Hummelarten (Hym., *Bombus* et *Psithyrus*). *Entomologische Berichte* 1972, 85-90.
- Prys-Jones, O.E. and Corbet, S.A. (1987). *Bumblebees*. Cambridge University Press.
- Rasmont, P. (1988). *Monographie écologique et zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae)*. Unpublished PhD thesis, Faculté des Sciences agronomiques de l'Etat, Gembloux, Belgium.
- Saville, N.M., Dramstad, W.E., Fry, G.L.A. and Corbet, S.A. (1997). Bumblebee movement in a fragmented agricultural landscape. *Agriculture Ecosystems and Environment* 61, 145-154.
- Sepp, K., Mikk, M., Mand, M. and Truu, J. (2004). Bumblebee communities as an indicator for landscape monitoring in the agri-environmental programme. *Landscape and Urban Planning* 67, 173-183.
- Speight, M.C.D. (1974). *Bombus lapponicus*, *Parasyrphus lineola* and *Phaonia exoleta*: Insects new to Ireland. *Irish Naturalists' Journal* 18, 123-124.
- Stelfox, A.W. (1927). A list of the Hymenoptera Aculeata (sensu lato) of Ireland. *Proceedings of the Royal Irish Academy, Fifteenth Report from the Fauna and Flora Committee*, 201-355.
- Teagasc (2004). *Advances in biological control for soft fruit growers* (<http://www.teagasc.ie/publications/2004/20040428/paper01.htm>).
- Thomson, J.D. and Goodell, K. (2001). Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. *Journal of Applied Ecology* 38, 1032-1044.
- UK Biodiversity Partnership (2005). *UK Biodiversity Action Plan* (<http://www.ukbap.org.uk/species.aspx>).
- Walther-Hellwig, K. and Frankl, R. (2000). Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behavior* 13, 239-246.
- Williams, P. (2005). Does specialization explain rarity and decline among British bumblebees? A response to Goulson *et al.* *Biological Conservation* 122, 33-43.
- Williams, P.H. (1982). The distribution and decline of British bumble bees (*Bombus* Latr.). *Journal of Apicultural Research* 21, 236-245.
- Williams, P.H. (1986). Environmental change and the distribution of British bumble bees (*Bombus* Latr.). *Bee World* 67, 50-61.
- Williams, P. H. (1989). *Bumble bees - and their decline in Britain*. Ilford, Central Association of Bee-Keepers (<http://www.nhm.ac.uk/research-curation/projects/bombus/decline.html>).
- Willmer, P.G., Bataw, A.A.M. and Hughes, J.P. (1994). The superiority of bumblebee to honeybees as pollinators – insect visits to raspberry flowers. *Ecological Entomology* 19, 271-284.

Appendix 1: Irish Bumblebee Species 2005 'True' Bumblebees

Bombus distinguendus Morawitz
Bombus hortorum (Linnaeus)
Bombus jonellus (Kirby)
Bombus lapidarius (Linnaeus)
Bombus lucorum (Linnaeus)
Bombus magnus Vogt
Bombus monticola Smith
Bombus muscorum (Linnaeus)
Bombus pascuorum (Scopoli)
Bombus pratorum (Linnaeus)
Bombus ruderals (Müller)
Bombus sylvarum (Linnaeus)
Bombus terrestris (Linnaeus)

Parasitic 'Cuckoo' Bumblebees

Bombus barbutellus (Kirby)
Bombus bohemicus Seidl
Bombus campestris (Panzer)
Bombus rupestris (Fabricius)
Bombus sylvestris (Lepeletier)

Due to copyright restrictions the following publication is not included in the electronic version of this thesis

The published version is available at

<https://doi.org/10.1016/j.biocon.2006.11.012>

Biological Conservation

2007, 136 (2), pp. 185-194

Rarity and decline in bumblebees – A test of causes and correlates in the Irish fauna

Úna Fitzpatrick, Tomás E. Murray, Robert J Paxton, John Breen, Don Cotton, Veronica Santorum,
Mark J.F. Brown

CHAPTER 3: STUDY DESIGN AND BEE SAMPLING METHODS

PURPOSE OF THIS CHAPTER

This chapter explains the study design and methods used to capture bee data for the analyses of Chapters 8-10. These later chapters will explore the relative importance of anthropogenic and natural factors influencing wild bees in pastoral landscapes in southern Ireland.

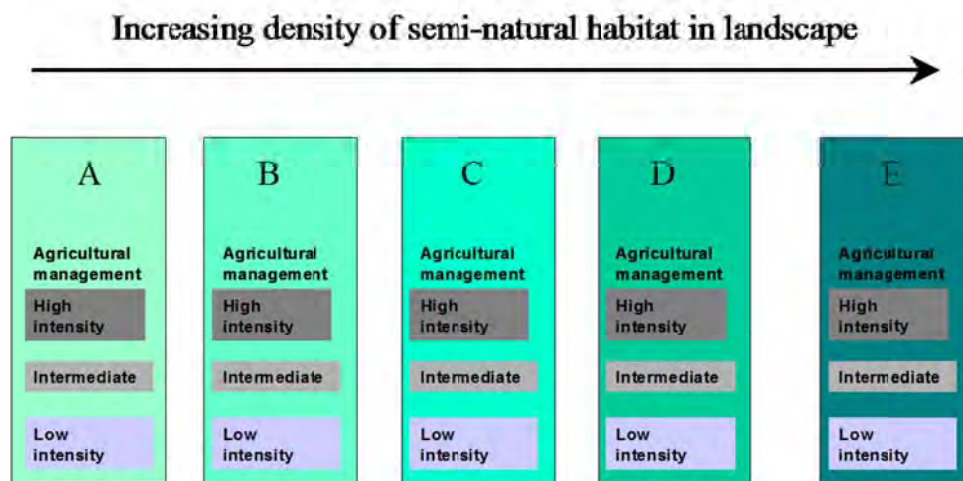


Figure 3.1. Sampling design showing how study farms were to be stratified along a gradient of agricultural management intensity and sampled in blocks of increasing semi-natural habitat area (A-E)

3. 1. SAMPLING DESIGN

A relatively homogenous area, 60km (North-South) x 70km (East-West) straddling County Limerick and the west of County Tipperary (Figure 3.2) and dominated by cattle farming, was studied. This study region, in the south of Ireland was regarded as sufficiently homogeneous, in altitude (range was 7m – 150m) and land-cover (dominated by agricultural grasslands), with no major geographical barriers such as large rivers or mountain ranges, that the regional species pool of bees would be uniform throughout the study area.

The ‘a priori’ hypothesis was that bee assemblage composition and bee abundances would not be particularly influenced by climatic conditions over the short distances encompassed by this particular study. Other local

influences were expected to explain more of the variance in species composition and abundances of bee assemblages.

RANDOMISED BLOCK DESIGN

A randomised block design (Hurlbert 1984), in which blocks were local areas with landscapes of varying habitat composition, was planned. Figure 3.1 illustrates the sampling design. This design aimed to control, in part, for spatial autocorrelation and dependence. It allowed some predictors that would be correlated for different blocks or areas to be omitted, reducing collinearity amongst variables (e.g. Kleijn *et al.* 2006; Concepcion *et al.* 2008; Williams 2011).

In the original sampling design, blocks A to E (Figure 3.1) represent landscapes differing in their proportions of semi-natural habitat. Identification of these landscape blocks within the study region was with the assistance of the National Parks and Wildlife service. Sampling was then stratified within these blocks in terms of management intensity. Within each landscape block a minimum of two fields, managed at different agricultural intensities, were selected as sampling units. Identification of extensively managed farms was with the assistance of the National Parks and Wildlife service and Teagasc, the agricultural advisory agency. Once 'low intensity' sites were located, a more intensively managed farm located within 2km was sought. The intensity of agricultural management imposed on each of the study fields represents the different treatments within each landscape block. A gradient of pastoral management, ranging from minimum input and outputs e.g. zero fertiliser and a late cut of hay and light grazing, through to intensive management as on dairy farms with high fertiliser inputs, 21 day rotational grazing and silage harvesting was studied.

Unfortunately there was a scarcity of data describing seminatural habitat availability and agricultural management intensity across the study region with which to define the strata for sampling. When semi-natural habitat areas and intensity of agricultural management were measured it became apparent that the sampling design had not been achieved. These difficulties led to a need to measure landscape composition and agricultural management

intensity for each site and apply analysis methods more suited to continuous data.

The sample contained fifty-nine farms. At each farm, sampling was centered upon an individual field. The median size of field in which sampling was centred was 3.64 hectares (interquartile range = 2.07-6.37).

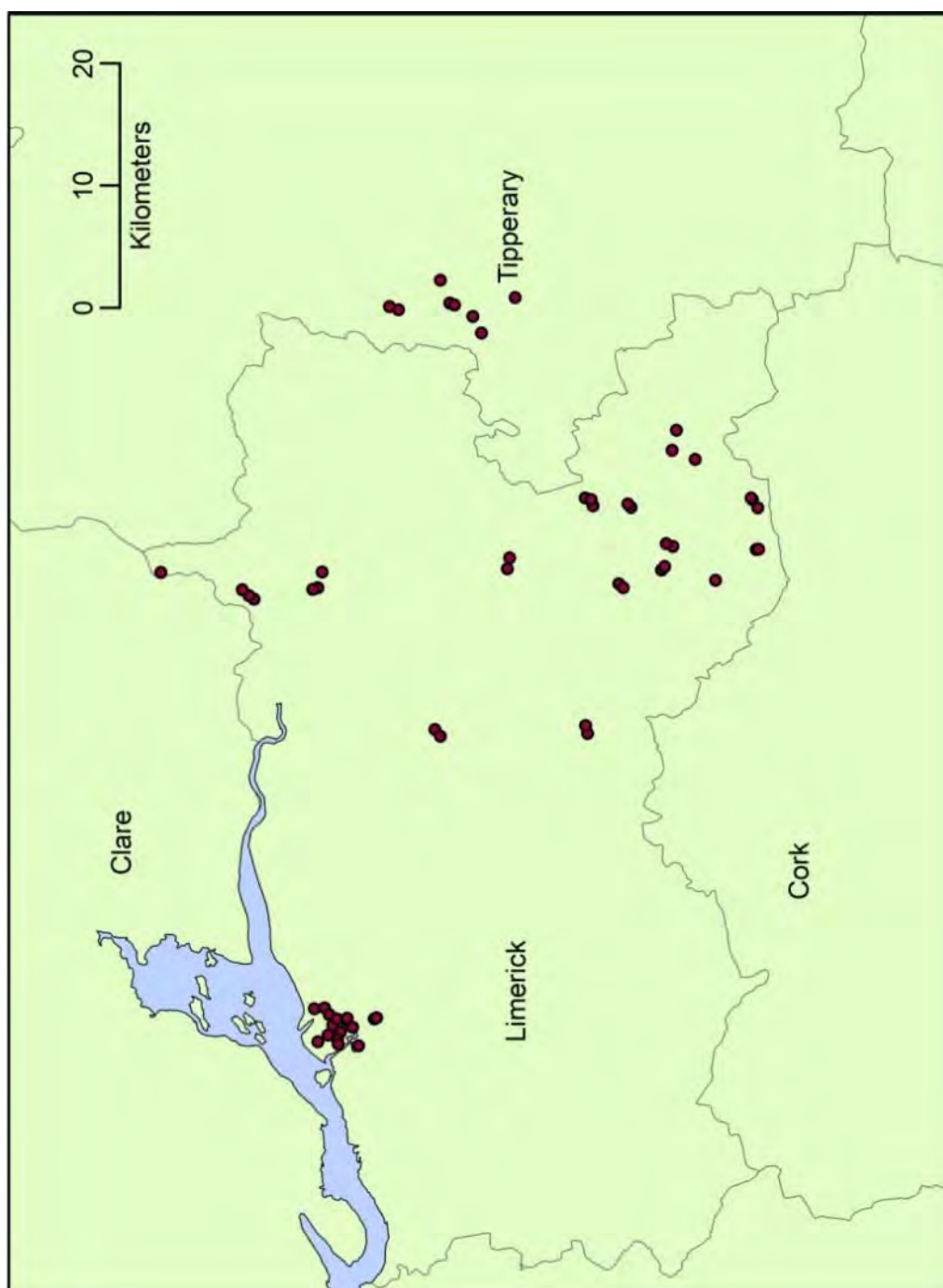


Figure 3.2. Map of study region showing location of sampling sites in Counties Tipperary and Limerick in the Republic of Ireland

3. 2. BEE DATA

Bees were sampled in 2005 using yellow pan traps (Calabuig 2000; Westphal *et al.* 2008), following a pilot study comparing their efficacy with transects in 2004 (Santorum & Breen 2005b and see Appendix 1). All bees captured were regarded as that site's assemblage of bees.

At each site, a yellow pan trap (35x27cm) with tethered, interlocking Perspex windows (30x30 and 22x30 cm) was established within 2m of a south-facing hedgerow bounding a grassland field in early May 2005. The traps were elevated above the vegetation, about 70cm from ground level, and filled to ~3cm depth with a solution of water, common salt (sodium chloride) and detergent (salt was added to help preserve the insects and detergent to reduce the surface tension. Salt was used rather than glycol to eliminate the risk of toxicity to farm animals).

Each site's sampling was timed relative to its full *Taraxacum officinale* ag. bloom (FTB) (Duelli *et al.* 1999) in order to standardize for temporal differences in bee emergence times between sites. This meant sampling was staggered by a few days between sites of different altitude (In 2005 in Co. Limerick, FTB (90%) at 10m above sea level ~ 22nd April; at 100m, FTB ~ 27th April and at 140m, FTB ~ 3rd May).

Each site was sampled for six weeks, two weeks in early summer, the first weeks trapping beginning two weeks after FTB (9th May -10th June), two weeks in midsummer (27th June – 29th July) and two weeks in late summer (8th August – 2nd September). Traps were open for two weeks during each period and emptied weekly. This extended sampling period aimed to cover the majority of Irish bee species flight periods, though some spring and early summer species were under-represented.

The length of time that pan traps were active, 6 weeks or 1008 hours, is much longer than is typical, e.g. 24 hours in Westphal *et al.* (2008) though Duelli *et al.* (1999) recommended a minimum of five x 1 week periods for a minimum sampling program for aculeate hymenoptera.

The longer sampling duration was also used to compensate for the effects of temporal variability in bee assemblages (Oertli *et al.* 2005; Tylianakis *et al.* 2005) and low bee densities observed on Irish farmland (Santorum & Breen 2005a; Purvis *et al.* 2010).

Bees were sorted from the pan catches and stored in 99% Industrial Methylated Spirits, IMS. Identification of bees was in the laboratory using several identification keys (Alford, 1975; Benton, 2006; Løken, 1972; Prys-Jones and Corbet, 1987 and Else (in prep.)).

Cryptic species, that were not readily distinguished visually, were grouped together. *B. lucorum*, *B. terrestris*, *B. magnus* and *B. cryptarum* (Carolan *et al.* 2012) were grouped together as *B. terrestris ag.* (Løken 1972). *Lasioglossum calceatum* and *L. fratellum* were also grouped together. *Apis mellifera* was excluded from analyses due to difficulties in distinguishing native populations from imported ones (Fitzpatrick *et al.* 2006b).

Response variables used for bees

The abundance of each species, of all bees and of solitary bees and abundance of bumblebees captured in 6 pan-trap weeks was used. Across all sites, the median number of bees observed with six sampling weeks = 22.0 bees, interquartile range = 13.0-29.9 bees, range = 5-211 bees). Details of subsequent transformations or omission of rare species are provided for each analysis in Chapters 8-10.

For bee diversity measures, that is species diversity and number of genera, it would have been preferable to have compared the diversity of sites for a constant number of bees (Magurran 2004) e.g. using rarefaction (Colwell *et al.* 2004) or using total species richness estimated with parametric or nonparametric extrapolation (e.g. Chao 1984; Walther & Morand 1998; Chiarucci *et al.* 2003; Melo 2004; Chao *et al.* 2006).

Species accumulation curves and nonparametric estimator curves were plotted using EstimateS 8.0 (Colwell 2006) to determine the sample size required to (a) estimate total species richness and (b) compare site species richness using rarefaction or extrapolation methods. In order to have sufficient data for these curves, data were pooled from nearby sites. Three

local areas were identified, from the broader survey, on the basis that sufficient sites had been sampled within an area of 8km radius allowing for data to be pooled. The areas were: Ballylanders, centred on Longitude -8.415 decimal degrees (DD), Latitude 52.367 DD and of radius 7.5km; Barrigone, centred on Longitude -9.0487 DD, Latitude 52.6122 DD and radius 3km and Tipperary, Longitude -8.1798 DD, Latitude 52.5293 DD and radius 5.3km. The minimum distance between sites from different local areas was 16km (closest sites in Ballylanders and Tipperary) but with Ballylanders and Barrigone were separated by 40km and Barrigone and Tipperary by 57km. The Tipperary area represented a higher disturbance area. The other two areas: Barrigone and Ballylanders, have a mixture of traditional and more intensive pastoral farming but differ in the proportion of seminatural habitat with Barrigone being richer in this respect.

Randomised species accumulation curves (Figure 3.3), have not reached an asymptote (best seen on the graphs drawn on the logarithmic scale (Longino *et al.* 2002)). This means that rare species have not been detected and that observed species richness is not equal to total species richness for any local area. This is also borne out by the nonparametric estimator curves which gave higher estimates of species richness than the observed species number (Figure 3.4), suggesting that species remain undetected within all three local areas. The species accumulation graphs drawn on a linear scale show that a considerable increase in sampling effort would be required to detect new species.

Using rarefaction (Colwell & Coddington 1994; Colwell *et al.* 2004) to determine a reduced sample size at which sites' species richness could be compared, it was estimated that sample sizes of 500 bees were required for the three areas' rarefaction curves to no longer cross (Lande *et al.* 2000) and comparisons to be stable. In the Tipperary area, the median number of bees captured per trap week was only two so 250 sampling weeks are required observe 500 bees.

Although the use of non-parametric Jackknife 2nd order or Chao 2 estimator curves could be used to reduce sample size to approximately 30 samples or

250 individuals to estimate total species richness in the Ballylanders area, this sample size was inadequate for the other two local areas.

The numbers of sampling units and bees observed at individual sites did not approach these sample sizes. Diversity was therefore compared for a constant sample size of six sampling units to provide some standardization.

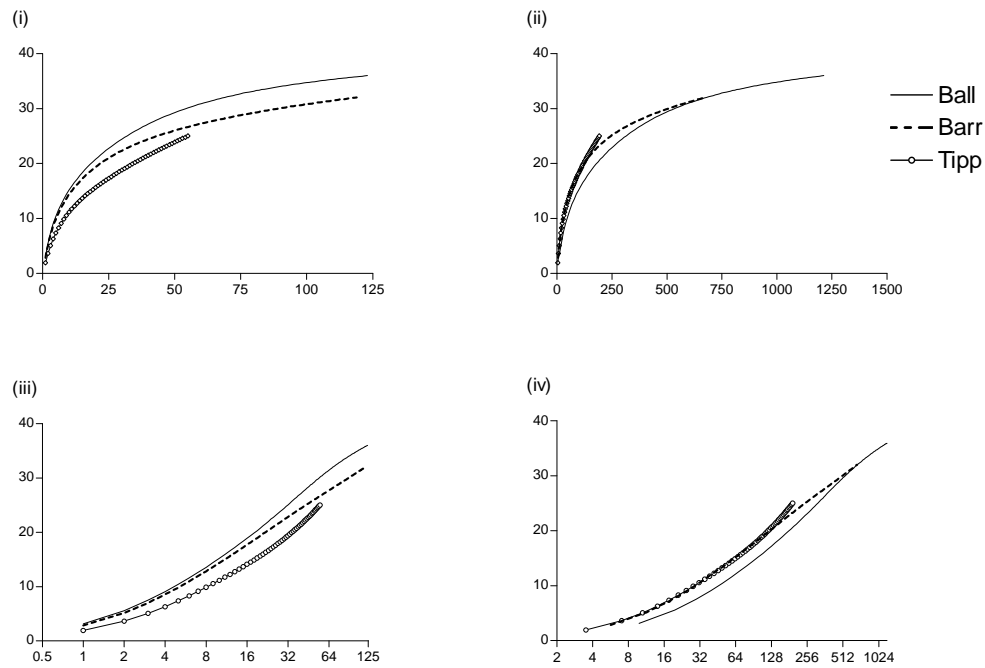


Figure 3.3. Randomised species accumulation curves for three local areas: Ball=Ballylanders, Barr= Barrigone, Tipp = Tipperary. X axis as follows: (i) x= samples on linear scale. (ii) x= individuals observed on linear scale. (iii) x= samples on log2 scale. (iv) x= individuals observed on log2 scale. Y axis = number of species observed.

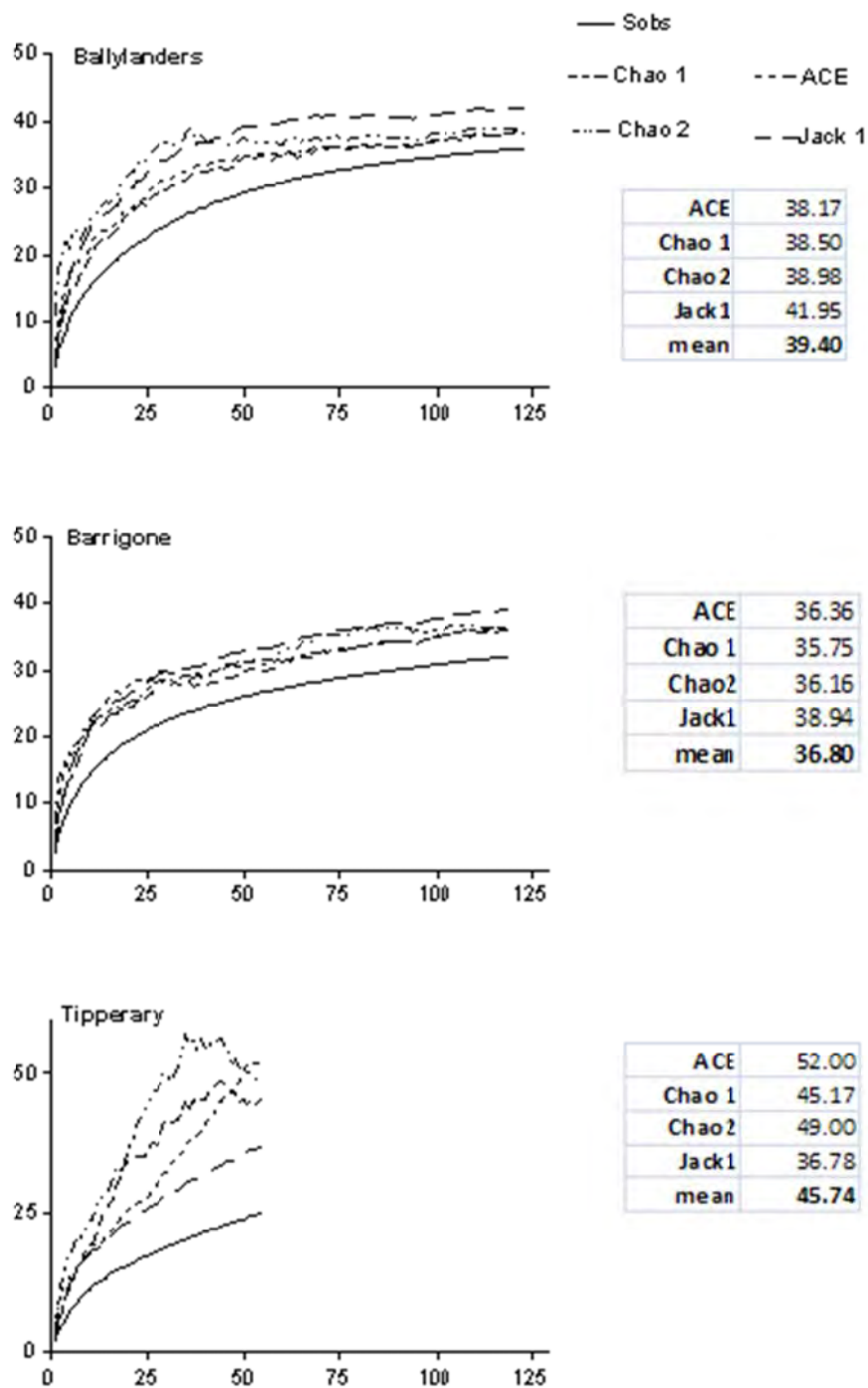


Figure 3.4. Nonparametric estimator curves (ACE, Chao1, Chao2 and Jack1) for three local areas: Ballylanders, Barrigone, Tipperary. X = number of sampling units. Y = estimated number of species. Mean = estimated total species richness calculated as mean of nonparametric estimates.

3. 3. ENVIRONMENTAL DATA

The major environmental factors identified from the literature as likely to influence bee assemblage composition, diversity and abundance were:

- *Landscape composition* in terms of habitat availability, as a measure of agricultural intensity at the landscape scale and other gradients in landscape composition.
- *Habitat quality* of grasslands
- *Habitat quality* of field boundaries
- *Agricultural management* at the field and farm scale

Each environmental influence is complex and may be described by a variety of variables. In order to select variables that (i) capture as much information about that environmental influence as possible and (ii) are not correlated with each other and (iii) are relevant to bees, each influence was studied thoroughly. Chapters 4- 7 explain the derivation of measures to summarise each environmental influence. The analyses of landscape and agricultural management showed the stratified block design originally chosen to be no longer relevant.

ASSUMPTIONS AND LIMITATIONS

ASSUMPTIONS ASSOCIATED WITH THESE METHODS

- Landowners responded honestly and accurately to questions about land management.
- Habitat maps were accurate.
- The sample of bees captured for each site was representative of the bees occurring there.

- Species abundance in trap is proportional to species abundance in field.
- Agricultural intensity as described at landscape scale was an accurate measure of agricultural management at this scale.

LIMITATIONS OF THE METHODS USED

- Floral abundance data had to be omitted due to the high number of missing values. (Volunteers did not record this information completely. However examination of model residuals for linear regressions in Chapter 10 does not suggest that a major influence was omitted.)
- The study was based upon a randomised block design survey with sampling stratified in terms of agricultural management intensity and proportion of habitat within the landscape. In practice this was difficult to implement due to lack of agricultural management data, especially for less intensely managed land, and of habitat maps for the study region.
- A single pan trap was used at each site, placed at the edge of each field. This did give an adequate sample for analyses. Ideally more pan traps would have been used, with sampling within the centre of the grassland field as well as at the periphery. Traps of different colour (Leong & Thorp 1999; Campbell & Hanula 2007; Gollan *et al.* 2011; Vrdoljak & Samways 2011) and the use of a combination of different sampling methods (Cane *et al.* 2000; Roulston *et al.* 2007) would also have increased the range of species captured.
- The earliest spring-active bee species (active before mid-May) were not sampled.
- Sites with missing data were removed from analyses in Chapters 8-10. This gave a sample of 49 farms. (Sites F113, F114, F704, F707, F721, F802 and F909 were removed due to missing farm management data; F713, F812 and F901 removed due to missing bee data.)

SPECIES NAMES: CONVENTION USED

In the text, common English names are used for some plants with the scientific name given the first time. Bumblebees is used interchangeably with *Bombus* (and includes the subgenus *Psithyrus*). The term, 'solitary bees' was used to refer to all other wild bee species. Not all of these bees are truly solitary, for example *Halictus rubicundus* lives colonially within the study area but the term served for convenience.

Species names of bees have been abbreviated to the first letter of their genus and the first six letters of their species name in figures and tables. For example, *Nomada marshamella* has been abbreviated to Nmarsha. The species names of plants have been abbreviated to the first three letters of genus followed by a dash and the first three letters of the species name. Thus, *Rubus fruticosus* ag. is abbreviated to Rub_fru. Where the plant was not identified to species level but only to genus, the first six letters of the genus name is given followed by _spp, for example *Betula*_spp. Lists of all plant and bee species observed are provided in Appendices 15 and 16.

CHAPTER 4: MEASURING LANDSCAPE COMPOSITION

4. 1. INTRODUCTION

This chapter describes the methods used to sample the landscape and identify appropriate variables to summarise landscape composition in terms of agricultural intensification and other major landscape gradients. The aim is that selected landscape variables should (i) capture as much information about landscape composition and (ii) be uncorrelated with each other and (iii) be relevant to bees.

Analyses were conducted in R (R Core Team 2012) using the base R package, vegan package (Oksanen *et al.* 2013) and ade4 package (Chessel *et al.* 2012).

4.1.1. DESCRIBING LANDSCAPE COMPOSITION

On a landscape level, intensification of farming activity is associated with a simplification of farmland as habitat patches are modified or removed to maximise the available area for farming (Robinson & Sutherland 2002; Benton *et al.* 2003; Persson *et al.* 2010). Agricultural intensification at a landscape level, was therefore classified by habitat composition and landuse.

Habitat loss, as well as reducing total habitat area, fragments remaining habitat patches, increasing edge relative to core and reducing connectivity between habitat areas (Tscharntke *et al.* 2002; Ewers & Didham 2006). A criticism of levelled at the majority of studies reporting biodiversity impacts due to habitat fragmentation is that they have not decoupled its effects from loss of habitat area (Harrison & Bruna 1999; Fahrig 2003; Yaacobi *et al.* 2007). Steffan-Dewenter (2003) did so for solitary bees and found habitat connectivity to be associated with the number of brood cells. Nevertheless as this study was exploratory, weighing the relative importance of multiple environmental factors, habitat was considered simply in terms of area and not pattern.

A number of alternative conceptual frameworks have developed to describe landscape. These can be summarised as ‘patches, gradients, and hierarchies’ (Talley 2007). They include the continuum model of landscape for fauna (Fischer & Lindenmayer 2006); hierarchical patch dynamics model (Wu &

Loucks 1995; Wu & David 2002) and hierarchical, patch-based model (Dunn & Majer 2007). Each model may have merit in particular study systems (Lindenmayer *et al.* 2007).

Most studies of bee responses to habitat availability within the landscape have been based on an implicit assumption of a binary or mosaic model of the landscape, in which habitat patches are considered to act as islands within a generally inhospitable matrix (Forman & Godron 1981; Haila 2002).

This has led to two main methodological approaches: (1) to study bee abundances and diversities at increasing distances from specified habitats or isolation gradients (as in the twenty-three studies reviewed by Ricketts (Ricketts *et al.* 2008) or (2) in landscapes with varying proportions of habitats, as for example in (Steffan-Dewenter *et al.* 2001; Steffan-Dewenter *et al.* 2002; Kleijn & van Langevelde 2006; Westphal *et al.* 2006; Garibaldi *et al.* 2011).

The ability of bees to utilise temporary or partial habitats to meet their life-cycle needs (Westrich 1996) means that the matrix is not entirely inhospitable to bees and cannot therefore be regarded as ‘nonhabitat’ (Blitzer *et al.* 2012). Temporal fluctuations and gradations in quality occur as for example with the mass flowering within a matrix composed of arable fields (Banaszak 1992; Westphal *et al.* 2009)

Bees have been shown to respond differently to habitat isolation depending on whether the matrix was arable, forest or mixed (Öckinger *et al.* 2012) or organic rather than conventional farmland (Williams & Kremen 2007; Holzschuh *et al.* 2008; Power & Stout 2011; Tscheulin *et al.* 2011). This compels researchers to move beyond a binary model of landscape for the study of bee responses to landscape factors as has been acknowledged in more recent times (Lonsdorf *et al.* 2009; Lander *et al.* 2011; Tscheulin *et al.* 2011).

Such advances have led to increasing sophistication in landscape models. For example, a goal in conservation ecology has been to identify critical thresholds (With & Crist 1995; Huggett 2005) of habitat area beyond which there is a dramatic shift in ecological response, such as abundance, diversity, stability, pollination service etc. Estimates of a critical threshold of 25% -30%

refuge habitats for bee conservation within a landscape (Banaszak 1992) and for the maintenance of pollination services (Kremen *et al.* 2004; Brosi *et al.* 2008) have been made based upon binary landscape models. Yet a meta-analysis of bee impact studies by (Winfree *et al.* 2009) showed declines in bee abundance and diversity were found only with habitat declines in regions where habitat loss was already very severe. This is closer to (Keitt 2009)'s computer simulations in which cultivated areas were not 'nonhabitat' but offered partial habitat for bees.

Further incongruities with regards to a binary representation of landscape for a pastoral study region are (i) the lack of contrast between semi-natural vegetation and the rest of the landscape in pastoral landscapes (McIntyre & Barrett 1992) and (ii) different habitat utilisation by various bee species (e.g. for bumblebees, Svensson *et al.* 2000).

For these reasons a binary representation of habitat and nonhabitat within the landscape was not used in this study.

Instead multivariate analysis was used to determine the dominant gradients in landuse within local landscapes and to establish if there was a gradient associated with agricultural intensity. This approach also allowed for other gradients in landscape composition to be identified from the data rather than being defined by my ideas of the landscape.

4.1.2. THE NEED TO CONSIDER SCALE

The scale used to describe landscape composition must be appropriate to bee behaviour and to the structuring of the landscape (Ludwig *et al.* 2000). The scale at which bees have been identified as responding to environmental factors ranges from a scale of tens of metres (Kohler *et al.* 2008; Albrecht *et al.* 2010; Samnegard *et al.* 2011) to kilometres (Steffan-Dewenter *et al.* 2002; Westphal *et al.* 2006).

This variation in scales of bee responses is likely to arise from (i) differences in the innate structuring over space of the environmental factor under study; (ii) differences in the scale at which the bees perceived and responded to the environment and (iii) the scale of the 'observational window' used by the researchers (Southwood 1988; Ludwig *et al.* 2000; Lechner *et al.* 2012). These

authors maintain that (i) and (ii) should contribute to determining (iii), the scale at which an ecological phenomenon is studied.

Correlations between the scale at which bees respond to landscape, their body size and foraging range have been observed repeatedly, with smaller bees tending to forage over shorter distances and to respond to factors measured at smaller scales within the landscape (van Nieuwstadt & Ruano Iraheta 1996; Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007; Tscheulin *et al.* 2011). Some studies have inferred that the scale at which there was the strongest correlation was a surrogate measurement of foraging distance (Westphal *et al.* 2006). However, the scale of an organism's perception of landscape is dependent not only on foraging distance (Bossenbroek *et al.* 2005).

Several studies suggest bees may respond to habitat availability within the landscape over distances much shorter than reported flight distances of many bees. For example, Albrecht *et al.* (2010) reported a 90% decay in bee abundance at a distance of 152 ± 34 m from 'Ecological Compensation Area' meadows. Samnegard *et al.* (2011) noted higher bee abundances and diversity when gardens were close by <15m compared to >140m away. (Kohler *et al.* 2008) found bee abundances and species richness to decline rapidly at 25-50m from nature reserves. Possibly responses over these relatively short distances may be because bees' foraging ranges reflect resource conditions (Connop *et al.* 2011; Carvell *et al.* 2012).

The scale at which bees perceive and respond to the landscape is dependent upon species, individual, caste, landscape, season and local resources. Individuals of the same species have been shown to cover very different distances (Wolf & Moritz 2008; Zurbuchen *et al.* 2010c).

I described the landscape at a smaller scale (100m radius circular sampling unit, sometimes referred to as grain size (Wiens 1989)) than typically used in bee studies. This scale is less than reported flight distances for bumblebees (Dramstad 1996; Saville *et al.* 1997; Osborne *et al.* 1999; Walther-Hellwig & Frankl 2000a, b; Westphal *et al.* 2006; Osborne *et al.* 2008a; Knight *et al.* 2009; Connop *et al.* 2011; Hagen *et al.* 2011; Carvell *et al.* 2012) and solitary

bees (Gathmann & Tscharntke 2002; Beil *et al.* 2008; Zurbuchen *et al.* 2010a; Zurbuchen *et al.* 2010c) which are in the order of hundreds of metres.

Many other researchers have not detected landscape structure effects on bees at this scale (Steffan-Dewenter 2003; Kleijn & van Langevelde 2006; Westphal *et al.* 2006; Knight *et al.* 2009) but these studies used a binary classification of habitat and non-habitat for bees.

I took a sample of the landscape by which to classify it rather than a measure of 'habitat available' or 'distance to habitat' within the area a bee might fly. I therefore anticipated that some studies (e.g. Albrecht *et al.* 2010; Samnegard *et al.* 2011; Kohler *et al.* 2008) did find correlations between landscape composition and bee diversity and abundance over distances of less than 100m that this scale would be adequate for the approach to landscape that I was taking.

4. 2. METHODS

4.2.1. DATA COLLECTION TO DESCRIBE LANDSCAPE COMPOSITION

Habitat maps were created for a sample of the landscape, a circle of 100m radius (Area = 3.142 ha) taken around each bee sampling point using a GIS established in Arcmap 9.2 (ESRI 2009).

The habitat maps were developed from aerial photographs and existing maps. The GIS was established initially with the following data layers:

- Orthorectified aerial photography from Ordnance Survey Ireland, 2000 and 2006 sets.
- Grid references of sampling points recorded with a Global Positioning System Magellan GPS 315
- All state and grant aided areas of forestry (Forest Service 1998)
- Maps of native woodlands (NPWS & BEC Consultants 2010)
- Areas with statutory protection: SACs (Special Areas of Conservation) and NHAs (Natural Heritage Areas) (NPWS 2010)

The habitat classification (See legend of Figure 4.1 and Appendix 2) used in the habitat maps was broader than the categories developed by (Fossitt

2000). This was because, at least for bumblebees, bees are not regarded as habitat specialists (Goulson *et al.* 2006). Instead I tried to take a bee's perspective and take a more functional view of habitat and classify it as a bee might see it (Dennis *et al.* 2003). For example, young coniferous plantations which did not have a closed canopy were classified together with semi-natural woodland and scrub due to the light that could penetrate and support a ground flora and the likely similarity in microclimate. A description of each habitat category and the procedure used for its mapping are provided in Appendix 2.

Automatic and manual digitising methods for the preparation of habitat maps from aerial photographs were trialled. Unsupervised classification (Appendix 3 gives details of the method) was used to automatically map hedgerows and wet grasslands. Unfortunately, the algorithms could not be repeated on every orthophotograph with equal success and had to be adjusted for each photograph. It was found to be more time efficient to manually digitise hedges and habitat areas.

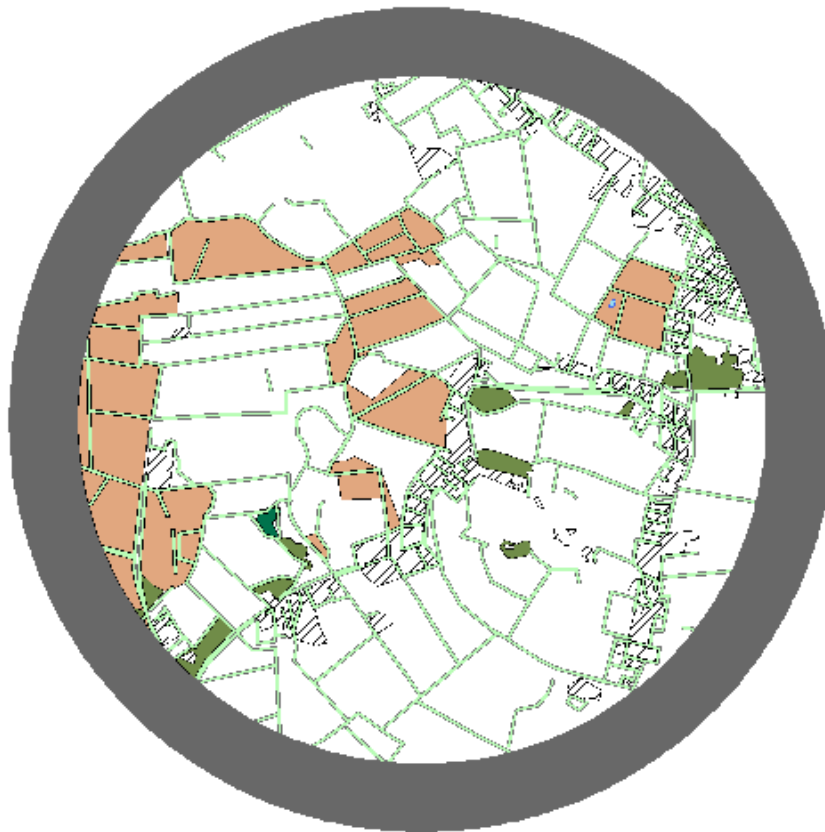
Aerial photographs were scaled to 1:2000 for the manual digitising of habitats. Boundary habitat was mapped as 2m wide lines and other habitats were mapped as polygons.

The quality of the habitat maps was maintained by using the snapping environment, advanced editing tools and map topology to reduce errors. The habitat map was edited to ensure that there was no overlap between habitats. Two sets of aerial photography were used. This allowed for cross-checking of mapping and facilitated the determination of some habitat classes, in particular semi-natural and 'semi-improved' (Sullivan *et al.* 2010) grasslands and boundaries.

A field survey was undertaken in late August-early September 2008 to validate the habitat maps. Discrepancies between observations in the field and habitats on the habitat maps were corrected. The proportion of grasslands that were misclassified in aerial photographs was also studied. It was found that though few (1.5%) intensively managed grasslands were wrongly identified as semi-natural and 'semi-improved' (Sullivan *et al.* 2010)

grasslands, approximately 20% of semi-natural and ‘semi-improved’ grasslands were misclassified as intensively managed (Appendix 5).

The total area of each habitat type was extracted from the GIS, for a sampling area of radius 100m around each site.



Legend

- Intensively managed grassland = IntensivGrass
- Field boundary = Bound
- Non-native coniferous forestry =NonNatFor
- Buildings, roads, car-parks, active quarries = Built
- Semi-natural woodland, scrub and young forestry plantations =SemiNatWood
- Semi-natural / semi-improved grassland = SemiNatGrass
- Water

Figure 4.1. Example of a habitat map , here for a 500m radius circle around the sampling point. Legend explains abbreviations used for habitat types throughout chapter.

4.2.2. METHODS OF ANALYSIS

DESCRIPTIVE STATISTICS TO DESCRIBE LANDSCAPE COMPOSITION WITHIN THE STUDY REGION

The median and interquartile range of each habitat's area were used to summarise the habitat availability within the local landscape.

Histograms were examined for normality. Most habitats had non-normal distributions in their areas and nonparametric analyses were used in subsequent analyses.

Spearman's correlations and graphing were used to examine associations between different habitat areas as a prelude to data reduction.

Principal components analysis was used to identify the trends in habitat composition of local landscapes and assess the strength of correlation between sampling location and landscape composition at the studied scale. Two principal component analyses, PCA and distance based PCA using Chord distances (dbPCA) were conducted upon the landscape composition dataset. The results were compared using Shepard Diagrams (Legendre & Legendre 1998; Zuur *et al.* 2010)(Appendix 6) Ordinary PCA was found to give distances between sites that were most faithful to the original Euclidean distances for the data matrix and I proceeded with this method.

The principal components of the first three axes were examined and the habitats driving the ordination identified.

The correlation of geographical location, treated as a categorical environmental variable = West Limerick, East Limerick, Central Limerick or Tipperary, Easting or X coordinate, Northing or Y coordinate and altitude, with landscape composition was assessed in the PCA ordination in an indirect gradient analysis (Ter braak & Prentice 1988; Ter Braak & Prentice 2004) using rotational vector fitting (Faith & Norris 1989).

The *envfit* function of vegan package (Oksanen *et al.* 2013) was used in R (R Core Team 2012). This function projected the environmental variables into the ordination space while ensuring maximal correlations between

environmental variables and ordination configuration. The strength and direction of correlations were visualised by plotting them as arrows onto the ordination plots. Permutation testing, based on 1,000 random permutations of the data, was used to evaluate the significance of the correlation coefficient and determine a ‘goodness of fit’ statistic, the *envfit* correlation coefficient.

ANALYSIS METHODS TO REDUCE LANDSCAPE VARIABLES TO A FEW SUMMARY VARIABLES

The methods used in the reduction of the landscape composition dataset were

1. PCA axes scores.
2. Landscape types: identified as clusters in the ordination or artificially determined.
3. One or more of the habitat areas to summarise overall landscape composition.

USING PCA AXES SCORES

The sum of eigen values of the first three axes of the PCA (see Section ‘Descriptive statistics to describe landscape composition within the study region’) was used to evaluate how much of the variability in landscape composition could be summarised by the first three axes. The loadings of each habitat area on the axes were studied to determine whether axes scores could be readily interpreted.

USING LANDSCAPE TYPES

The position of sites on the ordination plot was inspected to see if they were clustered into groups. This would indicate discrete types of landscape, classified at the 100m scale, within the study region.

In the absence of discrete natural groupings, artificial groupings were created and tested.

Generalised additive models (GAMs) were used to predict areas of each habitat type using the site scores on axes 1 and 2 as the predictor variables

(Simpson 2011). A smooth fitted surface showing the predicted area of each habitat type was overlain on the PCA biplot using the *ordisurf* function in *vegan* (Oksanen *et al.* 2013). This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use generalized cross-validatory selection of smoothness (GCV).

Cut-off points in predicted habitat areas were chosen that would slice the first axis of the PCA into thirds; with the group of ‘intensively managed’ landscapes at the negative extreme of axis 1, the group of ‘semi-natural’ landscapes at the positive extreme of axis 1 and ‘intermediate’ landscapes at the centre of the ordination.

The cut-off points used were:

- ‘intensively managed’ landscape group = >1.5ha of intensively managed grassland or > 47.7% of sampled area
- ‘intermediate’ landscape group = 1-1.5 ha of intensively managed grassland or 32-50% of sampled area
- ‘semi-natural’ landscapes group = >1.5ha of semi-natural and semi-improved grassland or > 47.7% of sampled area .

This process placed sites into three landscape groups determined by the type of grassland that dominated the 100m radius sampling area.

The capacity of these artificial groupings, which were based purely on grassland dominance, to summarise information about other habitats was evaluated. Three dimensional graphs showing the total areas of semi-natural / semi-improved grassland, semi-natural woodland and scrub, and area of boundary habitats were plotted for sites in each group. The distribution of sites classified as having an intensively managed, intermediate or semi-natural landscape within these three dimensional plots were compared.

Boxplots of the total area of semi-natural habitat for sites within each group were also plotted to check that the classification captured true differences in total habitat availability.

USING ONE OR MORE HABITAT AREAS MEASURED TO SUMMARISE LANDSCAPE COMPOSITION

Correlations between measured habitat areas and their contributions to the PCA axes were studied to determine which habitat areas could be used to summarise overall habitat composition. The *envfit* function of vegan package (Oksanen *et al.* 2013) was used to determine a goodness of fit statistic based on 1,000 random permutations of the data.

ANALYSIS METHODS TO SELECT THE BEST VARIABLES TO SUMMARISE LANDSCAPE COMPOSITION FOR BEE ANALYSES.

The data reduction process suggested several alternative approaches that could equally summarise the original matrix of variables describing habitat composition. Three types of summary variables, describing habitat composition, were evaluated. These were:

- Site scores on PCA axes: 3 continuous variables
- Landscape types: 3 ordinal variables, intensively managed landscape; intermediate landscape and ‘semi-natural’ landscape
- Areas of habitats: 3 or 2 continuous variables

These variables were tested for their strength of association with bee data from the same sites. Univariate and multivariate correlations were considered. The aim of this exploratory analysis was to determine which set of summary variables could explain the most information in the bee dataset.

UNIVARIATE ANALYSES

Three sets of generalised linear models to predict bee abundances were defined, each using a different set of variables to summarise landscape composition. Since geographical position was expected to also be an influence, XEast = Irish Grid Easting coordinate and YNorth = Irish Grid Northing coordinate were included in all models. Models with the same predictors were run for different bee response variables: bombus abundance, solitary bee abundance and number of bee genera (including *Psithyrus* as an additional genus).

As is typical of count data, there is over-dispersion in the bee data, i.e. the variance in the data is larger than the mean. Negative binomial regression models with a log-link were therefore used (Hilbe 2011). Analyses were conducted using the MASS package in R (Venables & Ripley 2002).

AICc values (Burnham & Anderson 2002b) for all models were compared to select the model and therefore method of summarising landscape composition that was most useful in predicting bee abundances and diversity.

The three model sets used were:

Model set 1: using PCA axes scores

```
M1<- glm.nb (BeeAbund~ XEast + YNorth + Axis1 + Axis2 + Axis3,  
link="log",data=Bee)
```

where Axis1,2,3 = site scores on first, second and third axes of PCA respectively

Model set 2: using landscape types

```
M2 <- glm.nb (BeeAbund~ XEast + YNorth + LandType,  
link="log",data=Bee)
```

where LandType = 3 ordinal variables describing landscape type as intensively managed landscape; intermediate landscape or 'semi-natural' landscape.

Model set 3: using areas of habitats

```
M3a <- glm.nb(BeeAbund~ XEast + YNorth + IntGrassA + Bound_woodA,  
link="log", data=Bee)
```

```
M3b <- glm.nb(BeeAbund~ XEast + YNorth + IntGrassA + WoodA +  
BoundA,link="log", data=Bee)
```

where IntGrassA = area of intensive grassland within 100m radius of site, WoodA = area of semi-natural woodland (including broadleaved woodlands composed of native species of trees, mixtures of native and nonnative trees growing on sites that have had continuous woodland cover for at least 160 years, orchards, transitional woodland scrub and recently planted coniferous forestry which did not have a closed canopy), BoundA= boundary area (hedgerows, earthen banks, ditches, walls and tree lines) and Bound_woodA= WoodA + BoundA.

MULTIVARIATE ANALYSES

Correlations between variables summarising landscape composition and bee assemblage composition were examined. Non-metric multidimensional scaling (NMDS) analyses were conducted for the solitary bee and the bumblebee datasets separately and the correlation of landscape variables with these analyses then examined.

Prior to the NMDS analyses, bee species that were only observed at one site were removed from the dataset. The Jaccard distance calculated using presence-absence data was used in the ordinations. The NMDS analysis was carried out with the *metaMDS* function in the *vegan* package of the *R* software (Oksanen *et al.* 2013). As well as using the random restarts provided by this function, each NMDS was repeated using the best solution from the first analyses. This was to ensure the global solution was reached by preventing the NMDS becoming trapped in local optima.

Stress, a measure of agreement between the original ecological distances and configuration of the ordination, was approximately 0.2 (the borderline between a ‘fair’ and ‘poor’ fit according to Kruskal’s rules of thumb (McCune & Grace 2002)) for two axes for both NMDS analyses. This was regarded as adequate and two axes configurations were used for all NMDS plots. Species were represented on ordination plots of NMDS solutions as centroids which were mapped using weighted averaging, following (Legendre & Legendre 1998).

The correlations of landscape, summarised as

- Site scores on PCA axes: 3 continuous variables
- Landscape types: 3 ordinal variables, intensively managed landscape; intermediate landscape and ‘semi-natural’ landscape
- Areas of habitats: 3 or 2 continuous variables

with bee assemblage composition summarized using NMDS, were assessed using the *envfit* function of *vegan* (Oksanen *et al.* 2013) to determine a goodness of fit statistic based on 1,000 random permutations of the data.

To determine whether correlations between landscape and bee composition were associated with sampling location or independent of it, permutation tests were carried out within blocks defined by location of sampling (4 blocks classes as West Limerick, East Limerick, Central Limerick or Tipperary) as well as across the entire dataset and p-values compared.

Correlations were visualised in ordination graphs, with arrows used to show the direction and strength of correlations. For landscape variables that were factors, the centroid was shown on the ordination diagram by the position of the label. Colour and size of points representing the site scores were also used to help with the interpretation of the ordination. For continuous landscape variables, the *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to check visually whether the correlation was a linear one. This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use cross-validatory selection of smoothness (GCV).

4. 3. RESULTS

4.3.1. OVERVIEW OF LANDSCAPE COMPOSITION

Table 4.1. Habitat areas (hectares) and proportion (%) within study region (based upon 59 samples of 100m radius circles).

Habitat category	Median	Interquartile range	Minimum	Maximum
Bound	0.49 (15.6%)	0.34 – 0.57 (10.8% - 18.1%)	0.14 (4.5%)	1.12 (35.6%)
NonNatFor	0.00	0.00 – 0.00	0.00	0.32 (10.2%)
SemiNatWood	0.00	0.00 – 0.25 (0- 8.0%)	0.00	1.74 (55.4%)
SemiNatGrass	0.89 (28.3%)	0.00 – 1.78 (0 – 56.7%)	0.00	2.60 (82.7%)
IntensvGrass	1.32 (42.0%)	0.41 – 2.30 (13.0% - 73%)	0.00	2.85 (90.7%)
Built	0.00	0.00 – 0.21 (0 – 6.7%)	0.00	0.56 (17.8%)
Water	0.00	0.00 – 0.00	0.00	0.28 (8.9%)

Grasslands and boundary habitat were the dominant habitat types within the study region (Table 4.1). The majority of sites had similar areas of boundary habitat comprising between 10.8 – 18.1% of the sampled area (interquartile range). This is very similar to the hedgerow habitat proportion of farmland reported by (Sheridan *et al.* 2011). (Though note that each sample area was centred on a point beside a boundary and not randomly placed, introducing a positive bias in the area of boundary.)

The low proportion of built land reflects the rural nature of the study region. Generally it did not exceed 6.7% (upper interquartile) of the sampled area.

Mature coniferous forestry was found within 100m of only two sampled sites although it is actually common in parts of the study region. Its omission from the sampled areas was due to survey design. (Study farms were below 170m and early plantings of commercial forests, that would now be mature, were on higher land. These early plantings were also on land owned by the state rather than farmers. The scale of 100m used in the study would often not reach beyond the farm under study. In more recent years the state has encouraged farm forestry but these younger plantings have been subsumed into the category ‘semi-natural woodland’ if their canopy had not yet closed.)

The first axis of the PCA distinguished landscapes with large proportions of semi-natural/semi-improved grassland from those dominated by intensively managed grasslands (Table 4.2, Figure 4.2, 4.3). The negative correlation between area of semi-natural/semi-improved grassland and area of intensively managed grasslands shown by the PCA was confirmed to be very strong by Spearman’s rank correlation $\rho = -0.91$, $p < 0.001$ (Appendix 7).

The area of boundary habitat and area of semi-natural woodland cover determined the second axis. These habitat areas were negatively correlated (Table 4.2, Figures 4.2 and 4.3 and Appendix 7). The extremes of the second axis were interpreted as separating enclosed landscapes from historically unenclosed or open landscapes.

The area of built upon land loaded very heavily on the third axis, with some contribution from boundary area.

Table 4.2. Principal component loadings for habitat variables on the first three axes of landscape composition PCA. Loadings are rotated and normed. Highlighted values indicate the variables which loaded most heavily on each axis.

	Comp1	Comp2	Comp3
Bound	0.08	0.65	0.38
NonNatFor	0.11	0.16	-0.21
SemiNatWood	0.21	-0.70	0.00
SemiNatGrass	0.67	0.12	0.00
IntensvGrass	-0.70	-0.01	0.07
Built	-0.05	0.24	-0.90

Location and habitat composition at the scale of 100m radius were shown to be correlated (Table 4.3). This was true whether location was considered as Easting or Northing coordinates, altitude or local sampling area. The significant association was mainly due to two discrete clusters of sites from West Limerick and East Limerick, in the bottom right and top right of the ordination plot respectively (Figure 4.4).

The West Limerick sites had a more open landscape with semi-natural/semi-improved grassland and scrub and developing woodland and the East Limerick sites had an enclosed hedgerow rich landscape with high density of semi-natural / semi-improved grasslands. They were interpreted as being representative of the traditional landscapes typical of their local area.

However the correlations between location and the PCA of habitat composition were weak. Figure 4.4 shows that sites from all areas were dispersed across much of the ordination plot and particularly at the left-hand extreme of axis 1 indicating dominance of the local landscape by intensively managed grassland. Therefore all the local areas studied, i.e. Tipperary, West Limerick etc. all had local areas that were impoverished in terms of natural habitat availability at a 100m scale.

Table 4.3. Results of indirect analyses examining correlations between location parameters and PCA of landscape composition

Location variable	<i>Envfit</i> Correlation coefficient r^2	p
Easting or X coordinate	0.36	0.001
Northing or Y coordinate	0.19	0.002
Altitude	0.25	0.001
4 local areas: West Limerick, East Limerick, Tipperary and 'Other' Limerick	0.24	0.001

4.3.2. DATA REDUCTION OF LANDSCAPE COMPOSITION SET OF VARIABLES

HABITAT AVAILABILITY

Three ways of reducing six habitat area variables were considered: using PCA axes scores, identifying and using landscape types, using one or more of the habitat areas measured.

USING PCA AXES SCORES

Using the scores of the first three axes would account for 72.4% of the variance captured by the ordination of six variables and reduce it to three variables. These three variables would describe the grassland composition, woody composition and built environment of the local landscape very well (Table 4.2, Figure 4.2).

If only the first two axes were used, this would omit information about the built environment and some information about boundary habitat and would capture 55% of the variance of the complete dataset.

USING LANDSCAPE TYPES

The classification of landscapes as ‘intensive’, ‘intermediate’ and ‘semi-natural’, on the basis of the type of grassland dominating at the sampled scale, also captured differences in the composition of their semi-natural habitats and the total area of semi-natural habitat (Figure 4.5 and 4.6).

Sites classified as ‘intensive’ were similar in their semi-natural habitat composition, with some hedgerow or some semi-natural woodland or scrub present at all sites but not at high densities. Semi-natural / semi-improved grassland was rare. Sites from all localities were represented in this group.

In the 'intermediate' landscape group, sites had more boundary habitat and/or semi-natural woodland and scrub habitat than the 'intensive' group. Densities of semi-natural / semi-improved grassland habitat remained low and comparable with the 'intensive' group.

The group classified as 'semi-natural' did have higher proportions of *all* semi-natural habitats, not just semi-natural / semi-improved grassland which was used to define the class. In this group, sites from the each local area clustered together in their composition of semi-natural habitats (Figure 4.5) and were separate from other local areas.

USING ONE OR MORE HABITAT AREAS MEASURED TO SUMMARISE LANDSCAPE COMPOSITION

The areas of intensive grassland and semi-natural / semi-improved grassland were very strongly negatively correlated with each other and were also driving the first axis of the ordination (Table 4.2, Figure 4.2 and 4.3, Appendix 7 and Spearman's rank correlation $\rho = -0.91$, $p < 0.001$). Either could therefore be used to summarise this aspect of landscape composition.

The negative correlation between the area of semi-natural woodland and the area of boundary habitat, though significant, was relatively weak (Table 4.2, Figures 4.2 and 4.3, Appendix 7 and Spearman's correlation $\rho = -0.38$, $p = 0.004$). Using one as a variable, would not give sufficient information about the other, meaning that both would be necessary to summarise the second axis of the PCA.

However it is debatable whether bees would perceive semi-natural woodland and scrub very differently from boundary habitat, which in this study region was predominantly hedgerow. Two options were therefore proposed. (1) use two habitat variables = Area of intensive grassland and (area of semi-natural woodland + area of boundary habitat) or (2) use three habitat variables = Area of intensive grassland and area of semi-natural woodland and area of boundary habitat. The results from tests of these two options as well as other approaches to summarizing landscape are described in the next section.

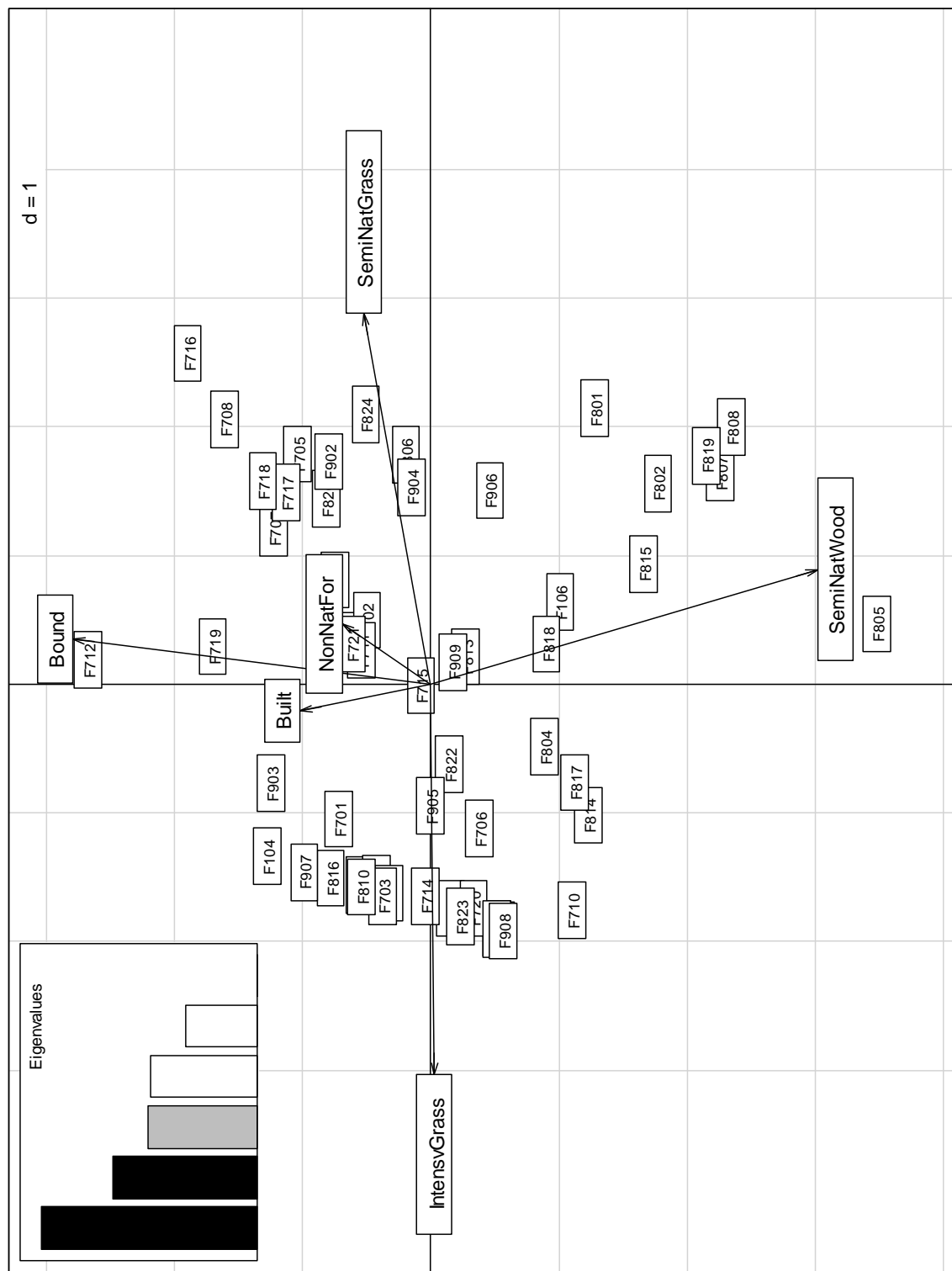


Figure 4.2. PCA of habitat composition (within 100m radius of each sampling point) showing major landscape gradients distinguishing study farms.

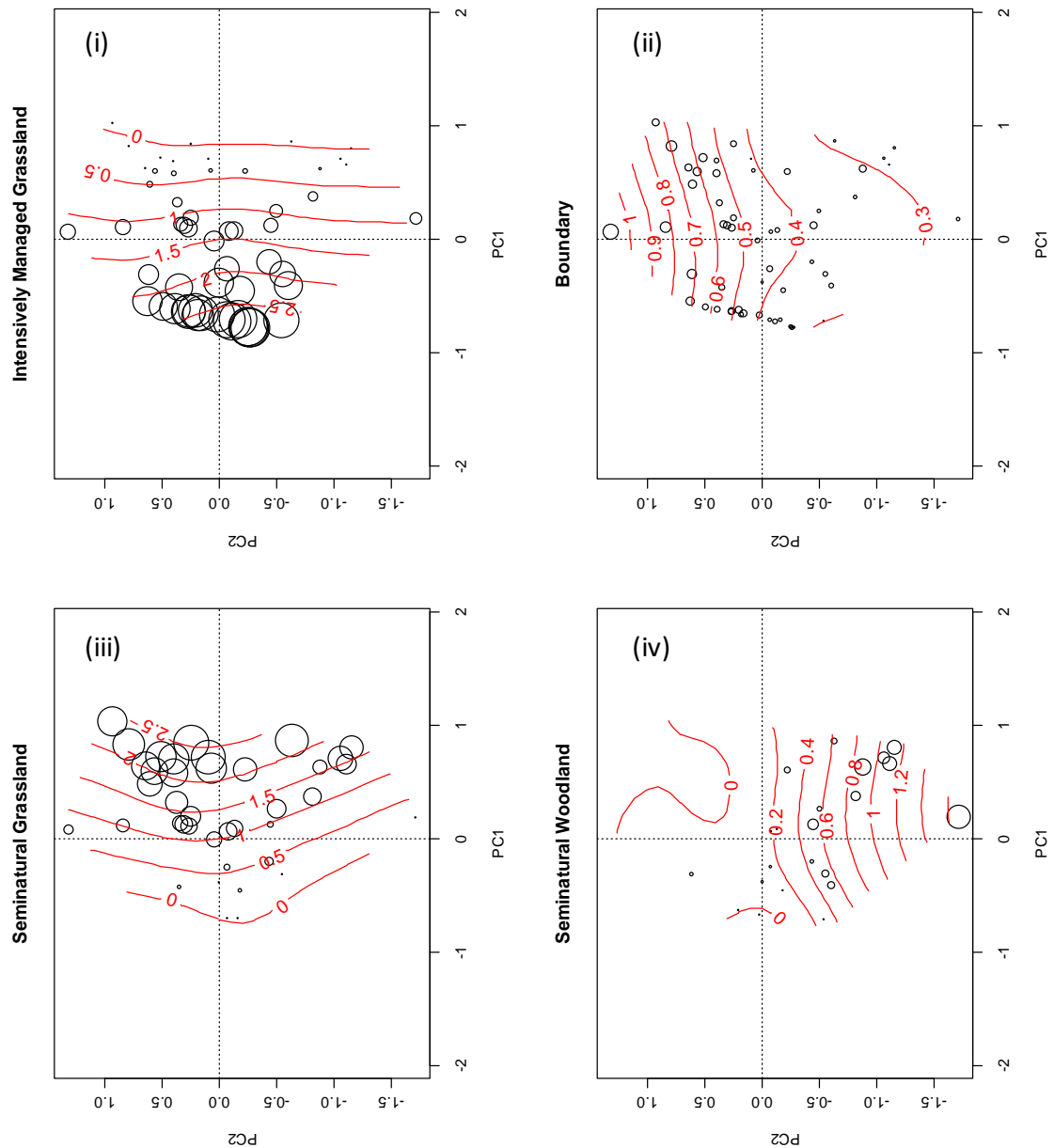


Figure 4.3. PCA correlation biplot of landscape composition showing areas of habitats and landuse at each site: (i) intensively managed grassland, (ii) boundary habitat, (iii) semi-natural / semi-improved grassland and (iv) semi-natural woodland, scrub and young forestry. Size of bubble represents relative area of habitat component around that site. Red contour lines show a smooth fitted surface of estimated area for each habitat type, fitted using a generalized additive model using the R function *ordisurf*.

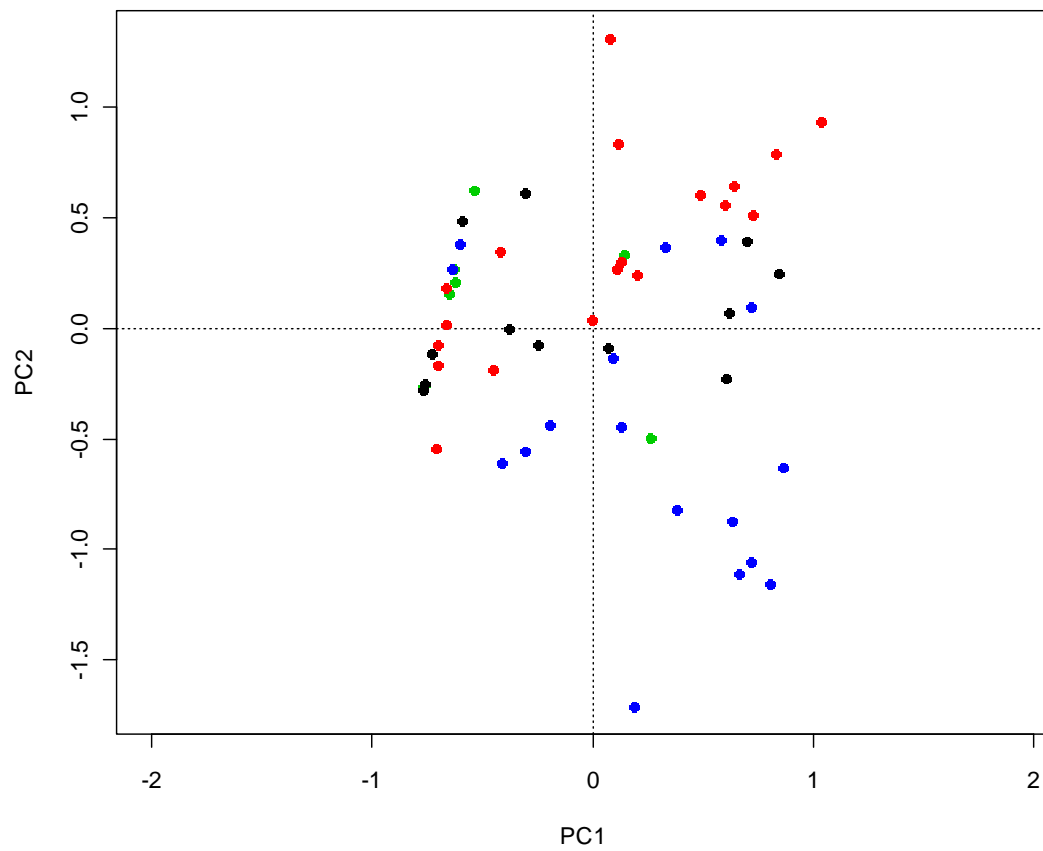


Figure 4.4. PCA correlation biplot of sites' habitat composition showing sampling location: blue=West Limerick; red =East Limerick; black = Central Limerick and green= Tipperary .

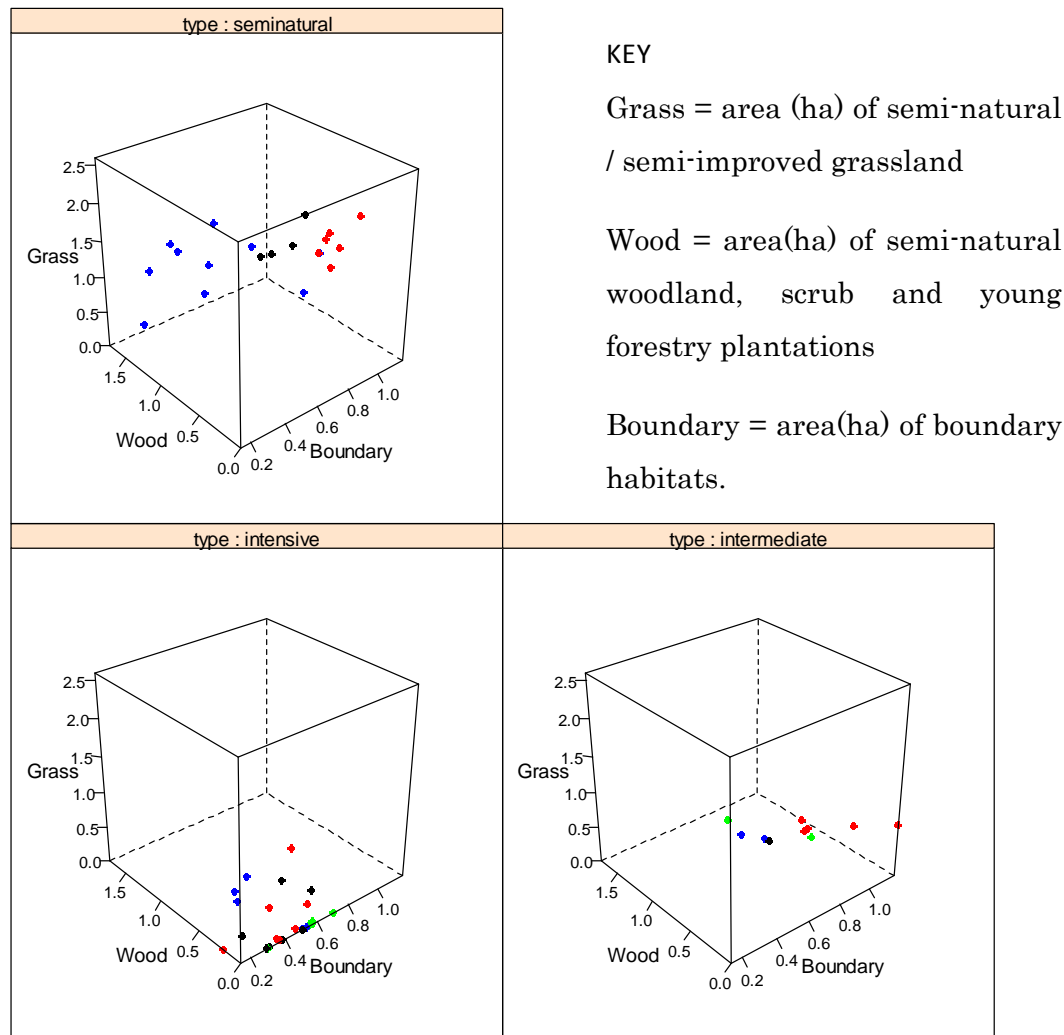


Figure 4.5. Three dimensional graphs showing areas of semi-natural habitats in three landscape types. Intensive landscapes (Type 1) were defined as >1.5ha intensive grassland area, intermediate landscapes (Type 2) as >1ha & <1.5ha intensive grassland, semi-natural landscapes (Type 3) as <1ha intensive grassland. Colours show location: blue=West Limerick; red =East Limerick; black = Central Limerick and green= Tipperary.

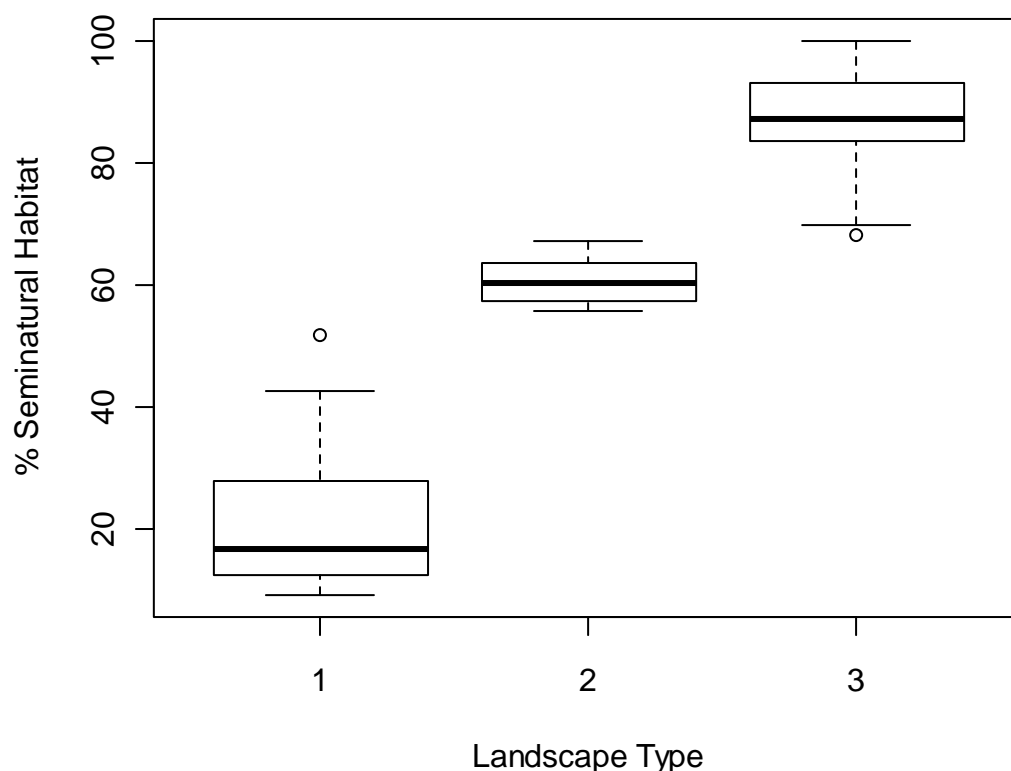


Figure 4.6. Boxplots showing area of semi-natural habitat present in each landscape type: Type 1= Intensive landscape (mean=21.1% semi-natural habitat, std.dev=11.8, n=26) Type 2=Intermediate landscape (mean =60.3% semi-natural habitat, std.dev=3.7, n=10) Type 3=Semi-natural landscape (mean =87.1% semi-natural habitat, std.dev=9.2, n=20)

4.3.3. BEST VARIABLES TO DESCRIBE LANDSCAPE COMPOSITION FOR BEE ANALYSES

UNIVARIATE ANALYSES

AICc values for each set of models, e.g. bee abundance models or bombus abundance models etc., were similar (Table 4.4) regardless of which approach was used to summarise habitat composition. This means the models were fairly equivalent in their capacity to summarise habitat composition and explain differences in bee abundances and diversity. Landscape type was the measure of landscape composition that most frequently gave the lowest AICc value in the models of bee abundances and diversity. This was partly because

there were fewer variables/ degrees of freedom in the model. Each additional variable incurred an AICc penalty of +2.

Table 4.4. AICc values for models of bee abundance and diversity that use different methods to summarise landscape composition in the models

Landscape variables	df	Bee abundance models	Bombus abundance models	Solitary abundance models	Number of bee genera models
PCA axes scores	7	470.4	391.5	413.8	219.2
Landscape types	6	470.6	389.2	411.9	215.1
Areas of habitats: 2 variables	6	469.9	392.3	411.6	216.7
Areas of habitats: 3 variables	7	471.6	391.8	414.2	219.2

MULTIVARIATE ANALYSES

Bumblebee composition was correlated with landscape PCA axis 2 scores and with area of semi-natural woodland and scrub (Table 4.5 and Figure 4.8). These two environmental variables were themselves correlated (Table 4.2 and Figure 4.3).

Solitary bee composition was also correlated with area of semi-natural woodland and with area of coniferous forestry (Table 4.5 and Figure 4.7).

The correlations of bee composition with area of semi-natural woodland and scrub were associated with sampling location as upon permutation testing within blocks defined by location, the correlations were no longer significant.

The correlation between solitary bee composition and forest area remained significant upon testing within blocks but the numbers of cases in the sample with areas of forestry were very few.

There was also a weak correlation between bumblebee composition and area of 'built environment' (Table 4.5 and Figure 4.8). This became significant upon testing within blocks suggesting that the correlation was independent of sampling location.

Table 4.5. Results of indirect analyses examining correlations between landscape variables and bee assemblage composition, with significance testing across entire dataset (p_{entire}) and within blocks defined by sampling location (p_{blocks}).

Correlations	Solitary bees			Bumblebees		
	<i>Envfit</i> r^2	p_{entire}	p_{blocks}	<i>Envfit</i> r^2	p_{entire}	p_{blocks}
Landscape PCA Axis 1 scores	0.006	0.857	0.941	0.06	0.186	0.258
Landscape PCA Axis 2 scores	0.08	0.142	0.751	0.16	0.008	0.108
Landscape PCA Axis 3 scores	0.10	0.063	0.094	0.05	0.284	0.198
Landscape types	0.08	0.074	0.186	0.08	0.125	0.186
Area of improved grassland	0.01	0.726	0.901	0.05	0.233	0.341
Area of semi-natural / semi-improved grassland	0.03	0.456	0.556	0.04	0.336	0.320
Area of semi-natural woodland & scrub =a	0.16	0.013	0.353	0.14	0.023	0.289
Area of boundary habitat=b	0.04	0.360	0.547	0.06	0.200	0.249
Area of a+b	0.12	0.039	0.312	0.07	0.157	0.499
Area of coniferous forestry	0.21	0.002	0.001	0.02	0.540	0.338
Area of built environment	0.06	0.205	0.190	0.09	0.084	0.049

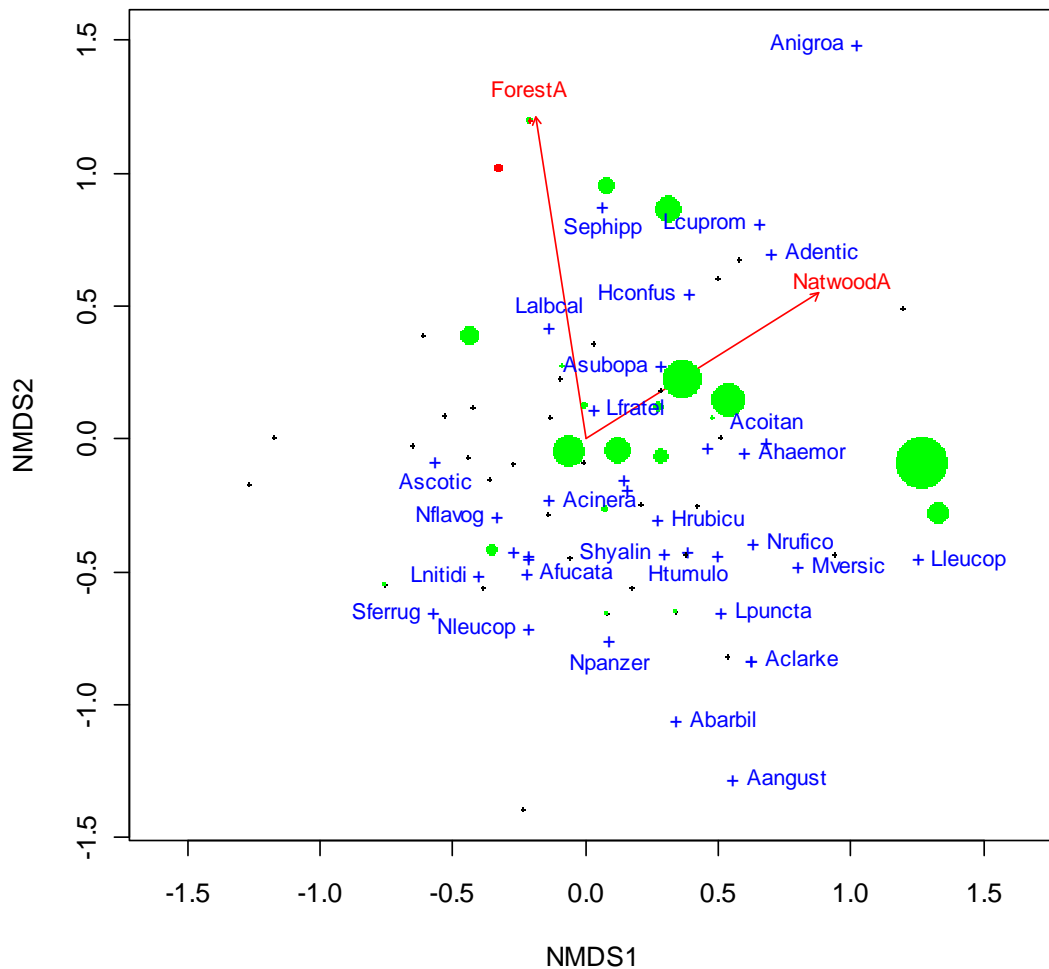


Figure 4.7. Solitary bee NMDS (Jaccard distances for presence-absence data) showing significant correlations with landscape composition at a scale of 100m radius (permutation testing across entire dataset). Length and direction of arrows show correlations with: ForestA = area of coniferous forestry; NatwoodA= area of semi-natural woodland, scrub and very young forestry plantations. Size of symbol reflects area of habitat around that site. Sites with no nearby woodland or forestry are shown as black crosses. Green= Sites with nearby woodland. Red (2 only)= Sites with mature coniferous forestry nearby.

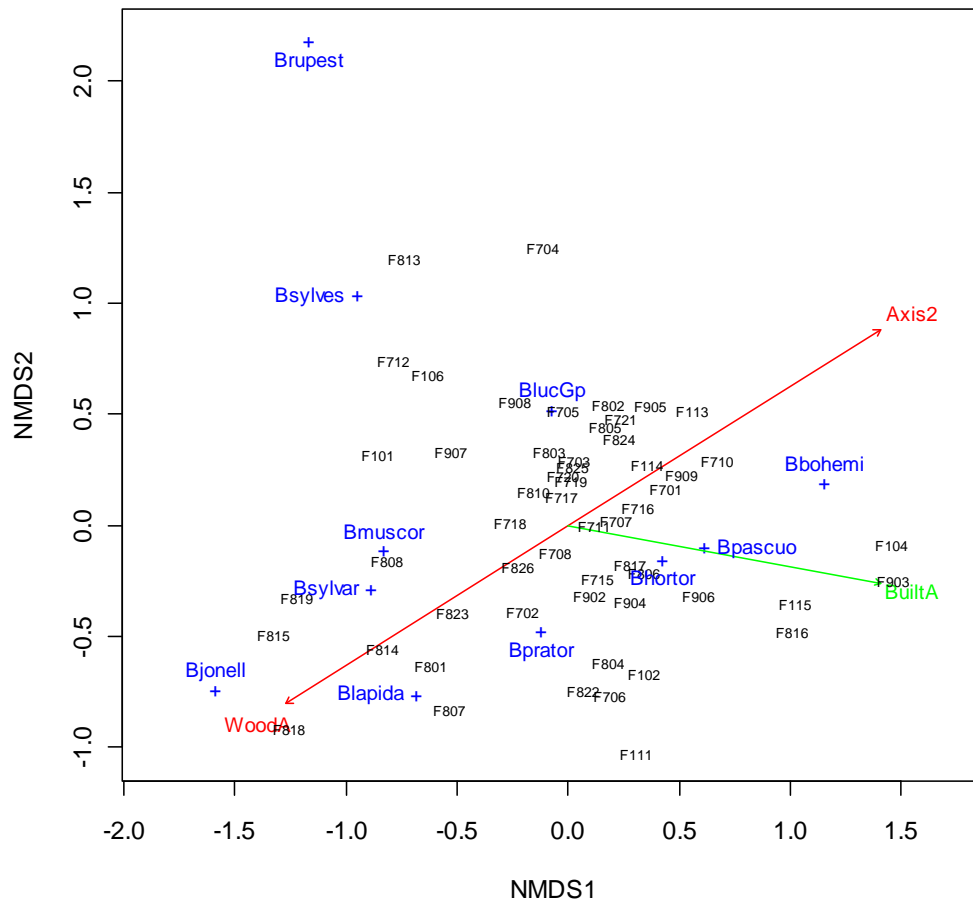


Figure 4.8. Bumblebee NMDS (Jaccard distances for presence-absence data) showing significant correlations with landscape composition at a scale of 100m radius (red = significant at $p=0.05$ with permutation testing across entire dataset, green= significant at $p=0.05$ with permutation testing in blocks defined by sampling location). Length and direction of arrow show correlations with: (a) Axis 2 = site scores on 2nd axis of landscape composition PCA which reflected a gradient from historically unenclosed and now wooded landscape to historically enclosed landscape; (b) WoodA= area of semi-natural woodland, scrub and very young forestry plantations; (c) BuiltA = area of buildings, roads, car-parks and active quarries.

4. 4. DISCUSSION AND CONCLUSIONS

Three landscape gradients were identified. The strongest gradient was that describing grassland type along a gradient of domination by improved agricultural grasslands to domination by semi-natural and semi-improved grassland as defined by (Sullivan *et al.* 2010). This is a gradient in agricultural management intensity at the landscape level. The second gradient was from previously open and now becoming wooded to enclosed

landscapes. The weakest but still discernible gradient was in landscapes with built land to areas with none. The literature indicates that all three of these gradients could be important to bees (e.g. Carré *et al.* 2009).

A number of alternative approaches to summarising landscape composition appeared equally suitable. When the variables arising from each method were tested for their strength of association with bee data, no one measure of landscape composition emerged as the best. These very preliminary investigations suggested that total bee abundance may be sensitive to different components of landscape compared to bee assemblage composition.

Although the dominant landscape gradient was determined by the intensity of grassland management at a landscape scale, this gradient was not correlated with bee assemblage composition. Instead bee assemblage composition was correlated with the other landscape components, a gradient from open to enclosed landscapes and from built to undeveloped land.

Analyses of the relative importance of key environmental factors for bee assemblage composition (Chapter 9) used three variables to describe landscape: (1) Area of semi-natural woodland & scrub and young forestry, (2) Area of built environment, and landscape type. Landscape type captured the intensity of farm management at landscape level.

For analysis of the relative importance of landscape composition on bee abundance and diversity (Chapter 10), landscape was summarized using (1) Area of improved grassland and (2) Area of woodland, scrub and young forestry. Area of improved grassland captured the intensity of farm management at landscape level.

CHAPTER 5: MEASURING FIELD BOUNDARY STRUCTURE AND BOTANICAL COMPOSITION

5. 1. INTRODUCTION

Field boundaries are a common feature of the Irish farmed landscape (Aalen *et al.* 1997). The dominant form of field boundary in the study region is a hedgerow although walls, earthen banks and tree lines also occur.

Hedgerows are regarded as the most abundant semi-natural habitat in farmland in the study region (Sheridan *et al.* 2011). Hedgerows may vary considerably in their species diversity and composition as well as their physical structure (Forman & Baudry 1984), with features such as walls, banks and drains often being associated with them in Ireland (Murray & Foulkes 2006; Santorum & O'Sullivan 2006).

This section describes the variation in botanical composition and structure of hedgerows within the study region. It tests a number of data reduction approaches to summarising botanical and structural information.

A difficulty for the study of associations between plant and animal assemblages has been the lack of methods that allow the use of the plant species composition of the entire community as a predictor (Schaffers *et al.* 2008). Species richness or diversity measures (Magurran 2004), for example, only summarise diversity. Species composition of plant assemblages can integrate information on environmental conditions, on vegetation structure and on site history (Schaffers *et al.* 2008).

The variables derived in this section, describing botanical composition and structure of hedgerows of boundaries, are to be used in subsequent analyses of correlations with bee abundances, diversity and assemblage composition in Chapters 8, 9 and 10.

Analyses were conducted in R (R Core Team 2012) using the base R package and vegan package (Oksanen *et al.* 2013).

5. 2. METHODS

5.2.1. DATA COLLECTION METHODS

A structural survey and botanical survey were conducted.

STRUCTURAL SURVEY

At each study site, the boundary immediately adjacent to each bee sampling point was surveyed. The structure of the boundary immediately adjacent to the bee sampling point was surveyed using the Field Boundary Evaluation and Grading System (FBEGS) Index (Collier & Feehan, 2003). The system was not used in its entirety as some measurements were not considered of importance to bees e.g. 'Boundary to wall connectivity' and 'percentage of gaps' The categories used in the FBEGS survey to score each observation were regrouped into a smaller set of categories for some observations, to improve the spread of cases and when it made sense ecologically.

The structural variables that were included in analyses were boundary type, height, width, structural complexity of vegetation, height of earthen bank and presence of drain. These are described further in Appendix 4.

BOTANICAL SURVEY

A 20m length along each boundary with a 'woody' component, i.e. tree line or hedgerow, was surveyed (50 of the 56 boundaries studied). Each shrub, tree or woody climber growing along this stretch was identified and the percentage of this length which it occupied estimated.

Some species were recorded only to the level of their genus as this was considered sufficient for the objectives of this study and allowed for quicker identification in the field (e.g. Birches, Cotoneasters, Gorse, Poplars, Oaks, Crab apples, Willows and Elms). Thirty-one woody species and species groups of trees, shrubs and climbers were identified.

Environmental conditions were measured in order to study their association with the botanical composition and structure of the hedgerows. The following

environmental variables (Table 5.1) were sampled in the field adjacent to the boundary (where the bee sampling was also carried out).

Table 5.1. Supplementary environmental variables used in analyses of composition of hedgerow and grassland vegetation

Group of environmental variables	Variables used	Type of variable
Geographical location	Easting (X) of Irish grid reference Northing (Y) of Irish grid reference Altitude (m) One of four local areas: West Limerick, East Limerick, Central Limerick and Tipperary	Continuous Continuous Continuous Factor
Soil chemistry	Phosphates (P) (mg/l) Potassium (K) (mg/l) Magnesium (Mg) (mg/l) pH Organic matter	All continuous
Grass management (derived from structured interview with farmers, see Appendix 13)	Reseeded within 15 years(Yes/No) One of five cutting and grazing categories (see Appendix 14 for details) Total N fertiliser applied to field (kg/ha)	Factor Factor Continuous

METHODS USED TO MEASURE SUPPLEMENTARY ENVIRONMENTAL DATA

GEOGRAPHICAL LOCATION

Grid references of sampling points were recorded with a Global Positioning System Magellan GPS 315

SOIL CHEMISTRY

Soil samples from the first few centimetres of topsoil were collected using an auger from across the field being sampled. They were bagged and labelled immediately and frozen on return to the laboratory. Soils were then defrosted, air dried, sieved through a 5mm-soil sieve with the aid of a pestle and mortar and then stored in labelled paper bags. In this state the samples could be stored satisfactorily for months. Soil pH and organic matter were measured by (Keegan 2007). Testing for phosphorous, potassium, magnesium was carried out in the ‘Soil and analytical services department’ in Johnstown Castle in Co. Wexford.

FERTILISER APPLICATION AND GRASS MANAGEMENT

Data regarding field management were extracted from interviews with farmers. See Chapter 7 and Appendices 2.M and 2.N for details.

5.2.2. METHODS OF ANALYSIS

DESCRIPTIVE ANALYSES TO PROVIDE AN OVERVIEW OF FIELD BOUNDARIES WITHIN THE STUDY REGION

FIELD BOUNDARY STRUCTURE

The types of field boundaries present within the study region and their relative frequencies are presented. The ranges of hedgerow heights, widths, presence of associated drain etc. are summarized to give an overview of boundary structure within the region.

Correlations between these structural descriptors were examined. As variables were a mixture of nominal and ordinal data, with three or fewer categories, the following methods were used to test for correlations:

- When one or both of the variables were nominal; Fisher's Exact Test was used to test for a significant correlation. The post-tests used were Phi if the variables were both dichotomous and Cramer's V if one variable had more than two levels.
- For two ordinal variables; Goodman and Kruskal's gamma.

FIELD BOUNDARY BOTANICAL COMPOSITION

Non-metric multidimensional scaling analyses (NMDS) with indirect gradient analysis, cluster analysis and indicator species analysis were used to understand the composition of hedgerows in the study region.

The species composition dataset was transformed (\log_{10}) and a Bray Curtis dissimilarity matrix of sites calculated. This data matrix was used in the following analyses.

Non-metric multidimensional scaling analyses (NMDS) was carried out using the *metaMDS* function of *vegan* (Oksanen *et al.* 2013). After the automatic iterations of *metaMDS*, the NMDS was repeated manually, using the best solution from the first run as a baseline for comparison. This process was repeated for ordinations with increasing numbers of axes in order to determine how many axes to present.

The correlations between environmental variables and botanical composition of hedgerows were examined using the *envfit* function of *vegan* (Oksanen *et al.* 2013) to determine a goodness of fit statistic based on 1,000 random permutations of the data. (Samples with missing values in ordination scores or environmental variables were removed from the analysis.)

The strength and direction of correlations were visualised as arrows on the ordination plot. For continuous environmental variables, the *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to check visually whether the correlation was a linear one. This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use cross-validators selection of smoothness (GCV).

Hierarchical cluster analysis was conducted using the *hclust* function of the R base package (R Core Team 2012). A cluster dendrogram was produced using average agglomeration. The groups identified in this analysis were superimposed upon the NMDS ordination plot.

The indicator values of species, for the two major types of hedgerow identified using cluster analysis, were calculated using Dufrene-Legendre Indicator Species Analysis (Dufrene & Legendre 1997). In this analysis, an indicator value equal to the product of relative frequency and relative average abundance in clusters is calculated together with the probability of obtaining as high an indicator value as observed over a specified number of iterations, in this case 1000. The software used was *indval* function of *Labdsv* package (Roberts 2013) in R (R Core Team 2012).

ANALYSIS METHODS TO SUMMARISE FIELD BOUNDARY STRUCTURE AND COMPOSITION TO A FEW VARIABLES

In order to find a small number of descriptive variables that could summarise field boundary structure and botanical composition effectively for bee analyses, they were considered separately and together.

For field boundary structure I examined whether:

- one or two of the structural descriptors were strongly correlated with the other variables and could account for the whole set;
- a few discrete types of hedgerow in terms of structure existed;
- a 'Structural Index' could be calculated and used to summarise structure.

For field boundary composition, I considered the results of cluster analysis of species-abundance data, indicator values of species, indices and PCO axes scores as options for variables that might summarise botanical composition.

Since it was possible that structure and botanical composition were associated and that discrete types of hedgerow with a particular structure and botanical composition existed, I also examined correlations between the botanical composition of wooded boundaries and boundary structure. The methods used for each of these analyses are outlined below.

SUMMARISING FIELD BOUNDARY STRUCTURE

For wooded field boundaries, the correlation matrix for variables describing structure (Table 5.2) was examined to see if one or two of the structural variables could account for the whole set.

To examine whether boundary structure clustered into a few discrete types, three dimensional scatterplots of the heights, widths and complexity of hedgerows were drawn and coloured by presence of drain and height of bank. The scatterplot 3d package (Ligges & Mächler 2003) was used together with *jitter* function from base R package (R Core Team 2012) to plot these graphs.

A Structural Index for each hedgerow was calculated and tested to see how well it correlated with each individual variable describing structure. The Structural Index was derived by allocating a score to each possible category of the structural variables (see Appendix 4) and summing these for the hedgerow. The maximum possible score was 13 and the minimum was 3. The association between this Structural Index and the factors that contributed to it were examined visually in graphs and tested using Spearman's correlation coefficient (the Structural Index was regarded as an ordinal variable) to check that the index was truly representative of the hedgerow structure.

SUMMARISING BOTANICAL COMPOSITION OF WOODED FIELD BOUNDARIES

The results of cluster analysis and NMDS of the botanical dataset (Figure 5.1 and 5.2) were examined to determine whether field boundaries could be considered distinct types or whether they were better described with a continuous variable.

To capture continuous variation in the botanical composition of hedgerows, the following approaches or indicators were considered:

1. Species number (number of woody species observed within each 20m sample of field boundary)
2. Inverse Simpson's Index, $1/D$, calculated using the number and abundance of woody species within each field boundary. This index is regarded as particularly robust (Magurran 2004).
3. Abundance of a single indicator plant species or small number of species (those identified as indicators, using Dufrene-Legendre Indicator Species Analysis .
4. Principal Coordinates Analysis axes scores

Principal coordinates analysis (PCO) was conducted upon the Bray Curtis distance matrix for the plant species abundance matrix using the *capscale* function of *vegan* (Oksanen *et al.* 2013). Three axes were retained.

An ideal variable for the summary of hedgerow botanical composition was regarded as one that was strongly correlated with complete botanical composition, preferably having a linear relationship with it.

The correlation of each of the four indicators with the hedgerow NMDS solution was tested using the *envfit* function of *vegan* package (Oksanen *et al.* 2013) which gave a goodness of fit statistic based on 1,000 random permutations of the data.

The direction and strength of this correlation visualised as an arrow on the NMDS biplot. To check whether the relationship between indicator and ordination solution was linear, the *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to fit a generalised additive model (GAM) (Simpson 2011). I

used the default settings, which use cross-validated selection of smoothness (GCV).

SUMMARISING STRUCTURE AND COMPOSITION OF FIELD BOUNDARIES WITH ONE MEASURE

Correlations between field boundary structure and composition were examined to assess if one quality could capture both.

Correlations between variables describing boundary structure (Structural Index and individual structure descriptors) and the NMDS solution of wooded boundaries' botanical composition were tested using *envfit* correlation coefficients calculated using the *envfit* function of vegan package (Oksanen *et al.* 2013) which gave a goodness of fit statistic based on 1,000 random permutations of the data.

Correlations between Structural Index and species number and Inverse Simpson's Index were tested using Spearman's correlation coefficient.

ANALYSIS METHODS TO SELECT THE BEST VARIABLES TO SUMMARISE FIELD BOUNDARY COMPOSITION AND STRUCTURE FOR BEE ANALYSES.

The correlations between bee response variables and hedgerow PCO axes and hedgerow structure and composition indicator variables were tested using Spearman's correlations. These analyses checked whether field boundary structure and composition had indeed been captured in a way that was relevant to bees. They also served as a preliminary exploration of bee responses to field boundary qualities.

The bee response variables used were: solitary bee abundance ($\log_{10}+1$); bumblebee abundance ($\log_{10}+1$), number of bee genera; number of bee species; number of solitary bee species and number of bumblebee species.

Correlations between hedgerow vegetation and bee assemblage composition are examined in depth in Chapter 8.

The correlation between hedgerow structure, summarised as the Structural Index, and solitary bee and bumblebee assemblage composition was assessed using indirect gradient analysis. Non-metric multidimensional scaling

(NMDS) analyses were conducted for the solitary bee and the bumblebee datasets separately. Prior to the NMDS analyses, bee species that were only observed at one site were removed from the dataset. The Jaccard distance calculated using presence-absence data was used in the ordinations. The NMDS analysis was done using the *metaMDS* function in the *vegan* package of the R software (Oksanen *et al.* 2013). As well as using the random restarts provided by this function, each NMDS was repeated using the best solution from the first analyses. This was to ensure the global solution was reached by preventing the NMDS becoming trapped in local optima.

Stress, a measure of agreement between the original ecological distances and configuration of the ordination, was approximately 0.2 for two axes for both NMDS analyses. This was considered acceptable and two axes configurations were used for all NMDS plots. Species were represented on ordination plots of NMDS solutions as centroids which were mapped using weighted averaging, following (Legendre & Legendre 1998).

The influence of the hedgerow Structural Index, was assessed in the NMDS, using the *envfit* function of *vegan* to determine a goodness of fit statistic based on 1,000 random permutations of the data. The correlation was visualised in ordination biplot, with arrows used to show the direction and strength of correlations. The *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to check visually whether the correlation was a linear one. This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use cross-validated selection of smoothness (GCV).

5. 3. RESULTS

5.3.1. AN OVERVIEW OF FIELD BOUNDARY STRUCTURE AND COMPOSITION WITHIN THE STUDY REGION.

STRUCTURE OF FIELD BOUNDARIES IN THE STUDY REGION

In the study region, hedgerows were the dominant type of field boundary and stone walls, unplanted earthen banks and water-filled ditches were less common. 89% of boundaries (56 surveyed) had a woody component and the majority of these (45) were hedgerows. Other types of wooded boundaries observed were two treelines (one was naturally occurring along a river and the other was a line of planted Poplars); two walls that had shrubs growing along them due to field abandonment (spontaneous hedgerows of (Forman & Baudry 1984)) and one woodland/scrub edge. Of the 11% of boundaries that did not have trees or shrubs, these were earthen banks (3); drystone wall (1) or ditches/drains with occasional trees or shrubs (2).

Earthen banks were a common feature of wooded boundaries, being associated with 76% of them. This was in addition to occurring more rarely without trees or shrubs.

Forty percent of wooded boundaries had open ditches or drains associated with them.

The heights of hedgerows and other wooded boundaries ranged from cut to almost ground level to taller than four meters and were evenly distributed over this range: 30% were between 0.5 and 2m high; 34% were between 2 and 4m high and 36% were taller than 4m.

The width of wooded boundaries, at their base, ranged from 0.5m to wider than four meters: 42% were between 0.5 and 2m wide; 30% were between 2m and 4m wide and 28% were wider than 4m.

Wooded boundaries showed a range of complexity in their structure. 36% were scored as having simple structure; 26% as having intermediate complexity of structure and 38% as having complex structure.

There was a strong correlation between structural complexity and width of wooded boundary (Table 5.2). Presence of drain and earthen bank were correlated with height.

Table 5.2. Correlation matrix between variables describing structure of wooded field boundaries

	Width	Complexity	Bank	Drain
Height	NS	NS	NS	Fisher's Exact Test $p=0.040$ Cramer's V = 0.36
Width		Gamma = 0.83 $p<0.001$	NS	NS
Complexity			NS	NS
Bank				Fisher's Exact Test $p=0.028$ Cramer's V = 0.38

BOTANICAL COMPOSITION OF FIELD BOUNDARIES IN STUDY REGION

Wooded boundaries were separated into two main groups by cluster analysis (Figures 5.1, 5.2) (three boundaries fell outside of these groups: F903= tree line, F906 =line of Poplars, F817= stone wall with scrub).

Group one boundaries, were the more common form of wooded boundary and were more species-rich with tree and shrub species whereas group two were species-poor and dominated by shrubs such as hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) (Figures 5.2, 5.3 and Table 5.3). Both groupings are similar to Ash woodland in composition (Rodwell 1991).

The botanical composition of field boundaries was strongly correlated with Easting coordinate (*envfit* $r^2=0.43$, $p=0.001$) and altitude (*envfit* $r^2=0.32$, $p=0.002$) and more weakly with Northing coordinate (*envfit* $r^2=0.22$, $p=0.004$) and soil pH (*envfit* $r^2=0.22$, $p=0.004$) (Figure 5.2).

Indicator species for group one boundaries were ivy (*Hedera helix*); hawthorn (*Crataegus monogyna*); dog rose (*Rosa canina*) and ash (*Fraxinus excelsior*)

(Table 5.3, Figure 5.3). Burnet rose (*Rosa pimpinellifolia*) was a significant indicator species for Group 2 hedgerows but only occurred in one third of boundaries within the group.

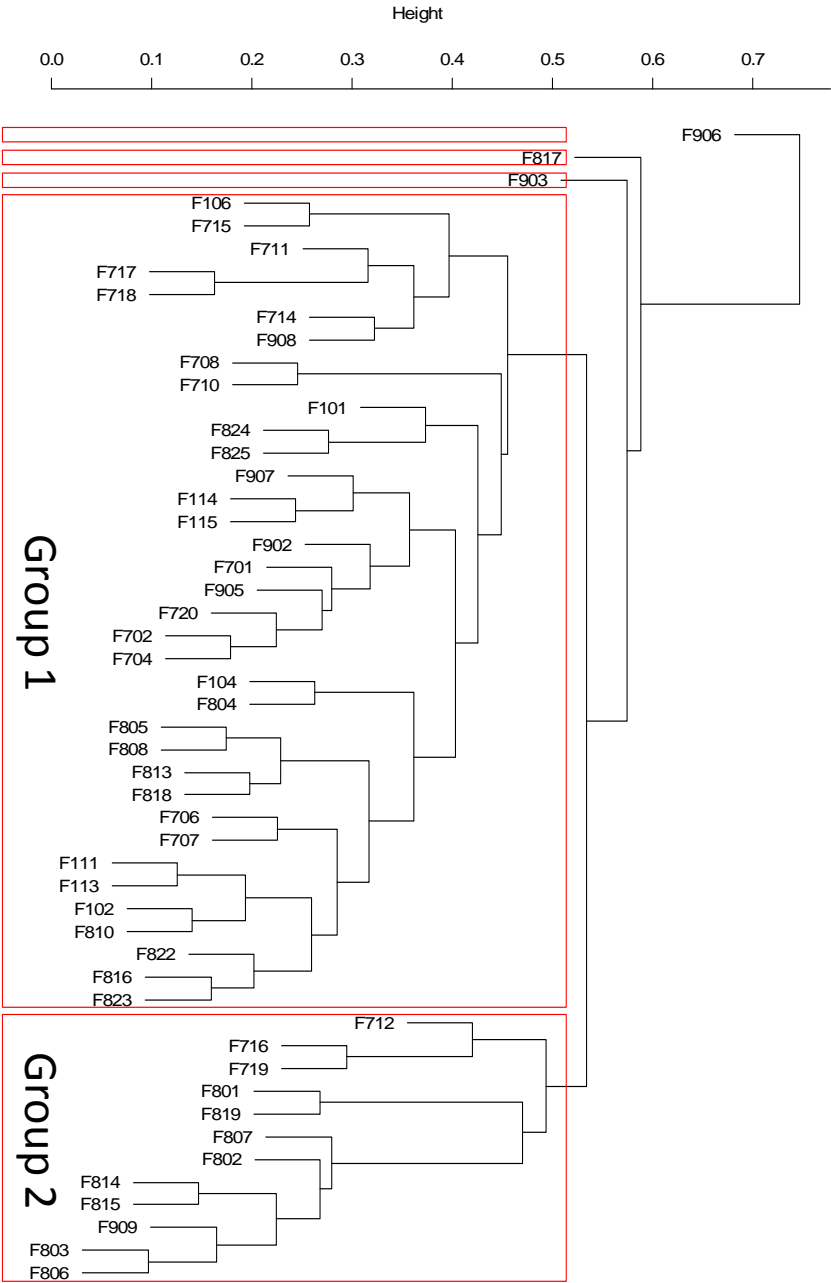


Figure 5.1. Cluster dendrogram of sites based upon their field boundary's woody vegetation (hierarchical cluster analysis using average agglomeration on Bray Curtis dissimilarity matrix).

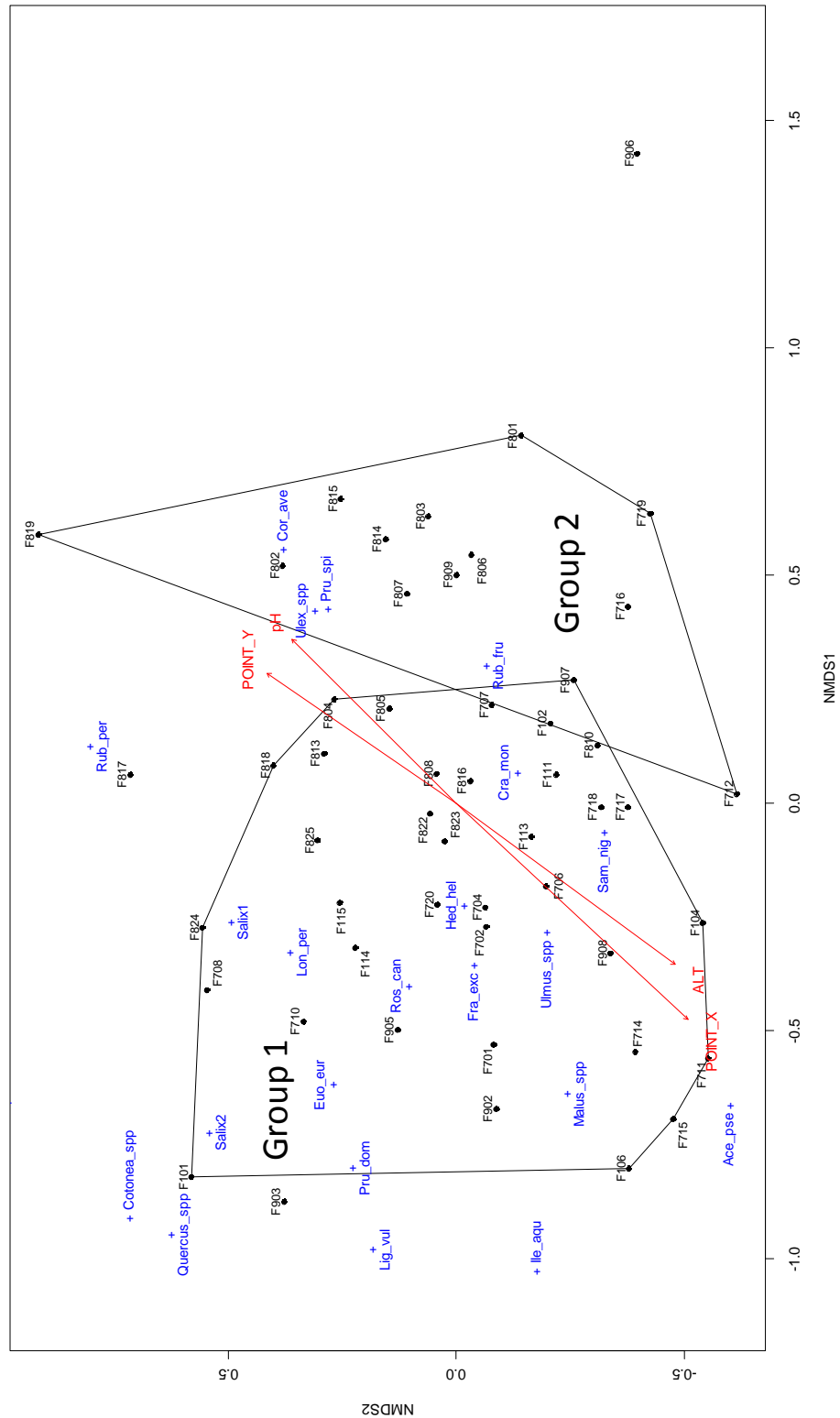


Figure 5.2. Biplot of NMDS of woody vegetation of field boundaries showing species and sites associated with the two hedge groups identified by cluster analysis together with correlations with altitude, location and soil pH. (POINT_X= Easting coordinate, POINT_Y= Northing coordinate, pH= soil pH, ALT=altitude.)

Table 5.3. Indicator values (IndVal percentage) for plant species in the two major groupings of hedgerows identified in cluster analysis. (An IndVal of zero does not mean that the species was absent from that hedgerow group, but that it has no indicator value in comparisons of the two hedgerow groups.) p-value is based on 1000 permutations and tests the statistical significance of the species associations with each group.

Species	Abbreviation	Group 1	Group 2	p- value
<i>Hedera helix</i>	Hed_hel	0.97	0	0.001
<i>Crataegus monogyna</i>	Cra_mon	0.75	0.25	0.001
<i>Rosa canina</i>	Ros_can	0.58	0	0.006
<i>Fraxinus excelsior</i>	Fra_exc	0.53	0	NS
<i>Rubus fruticosus ag.</i>	Rub_fru	0.48	0.52	NS
<i>Sambucus nigra</i>	Sam_nig	0.39	0	NS
<i>Lonicera periclymenum</i>	Lon_per	0.26	0	NS
<i>Acer pseudoplatanus</i>	Ace_pse	0.25	0	NS
<i>Malus species</i>	Malus_spp	0.19	0	NS
<i>Prunus spinosa</i>	Pru_spi	0.17	0.45	NS
<i>Salix species 1</i>	Salix1	0.17	0	NS
<i>Ulmus species</i>	Ulmus_spp	0.17	0	NS
<i>Symphoricarpos albus</i>	Sym_alb	0.17	0	NS
<i>Euonymus europaeus</i>	Euo_eur	0.14	0	NS
<i>Quercus species</i>	Quercus_spp	0.14	0	NS
<i>Salix species 2</i>	Salix2	0.11	0	NS
<i>Ilex aquifolium</i>	Ile_aqu	0.08	0	NS
<i>Ligustrum vulgare</i>	Lig_vul	0.08	0	NS
<i>Rubia peregrina</i>	Rub_per	0.08	0	NS
<i>Cotoneaster species</i>	Cotonea_spp	0.06	0	NS
<i>Ulex species</i>	Ulex_spp	0.05	0.25	NS
<i>Rosa pimpinellifolia</i>	Ros_pim	0	0.33	0.002
<i>Corylus avellana</i>	Cor_ave	0	0.15	NS
<i>Ligustrum ovalifolium</i>	Lig_ova	0	0.07	NS

RELATIONSHIP BETWEEN INDICATOR SPECIES ABUNDANCES, COMPOSITION INDICES AND NMDS OF FIELD BOUNDARY WOODY VEGETATION

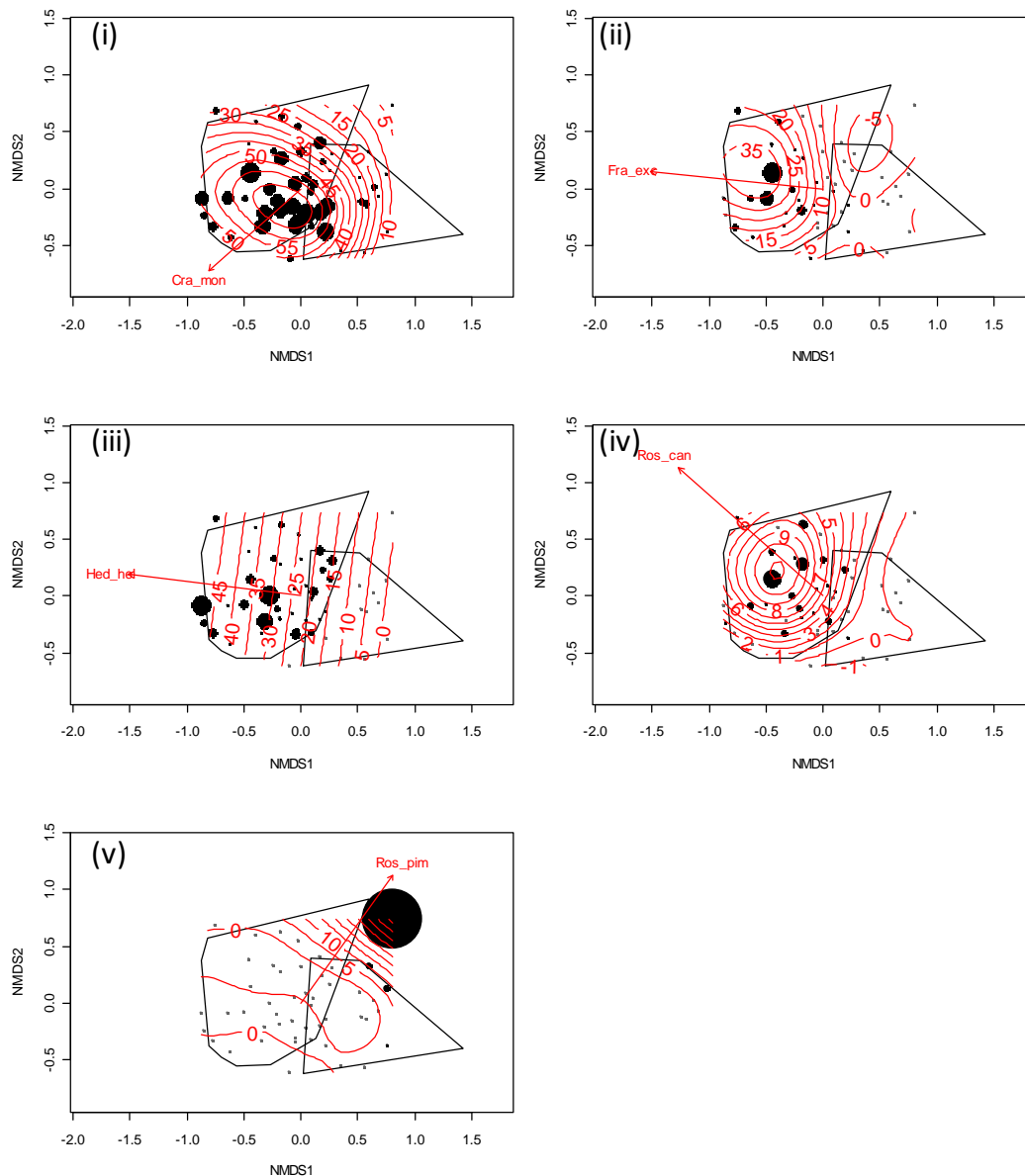


Figure 5.3. NMDS graphs showing the observed and modeled abundance of Indval Indicator Species (i) *Crataegus monogyna*, (ii) *Fraxinus excelsior*, (iii) *Hedera helix*, (iv) *Rosa canina*, (v) *Rosa pimpinellifolia* at sites in the two hedgerow groups identified by cluster analysis. The size of symbol is proportional to observed abundance of indicator species. The two hedge groups described are delineated in black. Red arrows indicate the strength and direction of significant linear correlations between species abundance and the ordination. Red contour lines show a smooth fitted surface of estimated abundance of each indicator species, fitted using a generalized additive model using the R function *ordisurf*.

5.3.2. DATA REDUCTION OF FIELD BOUNDARY STRUCTURE AND COMPOSITION

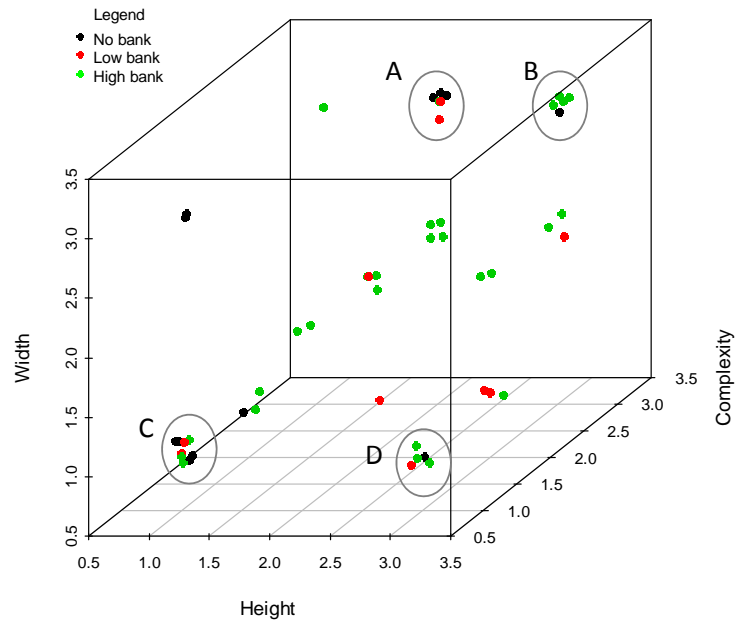
Summarising field boundary structure

Although there was a strong correlation between structural complexity and width of wooded boundary (Table 5.2), correlations between other dimensions of boundary structure were weak and it was concluded that one or two structural variables could not be selected to summarise the whole set.

Figure 5.4 showed that *some* hedgerows, marked in groups A-D, fell into structural types that could be defined by their height, width and complexity. Boundaries within some of these groups had other features in common. For example, Group B hedges which were tall, wide and complex, generally also had a high bank and a drain present, whereas within group C, hedges were low in height, relatively narrow and not complex in structure and rarely had an associated drain. They were variable with regards to the presence of an earthen bank. The graphs also show a linear trend, between height, width and complexity, for boundaries with a bank. This, together with the fact that many boundaries did not fall within clusters, suggested that a continuous variable may be more appropriate to describe structure rather than types.

The Structural Index was strongly correlated with all evaluated aspects of structure (Figure 5.5). As correlation coefficients were similar in size, each characteristic of boundary structure was considered to have loaded similarly onto the Structural Index, as was desired. The Structural Index was therefore considered to have summarized the structure of wooded boundaries very effectively.

[i]



[ii]

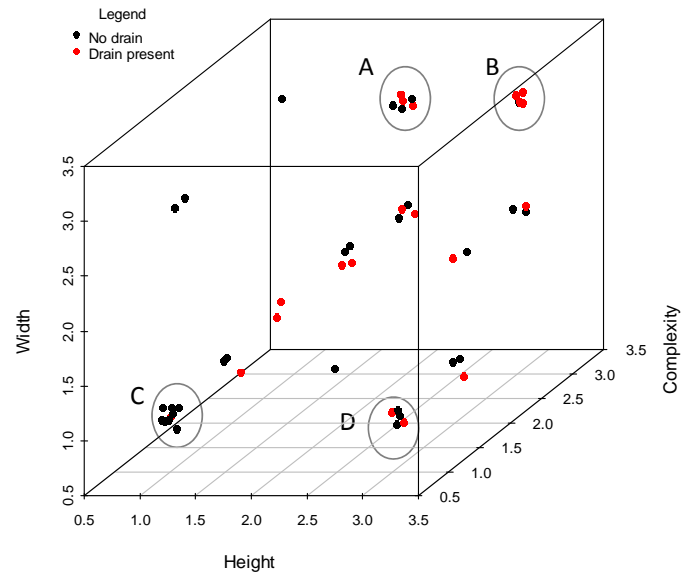


Figure 5.4. Scatterplots (3d) of variables describing field boundary structure. Jitter has been applied to keep all datapoints visible. Boundaries are coloured by [i] earthen bank height and [ii] presence of drain. Group A hedges were wider than tall and structurally complex. Group B hedges were tall, wide and complex, and generally also had a high bank and a drain present. Group C hedges were low, narrow and simple in structure. Group D hedges were tall, narrow and of low structural complexity.

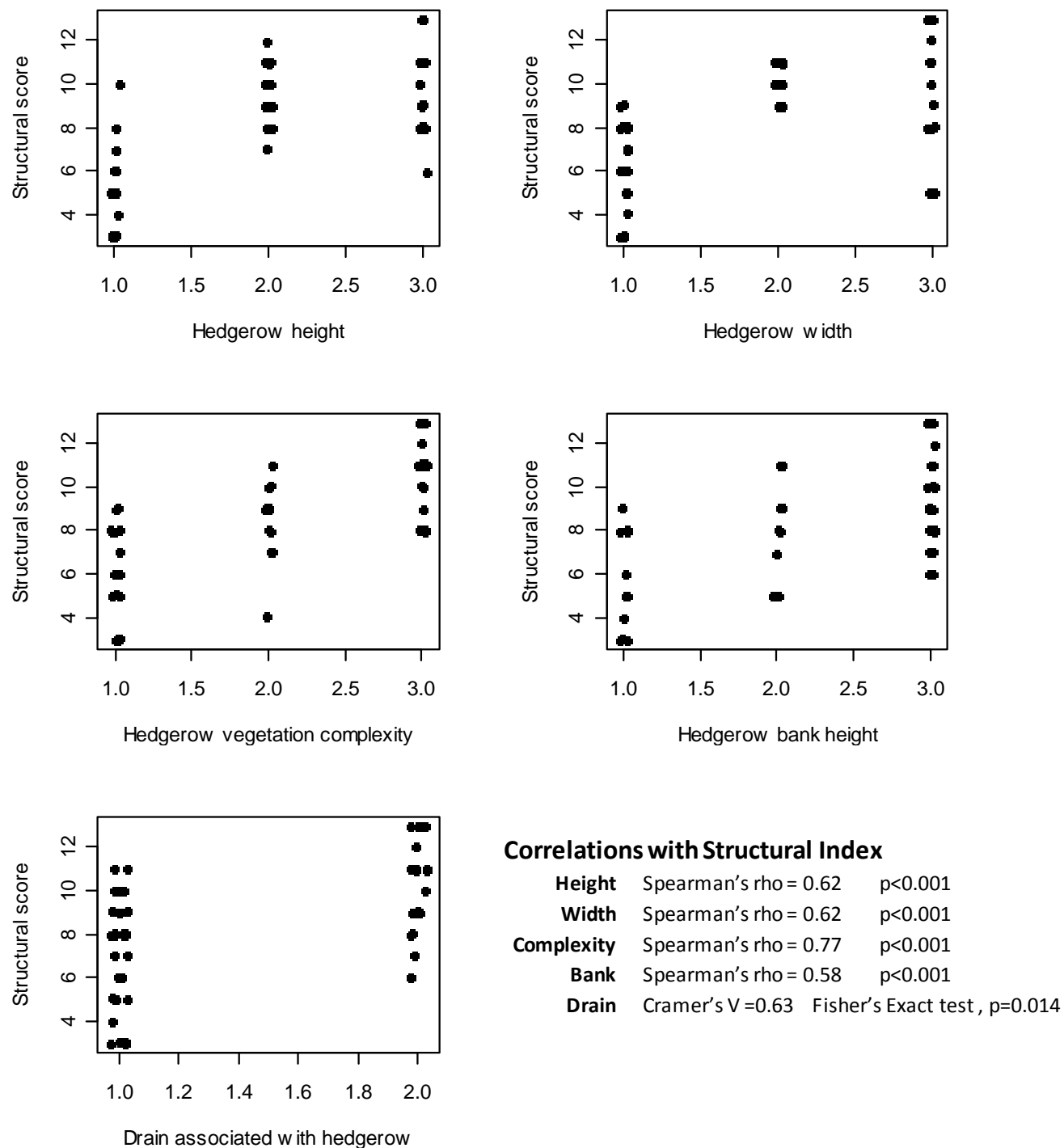


Figure 5.5. Correlations and dotplots showing how the Structural Index is associated with variables describing field boundary structure:.

Summarising botanical composition of wooded field boundaries

Although two broad botanical types of wooded field boundary were identified by cluster analysis, these were not completely distinct as shown by their overlap in the ordination plot (Figures 5.2, 5.3). It would be preferable not to assign boundaries to types based on composition but to use a continuous variable that allows for a gradient in composition.

The correlations between abundances of Indval Indicator species and the NMDS, although significant ($p < 0.05$), were relatively weak, with the correlation coefficients ranging between 0.19 and 0.28 (Figure 5.3). Indicator species, while a useful aid for interpretation of the cluster analysis and NMDS and description of the range of boundaries in the study region, were not suitable for use as surrogate variables summarizing the composition of boundaries for subsequent analyses.

Species number and the Inverse Simpsons index were both highly correlated with the NMDS ordination ($envfit\ r^2 = 0.78$, $p = 0.001$, $envfit\ r^2 = 0.68$, $p = 0.001$ respectively) and were therefore considered the best available option for summarising botanical composition. Plots showing how these indices were associated with botanical composition are shown in Figure 5.6.

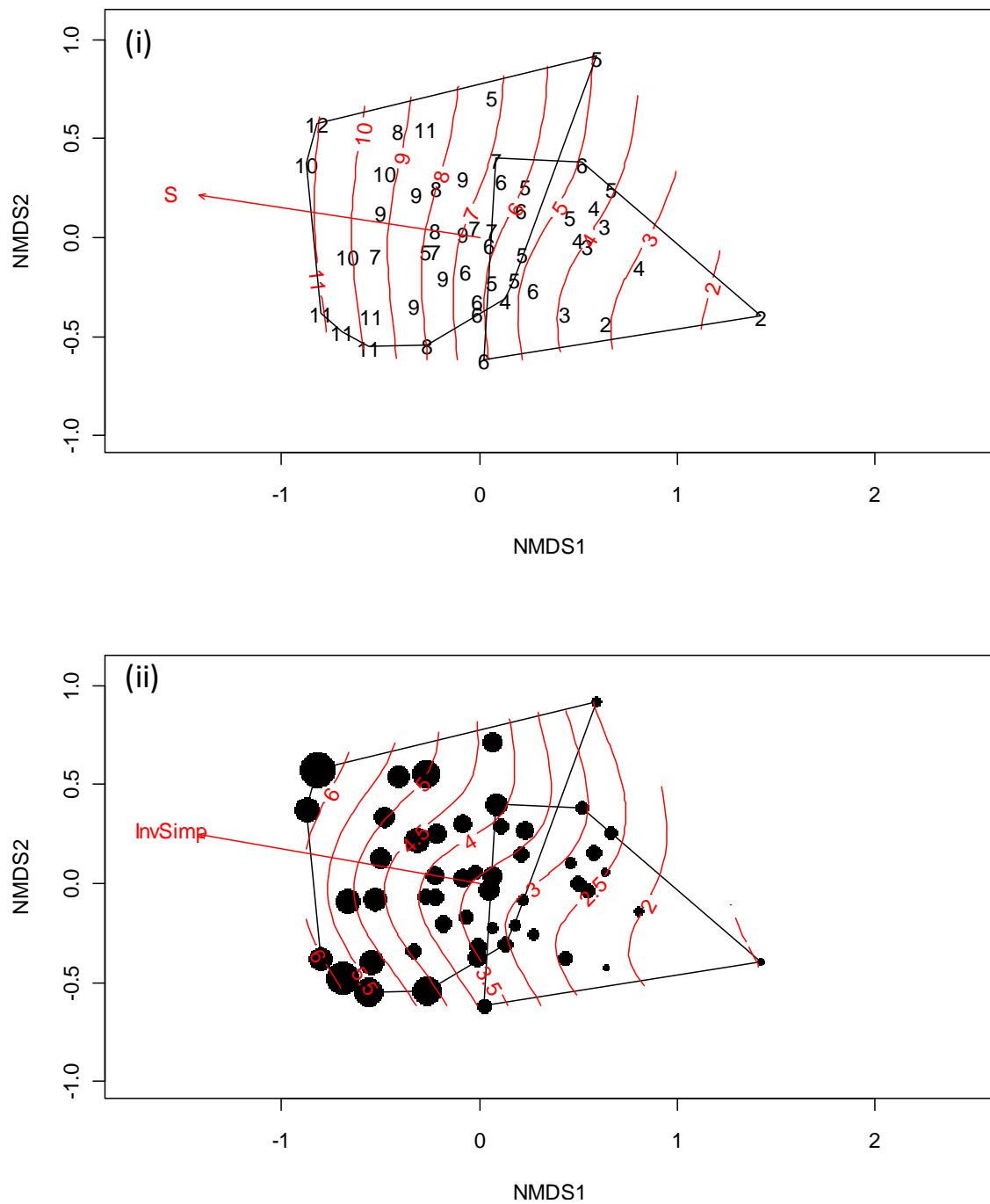


Figure 5.6. NMDS graphs of hedgerow composition showing (i) species number, S and (ii) Inverse Simpson's Index, $InvSimp$, at each site for the two main hedgerow groups. Arrows indicate the strength and direction of linear correlations between species number ($p < 0.05$) and Inverse Simpson's index ($p < 0.05$) and the ordination. Red contour lines show estimated values of S and $InvSimp$ fitted using a generalized additive model using the *vegan* function, *ordisurf*.

PCO OF FIELD BOUNDARY WOODY VEGETATION

The first three axes of the PCO analysis (Figure 5.7) explained only 35.5% of the variance in the composition of the woody component of hedgerow vegetation. This did not therefore seem an ideal way to summarise hedgerow composition for further analyses.

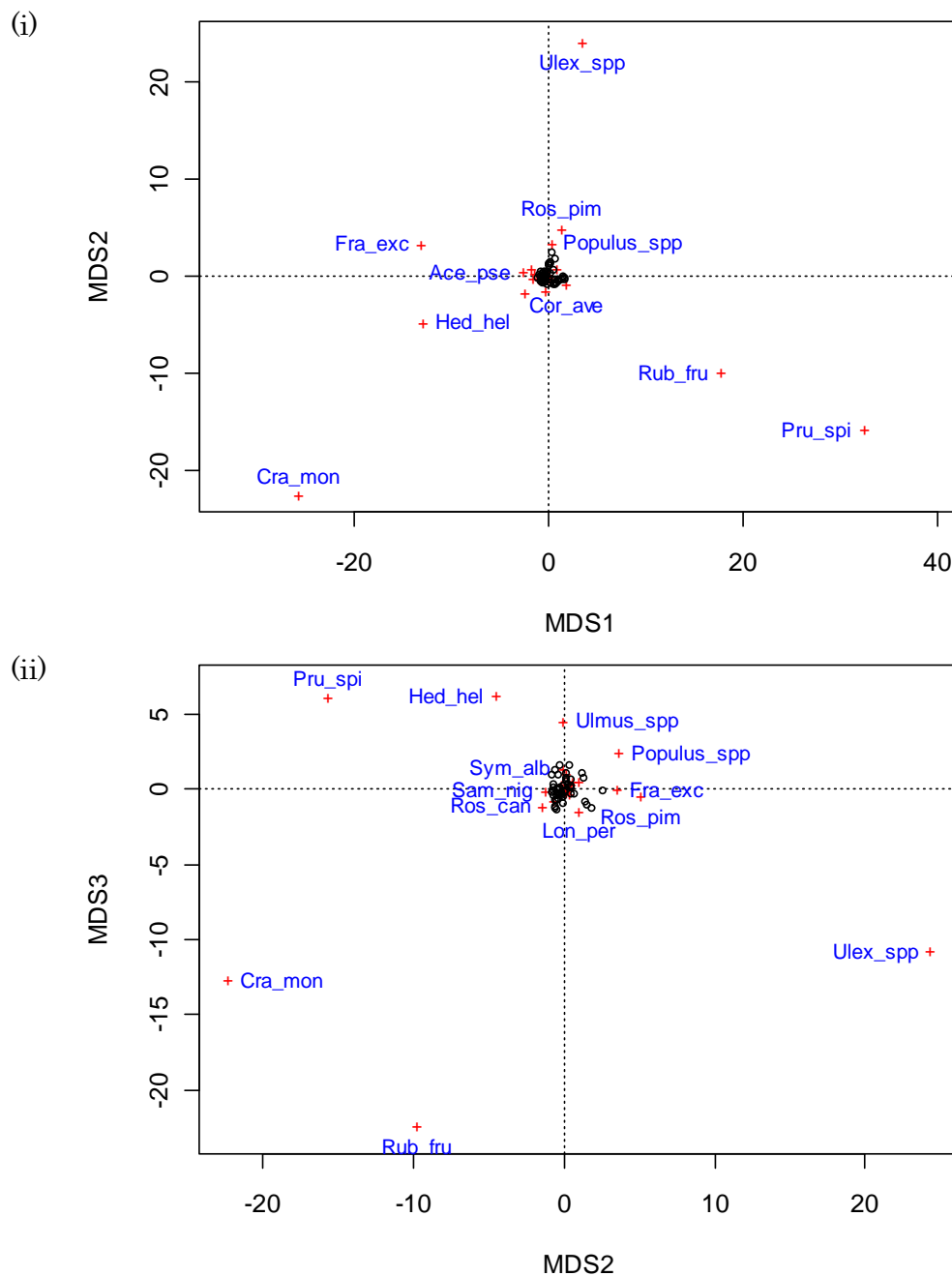


Figure 5.7. Biplots of hedgerow composition PCO, (i) first 2 axes of PCO, (ii) axes 2 and 3 of PCO.

Summarising structure and botanical composition of wooded field boundaries together

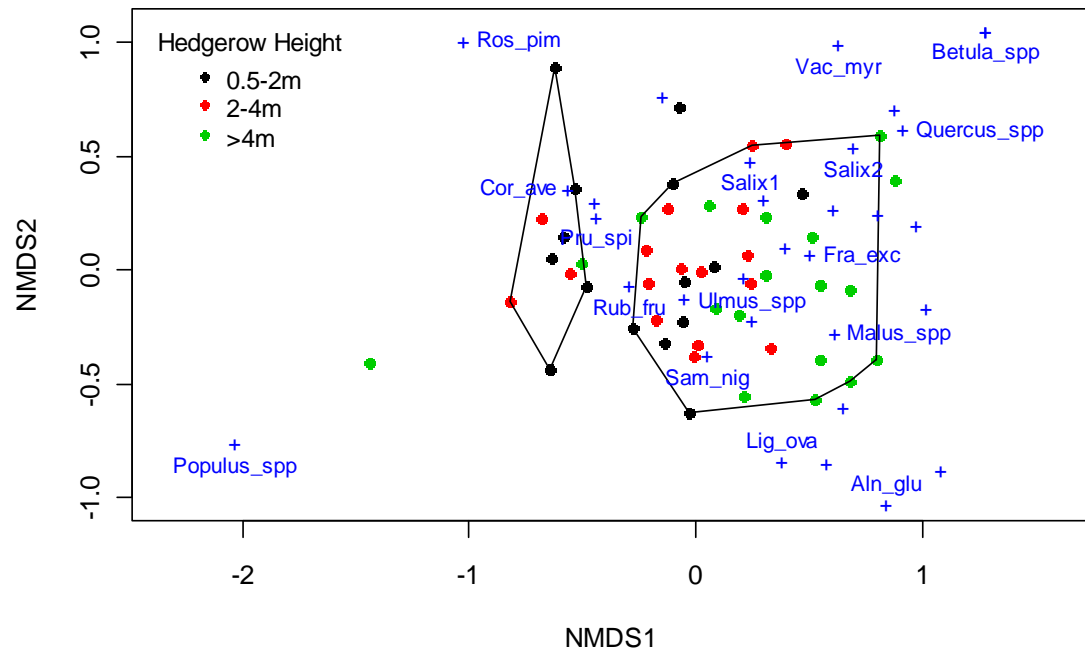
The structure and botanical composition of wooded field boundaries were correlated. This was shown by the significant correlation between Structural Index and number of woody species (Spearman's $\rho = 0.43$, $p=0.002$) and Inverse Simpson's Index (Spearman's $\rho = 0.50$, $p<0.001$) as well as correlations between individual structural characteristics and the vegetation NMDS solution (Table 5.4, Figure 5.8).

However no correlation was strong enough to indicate that one variable would be sufficient to describe both structure and botanical composition. Instead different variables are required to describe each of these boundary qualities. In these circumstances it would be more advantageous for the variables describing structure and composition not to be correlated.

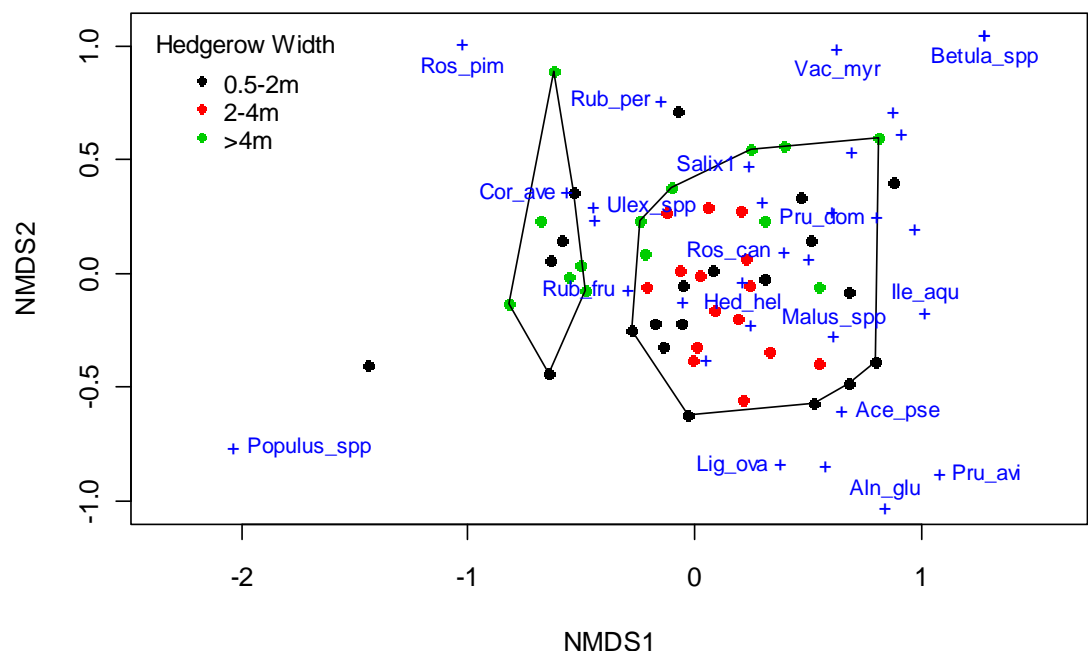
Table 5.4. Correlations between structural characteristics and botanical composition of wooded field boundaries

Structural variable	<i>Envfit</i> r^2	p-value
Height	0.15	0.002
Width	0.10	0.043
Complexity	0.05	0.233
Height of earthen bank	0.31	0.001
Presence of drain	0.02	0.430
Structural Index	0.30	0.069

(i)



(ii)



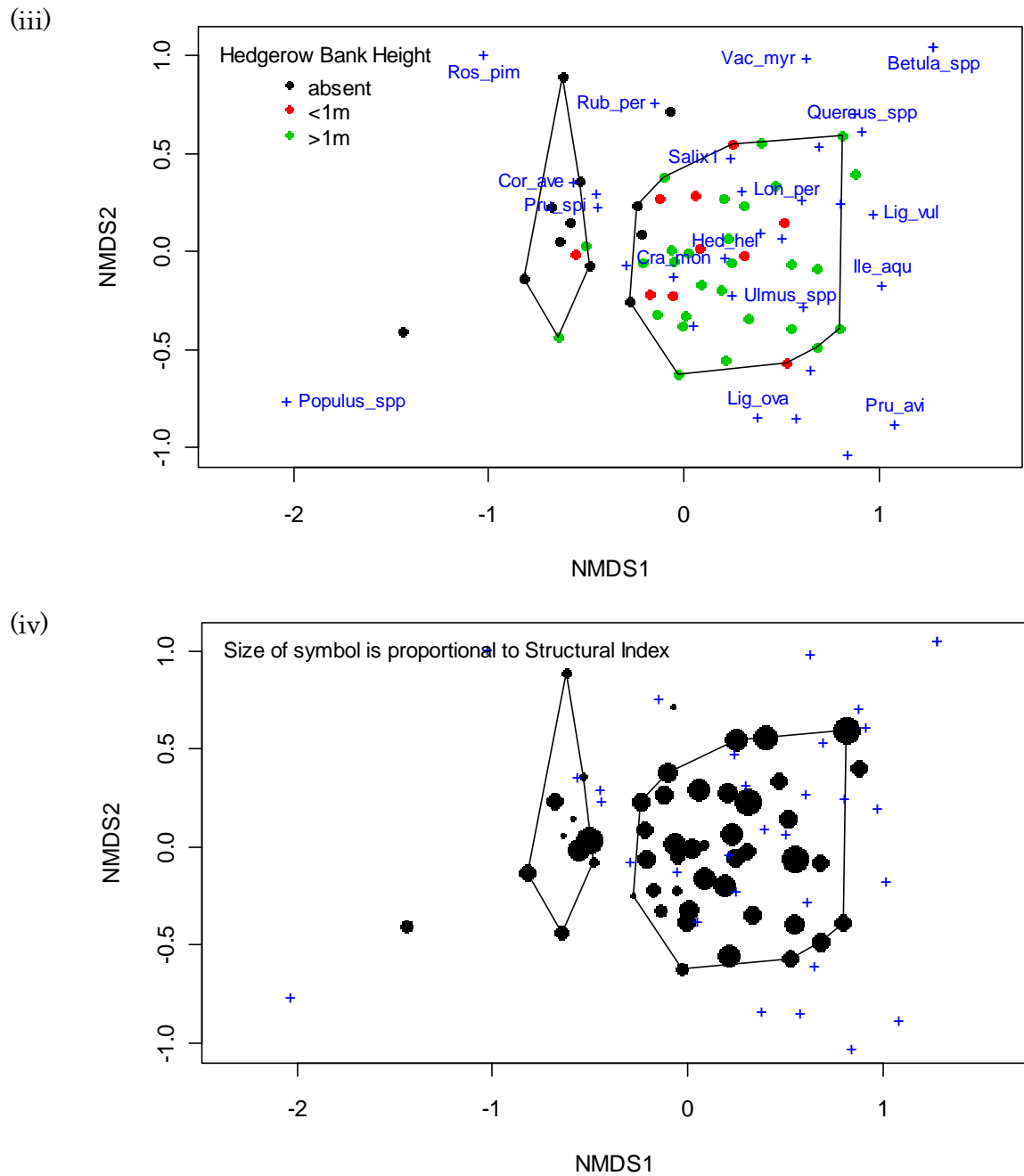


Figure 5.8. NMDS biplots of field boundary botanical composition showing how structural characteristics of field boundaries are correlated with woody vegetation (i) hedgerow height, *envfit* $r^2=0.15$, $p=0.002$, (ii) hedgerow width, *envfit* $r^2=0.10$, $p=0.043$ (iii) bank height, *envfit* $r^2=0.31$, $p=0.001$ and (iv) Structural Index, *envfit* $r^2=0.30$, $p=0.069$. The two main hedgerow groups described are delineated in black.

5.3.3. BEST VARIABLES TO DESCRIBE FIELD BOUNDARIES FOR BEE ANALYSES

The Structural Index, species number and Inverse Simpson's Index were identified as capturing the most information about hedgerow structure and composition.

However, they did not do so in a way that was meaningful to bee abundances or diversity (Table 5.5).

In contrast, the site scores on the first axis of the PCO of field boundary vegetation were significantly correlated with bumblebee abundances and species diversity (Table 5.5). This axis sorted boundaries along a gradient of high hawthorn (*Crataegus monogyna*) abundance and low blackthorn abundance (*Prunus spinosa*) to a situation where these abundances were reversed (Figure 5.7).

Table 5.5. Spearman's correlations between variables describing physical structure and botanical composition of field boundaries and bee abundances and diversity.

Variable	Structural Index	Species number	Inverse Simpsons	PCO Axis1	PCO Axis2	PCO Axis3
Solitary bee abundance (log10+1)	NS	NS	NS	NS	NS	NS
Bumblebee abundance (log10+1)	NS	NS	NS	rho = 0.39, p=0.006	NS	NS
Number of bee genera	NS	NS	NS	NS	NS	NS
Number of bee species	NS	NS	NS	NS	NS	NS
Number of solitary bee species	NS	NS	NS	NS	NS	NS
Number of bumblebee species	NS	NS	NS	rho = 0.47, p=0.0007	rho=0.26, p=0.073	NS

Structural Index of wooded field boundaries was significantly correlated with solitary bee composition (*envfit* $r^2 = 0.31$, $p = 0.002$, see Figure 5.9) and not with bumblebee composition. Chapter 8 examines correlations between the vegetation of field boundaries and solitary bee and bumblebee composition in much greater depth.

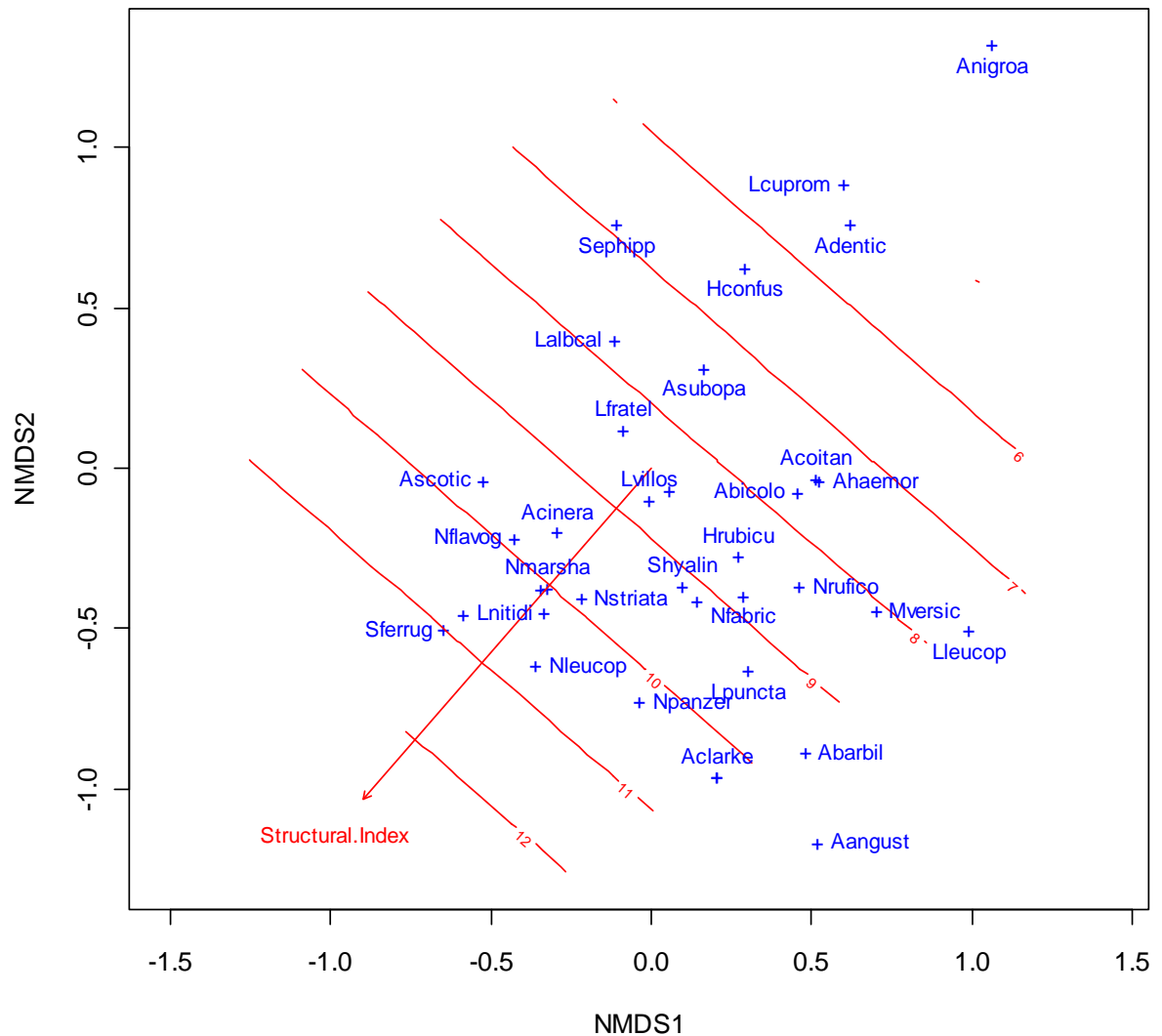


Figure 5.9. Indirect gradient analysis of correlation between physical structure of field boundaries and NMDS of solitary bee species (using Jaccard distances for presence/absence data (stress=0.19)) Arrow indicates the strength and direction of linear correlation between Structural Index and solitary bee composition, *envfit* $r^2 = 0.31$, $p = 0.002$. Red contour lines show estimated values of Structural Index fitted using a generalized additive model using the R function *ordisurf*.

5. 4. DISCUSSION AND CONCLUSIONS

Hedgerows were confirmed to be the most abundant form of field boundary on farms in the study area. They showed variation in structural complexity and in their botanical composition. Though structural complexity and botanical

composition were correlated, the association was not strong enough for one descriptor to capture both components of hedgerow variation.

In terms of physical structure, types could be discerned but many hedgerows differed from these common forms. A continuous variable was therefore more appropriate to capture this range in structure. The Structural Index was proven to be suitable for this purpose. The Structural Index was found to be correlated with the assemblage structure of solitary bees. It is used to describe the volume and complexity of field boundaries for the analyses of bee diversity, abundance and composition.

Hedgerows in the study region, like hedgerows in England (French & Cummins 2001) are dominated by hawthorn (*Crataegus monogyna*) or blackthorn, (*Prunus spinosa*).

Two hedgerow types were identified on the basis of their tree and shrub composition, both variants of Ash woodland (Rodwell 1991).

Indicator species that typified each group were also identified. One type of hedgerow could be recognised by its prevalence and the other its scarcity, of hawthorn (*Crataegus monogyna*), ivy (*Hedera helix*) and dog rose (*Rosa canina*).

However the groupings were not completely discrete so were discarded as a method of hedgerow classification.

Species number and Inverse Simpson's Index calculated for hedgerow shrubs and trees were found to be highly correlated with the ordination of hedgerow botanical composition using NMDS. Though these variables summarized the woody vegetation composition of hedgerows neither was associated with bee abundances or diversity.

But hedgerow botanical composition *is* correlated with bumblebee abundance and species diversity as shown by correlations between these response variables and the first axis of the PCO of hedgerow vegetation.

This discrepancy between the correlations of bee abundances and diversity with hedgerow composition indices versus PCO axis also describing hedgerow

composition, highlights the challenge in capturing the precise quality of hedgerow composition that is important to bees.

These analyses led to the selection of site scores on the first axis of PCO of boundary vegetation and Inverse Simpsons index to summarise the composition of woody vegetation in field boundaries and the Structural Index to describe the bulk and complexity of field boundaries for the analyses of bee diversity, abundance and composition.

CHAPTER 6: MEASURING THE BOTANICAL COMPOSITION OF GRASSLANDS

6. 1. INTRODUCTION

This section explains how the composition of grassland habitats was summarised so that bee responses to vegetation in grassland habitats could be investigated. An overview of grassland composition across the study sites is provided, together with a summary of the main environmental correlates with this composition. A number of alternative approaches to reducing grassland botanical composition to a small number of variables for bee analyses were tested. Analyses were conducted in R (R Core Team 2012) using the base R package and vegan package (Oksanen *et al.* 2013).

A difficulty in the study of associations between plants and animals has been the lack of methods that allow the use of the plant species composition of the entire community as a predictor (Schaffers *et al.* 2008). To summarise grassland vegetation a number of approaches were used that between them would capture several dimensions. Multivariate analyses were used to reduce dimensions to the dominant gradients in the vegetation (Legendre & Legendre 1998). Other dimensions of grassland vegetation were captured using Ellenberg scores (Ellenberg *et al.* 1991; Hill *et al.* 1999). The grassland community's score is calculated using Ellenberg values assigned to each plant species according to their association with various soil conditions such as soil moisture, soil nitrogen and soil pH, weighted by the species' abundance.

6. 2. METHODS

6.2.1. DATA COLLECTION METHODS

BOTANICAL SURVEY METHOD

Sampling was carried out in July-August 2005, with fields surveyed once.

At each study site, a 4x4m quadrat was placed in a 'typical' part of the field and the percentage cover of each plant estimated (Rodwell 1992).

In most cases, vegetative characters were used for identification as flowers had been removed by grazing and harvesting.

The total number of plant species observed was 134 species. Rare species that occurred at only one site were removed from the dataset and some closely related rare plants were combined into one group. The dataset was thus reduced to 77 plant species and groups for analyses.

METHODS USED TO MEASURE SUPPLEMENTARY ENVIRONMENTAL DATA

The supplementary environmental information that was used in Chapter 5 (Table 5.1) to facilitate interpretation of hedgerow vegetation classification was also used in grassland vegetation analyses.

6.2.2. ANALYSIS METHODS TO DESCRIBE GRASSLAND COMPOSITION WITHIN THE STUDY REGION

Non-metric multidimensional scaling analyses (NMDS) and indirect gradient analysis were used to understand the composition of agricultural grasslands within the study region.

Bray-Curtis similarity was used in the ordination. The NMDS was carried out using the *metaMDS* function of *vegan*) (Oksanen *et al.* 2013). Data were square root transformed and the Wisconsin double standardization applied (these were standard transformations applied by *metaMDS*) prior to NMDS. After the automatic iterations of *metaMDS*, the NMDS was repeated manually, using the best solution from the first run as a baseline for comparison. This process was repeated for ordinations with increasing numbers of axes in order to determine how many axes to present. A graph was plotted of stress levels against number of axes (Figure 6.1) and two axes were selected (stress = 0.21).

The correlations between supplementary environmental variables (Table 5.1) and composition of plant communities were examined using the *envfit* function of *vegan* to determine a goodness of fit statistic based on 1,000 random permutations of the data. (Samples with missing values in ordination

scores or environmental variables were removed from the analysis.) The strength and direction of correlations were visualised as arrows on the ordination plot. For continuous environmental variables, the *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to check visually whether the correlation was a linear one. This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use cross-validators selection of smoothness (GCV).

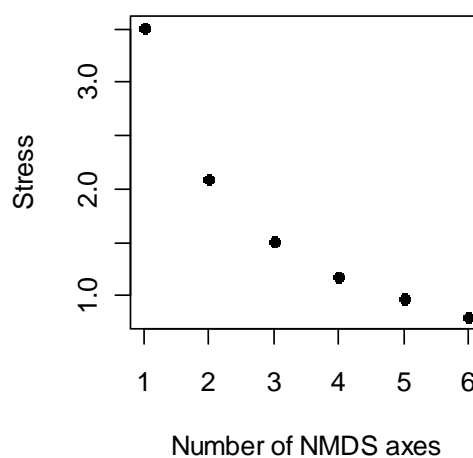


Figure 6.1. Level of stress associated with different numbers of axes in NMDS ordination of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization).

6.2.3. ANALYSIS METHODS TO REDUCE GRASSLAND BOTANICAL COMPOSITION TO A FEW SUMMARY VARIABLES

Since NMDS cannot be used for data reduction, two alternative approaches were considered to reduce the information contained in 77 species abundances to a smaller number of variables: PCO axes scores and indices.

Principal coordinates analysis (PCO) axes scores

PCO was conducted upon the Bray Curtis distance matrix for the plant species abundance matrix. A bar plot of axes' eigen values was used to select

an appropriate number of axes for the ordination and to evaluate the proportion of variance explained by the axes. A Shepard plot was drawn to evaluate whether the distances resulting from the ordination adequately represented those in the Bray Curtis distance matrix (Appendix 8). Analyses were conducted using Ade4 (Chessel *et al.* 2012) and vegan (Oksanen *et al.* 2013) packages in R (R Core Team 2012).

Correlations between the ordination and environmental variables were examined using the *ordifit* and *ordisurf* functions of vegan (Oksanen *et al.* 2013). This allowed interpretation of the PCO results and an evaluation of the capacity of the PCO axes to capturing the same variation in composition that was observed with the NMDS.

The NMDS results and PCO results were also compared directly using a Procrustes rotation. The function *procrustes* of the vegan package was used (Oksanen *et al.* 2013). Both solutions were scaled to unit variance prior to the rotation. The PCO matrix (first three axes) was rotated to maximum similarity with the NMDS matrix (first two axes). This was determined by minimising the squared differences between the two ordinations. Plots of the Procrustes errors, that is, the differences between the two ordinations for each site, were presented. The statistic m_{12} was calculated as a measure of the correlation between the two configurations.

The suitability of the PCO axes as new summary variables describing sward composition was evaluated by considering

- Proportion of variance in vegetation composition explained by the selected axes.
- Adequacy of ordination distances to represent those in the Bray Curtis distance matrix.
- Correlation with NMDS solution and environmental factors with which NMDS was correlated.

Indices

An index with a strong, and preferably linear, correlation with the NMDS ordination was required (the NMDS being viewed as the best available summary of the botanical composition of the grassland vegetation) to summarise as much information about the grassland composition as possible. The following were calculated for the grassland vegetation and evaluated by examining their correlation with the NMDS ordination using *envfit* and *ordisurf* functions of *vegan* (Oksanen *et al.* 2013).

- Number of plant species recorded within the 4mx4m quadrat
- Simpson's diversity index complement (see below)
- Ellenberg values for Nitrogen, soil pH and soil moisture (see below)

The complement of the Simpson Index (1-D) was calculated for each site, using all higher plant species recorded and their percentage cover.

Mean Ellenberg scores for each site's grassland were calculated using Turboveg (Hennekens & Schaminee 2001). Ellenberg values (Ellenberg *et al.* 1991), adapted for UK conditions (Hill *et al.* 1999), for nitrogen, soil pH and soil moisture for each observed plant species were weighted by its percentage cover in that relevé. The mean Ellenberg score for the relevé was then calculated from the Ellenberg scores of the species present.

6.2.4. ANALYSIS METHODS TO SELECT THE BEST VARIABLES TO SUMMARISE GRASSLAND BOTANICAL COMPOSITION FOR BEE ANALYSES.

Associations between bee abundances, diversity and assemblage composition and the measures selected as possible ways of summarising grassland vegetation composition at each site were tested.

The grassland summary variables that were considered were

- (i) site scores on the first three axes of the grassland vegetation PCO and

- (ii) grassland composition indices: number of plant species; Complement of Simpson's diversity index; Ellenberg values for Nitrogen, soil pH and soil moisture.

Spearman's correlations between these variables and solitary bee abundance ($\log_{10}+1$); bumblebee abundance ($\log_{10}+1$), number of bee genera; number of bee species; number of solitary bee species and number of bumblebee species were tested.

Correlations between bee assemblage composition and grassland vegetation composition and these indices are examined in more depth in Chapter 8.

6. 3. RESULTS

6.3.1. OVERVIEW OF GRASSLAND BOTANICAL COMPOSITION

Table 6.1. Results of indirect analyses examining correlations between supplementary environmental variables and grassland vegetation composition, summarized using NMDS and PCO.

Environmental supplementary variable	Correlation with NMDS (2 axes)		Correlation with PCO (3 axes)	
	<i>Envfit</i> r^2	p value	<i>Envfit</i> r^2	p value
Easting X coordinate	0.24	0.001	0.22	0.010
Northing Y coordinate	0.14	0.034	0.22	0.011
Altitude	0.12	0.042	0.20	0.011
4 local areas	0.22	0.001	0.14	0.013
Soil P	0.11	0.051		NS
Soil K	0.10	0.085		NS
Soil Mg	0.06	0.177	0.17	0.021
Soil pH	0.15	0.022	0.18	0.018
Soil Organic Matter	0.12	0.041		NS
Total N fertiliser	0.46	0.001	0.48	0.001
Grass Management	0.26	0.001	0.23	0.002
Reseeding	0.11	0.004	0.16	0.001

The first axis of the NMDS separated sites with grassland vegetation composed of modern-day agricultural forage species and weeds (such as *Lolium* spp., *Rumex* spp., *Poa annua* and *P. pratensis* and *Stellaria media*) from sites with semi-natural grasslands (to the right of the ordination plot).

In the centre of the ordination plot were sites with species typical of fields under intermediate levels of management intensity (Sullivan *et al.* 2010) e.g. *Holcus lanatus*, *Senecio jacobaea*, *Plantago major*, *Rumex acetosa*, *Anthoxanthum odoratum*, *Vicia cracca*.

The position of plant species along the first axis of the ordination indicates agricultural management to be the most important influence on the composition of grasslands within the study region.

Variables describing agricultural management: total nitrogenous fertiliser, reseeded, grass management category and total soil phosphate were significantly correlated and aligned with this first axis (Table 6.1, Figures 6.2 and 6.3). The amount of nitrogen applied was the most strongly correlated environmental variable with field vegetation composition. The first axis of the NMDS can therefore be regarded as a 'management' axis.

The second NMDS axis (Figures 6.1 and 6.2) positioned sites with grassland composition typical of more traditional management along a gradient of wet to dry soils. This was indicated by the positioning of species typical of damp meadows: *Senecio aquaticus*, *Galium palustre*, *Lotus pedunculatus*, *Equisetum spp.*, *Ranunculus lingua* at the top of the plot and herbs typical of drier conditions at the bottom e.g. *Leucanthemum vulgare*, *Galium verum*, *Odontites vernus*, *Daucus carota*, *Hypericum perforatum*. Some of these species also suggest a gradient in more neutral to basic soil conditions.

Soil pH and soil organic matter were correlated with the ordination (Table 6.1 and Figure 6.2). Together with soil moisture (which was not measured but was indicated by species composition), these edaphic factors were interpreted to be driving the second axis of the ordination. The second axis could be regarded as an 'environmental' or 'edaphic' gradient reflected in the field vegetation.

Sampling location, an East-West gradient and North-South gradient and altitude were significantly correlated with the composition of grassland vegetation (Table 6.1 and Figure 6.4) but the correlations were not strong. Sites from all sampling locations were distributed along the first 'management' axis, reflecting the stratified sampling protocol.

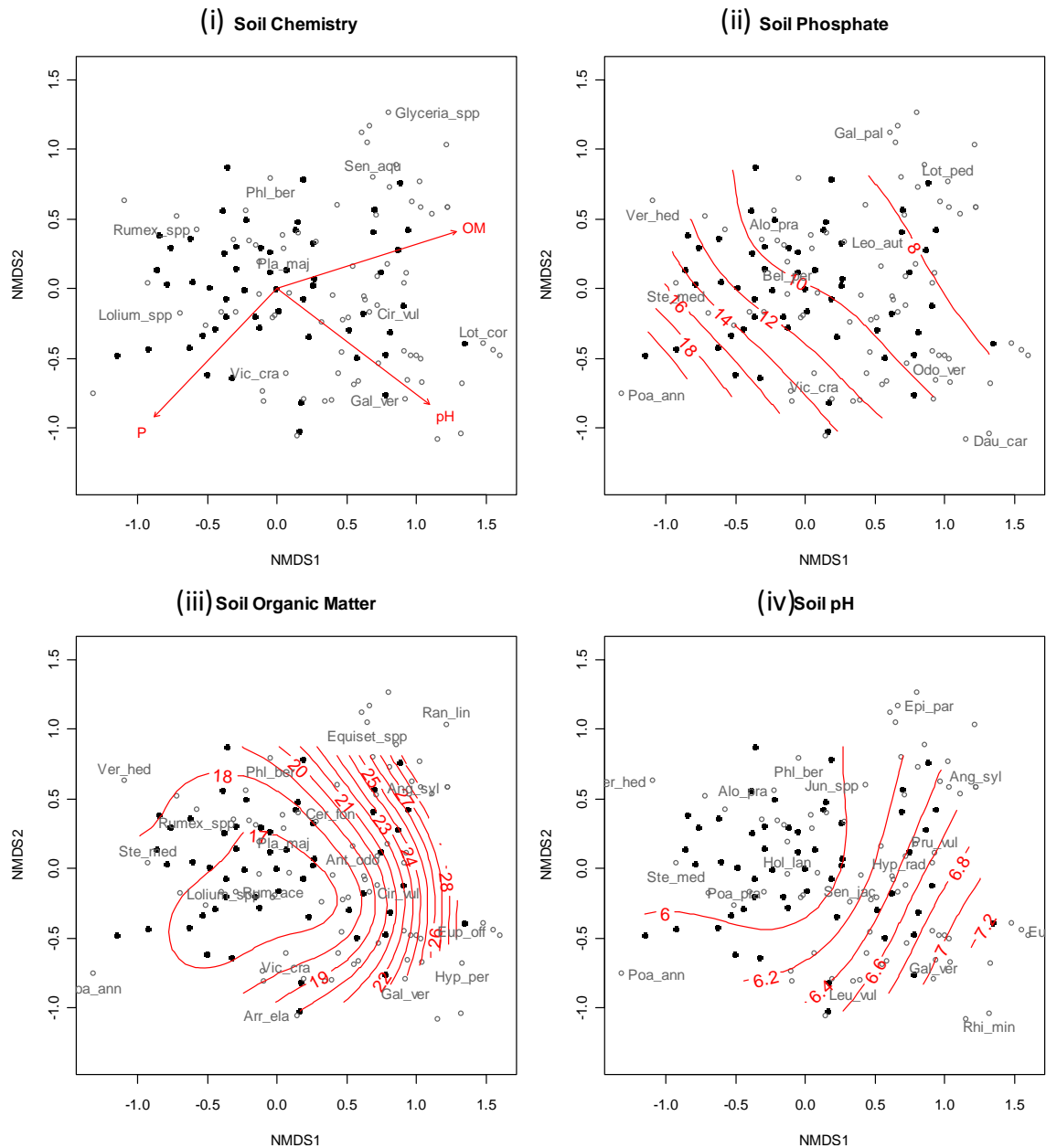
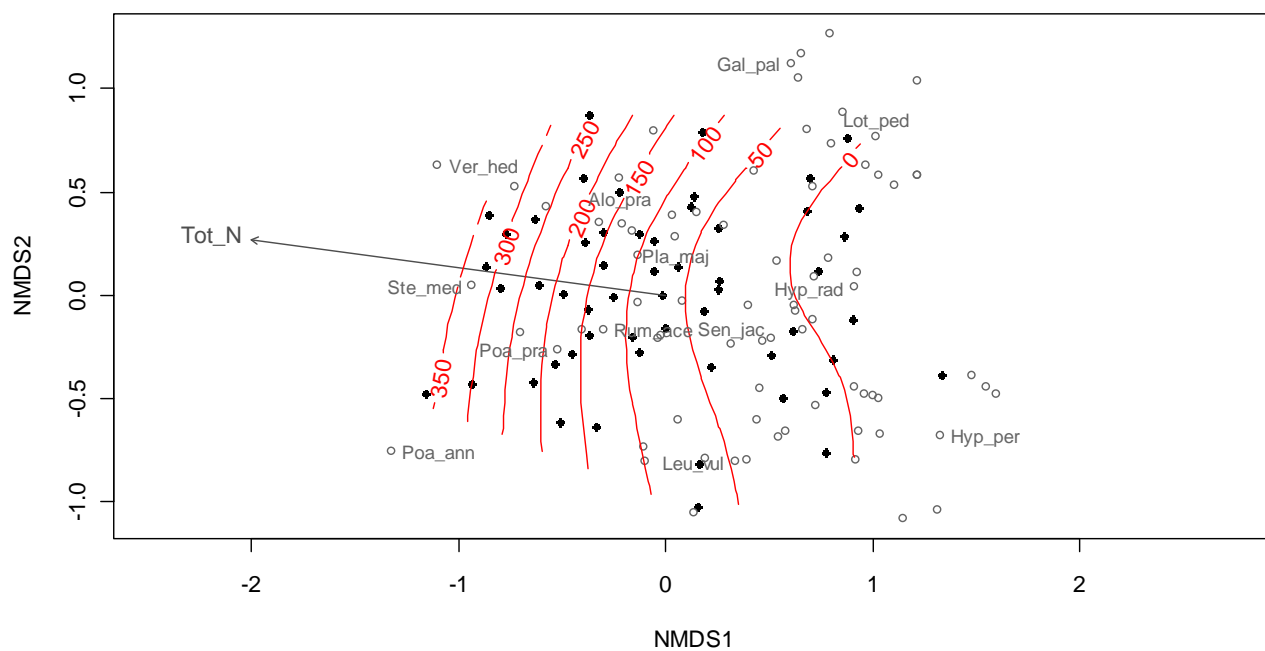
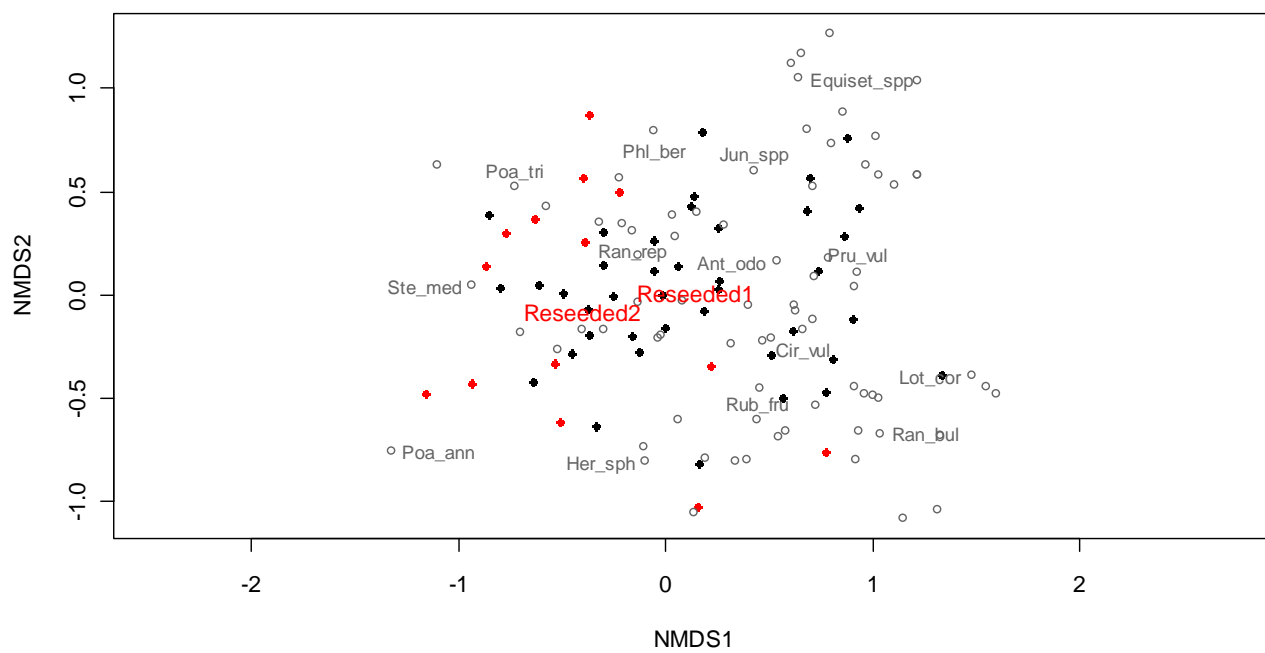


Figure 6.2. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21) showing correlations of soil conditions with botanical composition, [i] shows strength and direction of correlations with soil conditions, significant at $p=0.05$. Red contour lines in [ii]-[iv] represent a smooth fitted surface for each edaphic variable: soil phosphate (P), soil organic matter (OM) and soil pH (pH) respectively, fitted using generalized additive models using the R function *ordisurf*. Open circles = species, a selection of which are labelled. Solid circles = sites.

(i) N Fertiliser



(ii) Reseeding



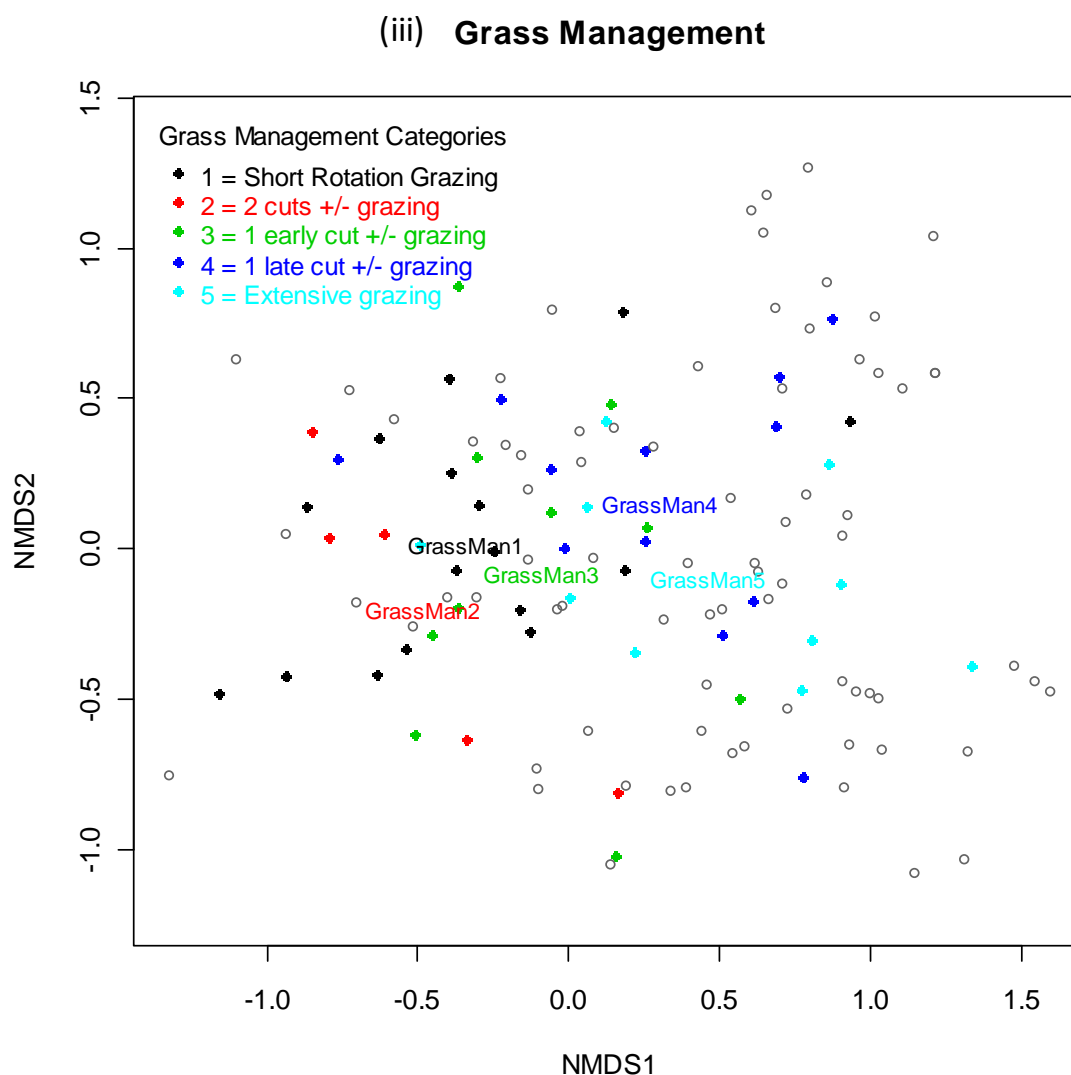


Figure 6.3. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21) showing correlations of field management with botanical composition. Open circles = species, a selection of which are labelled. Solid circles = sites. [i] Correlation with nitrogen fertiliser application. [ii] Correlation with reseeded (red = reseeded, black = not reseeded in previous 15 years). [iii] Correlation with grazing and cutting regime. Sites coloured by management, see legend.

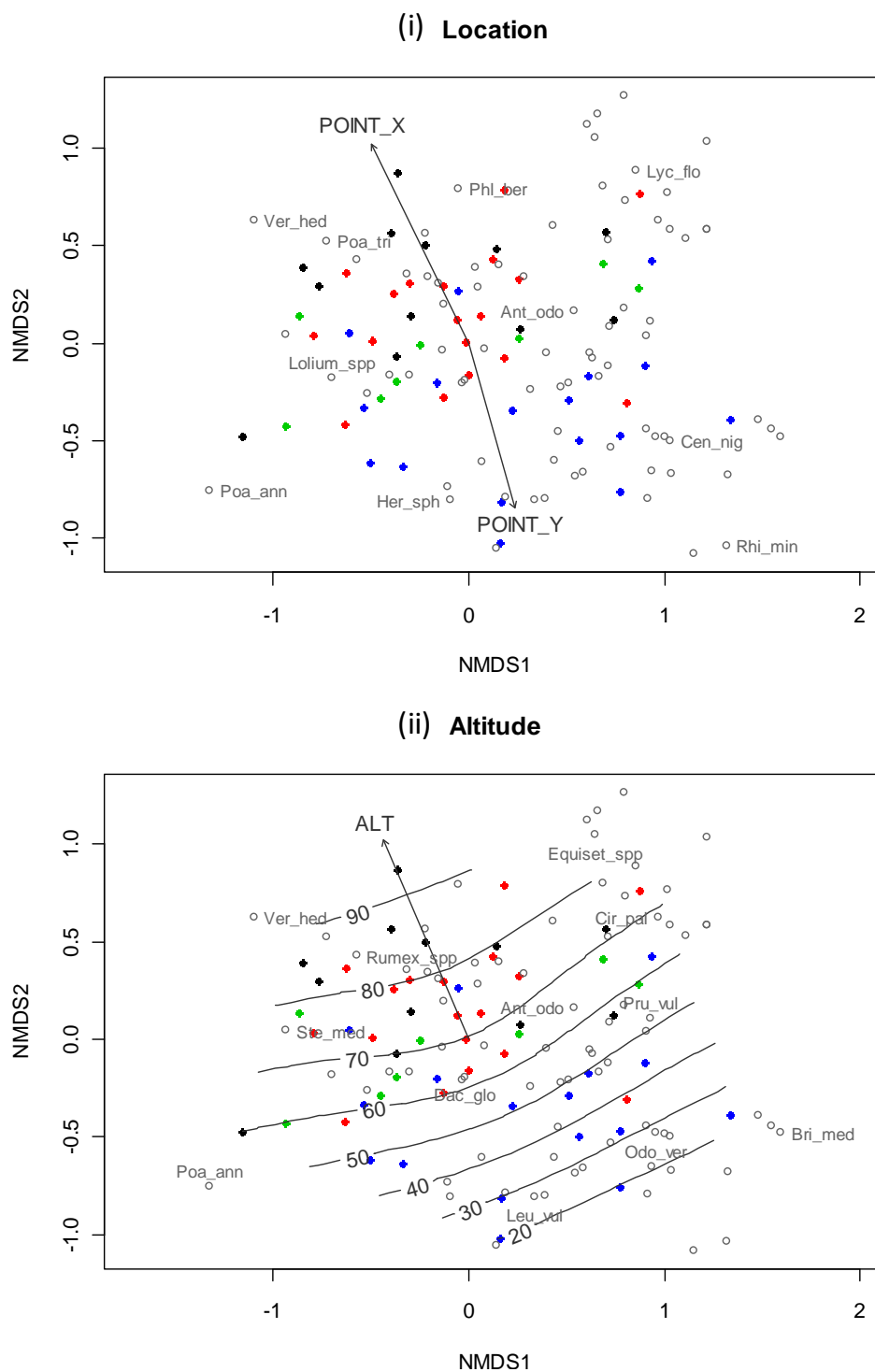


Figure 6.4. NMDS of grassland vegetation (Bray-Curtis similarity, square root transformed and Wisconsin double standardization) sampled by species composition and cover (stress = 0.21) showing correlations of geographical location with botanical composition. Open circles = species, a selection of which are labelled. Solid circles = sites, coloured by local area: blue=West Limerick, red =East Limerick , green =Tipperary and black= other areas of County Limerick. [i] Correlation with location summarised by Easting and Northing coordinates. [ii] Correlation with altitude in metres.

6.3.2. DATA REDUCTION OF GRASSLAND BOTANICAL COMPOSITION

PCO axes scores

As most points fell on a straight line in the Shepard plot (Appendix 8), the distances between sites resulting from the PCO were judged to be a reasonable representation of the Bray Curtis distances in the original distance matrix.

Three axes were selected for the PCO solution (based upon a bar graph of axes' eigen values). The proportion of the total variance explained by three axes was only 35.6%. Even with 8 axes only 56.3% of variance was captured.

When the results of the PCO were drawn in three dimensions, sites were seen to be positioned in a cone shape (Figure 6.5), with the narrow tip of the cone occupied by sites with very similar plant assemblages, dominated by *Lolium* species and few other grasses (Appendix 9). These sites typically received high levels of fertiliser, were often reseeded and many were managed as short-rotational grazing or for two cuts of silage (Figure 6.5, Tables 6.1, Table 6.2 and Appendix 10). The broad end of the cone was occupied by sites with dissimilar, species-rich plant assemblages.

As in the NMDS, the first axis of the PCO was correlated with variables indicative of management intensity. Soil pH was associated with the second axis of the PCO (Table 6.1, Table 6.2, Appendix 11).

Although environmental gradients that were evident in the NMDS were also apparent in the PCO, the Procrustes correlation statistic at $M_{12} = 0.58$ showed sites were not configured the same in the two analyses. A higher value of M_{12} would be expected if this were the case given that the same dataset was used in both analyses (Results of Procrustes analyses can be seen in Appendix 12).

When PCO axes are used as variables to summarise vegetation composition in subsequent analyses, it must be remembered that only a small amount of

information has been captured by three axes and the positioning of sites was not faithful to the NMDS. However, the environmental gradients reflected by the ordination are very similar to those indicated by NMDS (Table 6.1).

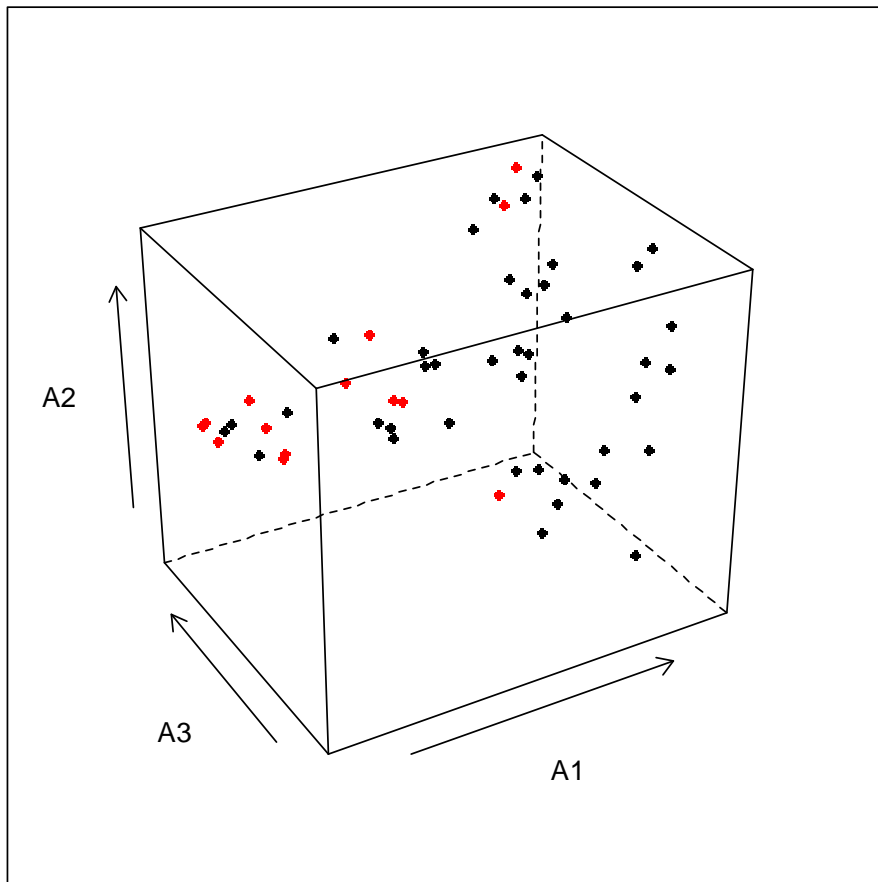


Figure 6.5. Three dimensional ordination plot of PCO of grassland vegetation (Bray Curtis distance) sampled by species composition and cover. 3 axes explained 35.6% total variance. Red= reseeded fields, Black = not reseeded within previous 15 years.

Table 6.2. Results of indirect analyses examining correlations between edaphic variables and grassland vegetation PCO axes 1-3.

	PCO Ax1	PCO Ax2	PCO Ax3	Envfit r2	Pr(>r)
Lime	-0.23	0.21	-0.95	0.16	0.0301
P	-0.99	-0.08	-0.13	0.08	0.2575
K	-0.91	0.02	-0.41	0.03	0.7261
Mg	-0.58	-0.39	0.71	0.17	0.0187
pH	0.25	-0.33	0.91	0.15	0.0416
E_cond	-0.68	-0.37	0.64	0.04	0.5302
OM	0.38	-0.71	0.60	0.09	0.1812

Indices

All of the indices were significantly correlated with the vegetation NMDS (Figure 6.6) and the PCO (Table 6.3).

The index most strongly correlated with vegetation composition was species number. Correlations between the NMDS and Ellenberg values for soil moisture (Ellen_Water) and soil pH (Ellen_pH), though significant, were not strong. The direction of these correlations (Figure 6.6) supports the interpretation that the second axis is driven by soil moisture and soil pH.

Table 6.3. Correlations of vegetation indices with grassland vegetation PCO axes 1-3.

	PCO Ax1	PCO Ax2	PCO Ax3	Envfit r2	Pr(>r)
Sw_Ellen_pH	-0.35	0.83	0.42	0.16	0.0266
Sw_Ellen_N	-0.83	0.52	-0.21	0.53	0.0001
Sw_Ellen_Water	0.71	-0.57	-0.43	0.54	0.0001
Simpsons	-0.91	0.41	-0.05	0.47	0.0001
SpNo	0.68	-0.62	0.40	0.63	0.0001

Table 6.4. Spearman's correlations between grassland vegetation indices and other measures of botanical composition and bee diversity and abundance

	PCO Axis1	PCO Axis 2	PCO Axis3	Species numbe r	Simpsons Index complemen t	Ellenber g soil moisture	Ellenber g soil nitrogen	Ellenber g soil pH
Solitary bee abundance (log10+1)	NS	NS	NS	NS	NS	NS	NS	NS
Bumblebe e abundance (log10+1)	NS	NS	NS	NS	NS	NS	NS	NS
Number of bee genera	rho=0.2 8 p=0.041	NS	NS	NS	NS	NS	rho =- 0.28 p=0.041	NS
Number of bee species	NS	NS	rho=0.3 8 p=0.005	NS	NS	NS	NS	NS
Number of solitary bee species	NS	NS	rho=0.2 8 p=0.035	NS	NS	rho= - 0.25 p=0.075	NS	NS
Number of bumblebe e species	rho=0.3 2 p=0.018	NS	rho=0.2 7 p=0.048	NS	NS	NS	NS	NS

6.3.3. BEST VARIABLES TO DESCRIBE GRASSLAND BOTANICAL COMPOSITION

Univariate analyses of bee abundances and diversity

Solitary bee and bumblebee *abundances* were not correlated with any of the variables used to summarise grassland vegetation composition (Table 6.4).

However bee *diversity* was associated with grassland composition.

The first grassland vegetation PCO axis, which reflected intensity of agricultural management in grassland composition, was correlated with the number of bee genera and number of bumblebee species (Table 6.4).

Ellenberg nitrogen values, also indicative of management intensity, showed a correlation with bee genera too. The third PCO axis was significantly correlated with the number of species of solitary bees and bumblebees. This axis distinguished sites' vegetation along a soil pH, lime and magnesium gradient.

A negative correlation between the number of solitary bees and the sward Ellenberg value for soil moisture was close to significance levels ($p=0.07$). This is likely to reflect preferences of the majority of bees for drier soil conditions.

Analyses of bee assemblage composition in relation to grassland vegetation composition are studied in depth and are presented in Chapter 8.

6. 4. DISCUSSION AND CONCLUSIONS

This chapter aimed to reduce 134 environmental variables (the plant species abundances observed within the study fields) to a small number of explanatory variables that could be used to describe the botanical composition of grasslands for analyses of bee abundances, diversity and assemblage composition. It was possible to reduce botanical composition to a few variables summarising the dominant gradients structuring vegetation.

Analyses showed the primary gradient structuring plant assemblages in fields was management intensity. Edaphic factors such soil organic matter, soil pH and soil moisture were identified as secondary gradients.

The methods used to summarise botanical composition were capable of capturing these gradients although they did not capture other components of the variance in plant composition (as shown by the low proportion of variance explained by PCO or the relatively weak correlations between indices and the NMDS solution).

Bee abundance appeared not to be associated with the composition of grassland vegetation, although diversity was.

The number of bee genera was correlated with the Ellenberg score for soil Nitrogen and the first axis of the PCO, two variables that reflected a shift in plant composition due to an intensification of agricultural management.

The number of species however, of solitary bees and of bumblebees, was correlated with natural gradients in vegetation composition, associated with edaphic factors.

Preliminary studies of the correlations of these variables with bee response variables led to the selection of site scores on grassland vegetation PCO Axis 1 (reflecting a field management intensity gradient) and PCO Axis 3 (reflecting a gradient in soil pH) for analyses of bee abundances and diversity. The relative importance of these associations compared to other factors is examined in Chapter 9.

Correlations between bee assemblage composition and the botanical composition of grasslands are explored in depth in Chapter 8 and 9.

CHAPTER 7: MEASURING AGRICULTURAL MANAGEMENT INTENSITY

7. 1. INTRODUCTION

This section provides an overview of farm management at the study farms. It tests a number of ways aimed at reducing information describing agricultural activity to a small number of variables. Ideal variables were considered to be those that captured the degree of intensification of management on the farm in a way that was ecologically meaningful for bees and readily understood by a general audience.

The R base package (R Core Team 2012); vcd package (Meyer *et al.* 2012); FD package (Laliberté & Shipley 2011) and vegan package (Oksanen *et al.* 2013) were used for graphing and statistical analyses.

Describing the intensity level of agricultural management

Agricultural intensification may follow different pathways (White *et al.* 2010) resulting in a “multivariate and interacting nature of farming practices” (Benton *et al.* 2003). It may also be classified at different scales (Firbank *et al.* 2008). A multiscale approach to ecological research has been recommended since the 1980s (e.g. Addicott *et al.* 1987; Blondel 1987; Wiens 1989 and has been applied by many researchers of bee ecology (e.g. Steffan-Dewenter *et al.* 2002; Dauber *et al.* 2003; Hines & Hendrix 2005; Kleijn & van Langevelde 2006; Westphal *et al.* 2006; Holzschuh *et al.* 2008; Tscheulin *et al.* 2011).

Understanding scale-dependence is essential for a more complete understanding of ecological processes and for effective conservation management (Ludwig *et al.* 2000; Bestelmeyer *et al.* 2003; Lindenmayer *et al.* 2008; Pelosi *et al.* 2010). For this study, field, farm and landscape scales of agricultural intensification were measured. This section describes the development of methods of classifying agricultural management intensity at field and farm levels. For the methods used to describe agricultural intensity at a landscape level, see Chapter 4.

At the field level, grassland management is flexible and may differ in timing, type and amount of fertiliser applications, reseeding, liming, drainage,

stocking densities, grazing regimes and timing and frequency of mechanical harvesting (Frame 1992; Creighton *et al.* 2011). These inputs alter the botanical composition of grasslands (O'Sullivan 1968; Tilman 1987; Crawley *et al.* 2005).

The structure of the sward is determined by the grass harvesting regime, whether by grazing or cutting. Short-term rotational grazing at high stocking densities and frequent cutting, for example, maintain a structurally and botanically uniform sward (Vickery *et al.* 2001).

Management intensity at the field level has been classified in many ways for the purposes of ecological studies. These include using a surrogate management variable such as total nitrogenous fertiliser or pesticide use to summarise field management intensity (e.g. Le Feon *et al.* 2010; Kovacs-Hostyanszki *et al.* 2011). Others have created categories of management, dependent on mowing regime and fertiliser application (Weiner *et al.* 2011) or indices of management intensity (Bluethgen *et al.* 2012) for example.

Management intensity has been categorised at the farm level, as organic versus conventional, by primary agricultural activity and size as in the European farm typology (EC 1985) which was extended to increase its environmental relevance (Andersen *et al.* 2007) or by participation in an agri-environmental scheme (Rural Environmental Protection Scheme, REPS in Ireland at the time of the study).

However farm management may be too diverse for such broad classifications (van der Ploeg *et al.* 2009). For example, farm intensification may lead to changes in the breeds of animals kept, increased reliance upon genetically engineered species, increased mechanisation e.g. resulting in more mechanical horsepower and reductions in labour, increased area of productive land compared to non-productive farmland e.g. by field boundary removal and subdivision of farm into electrified paddocks and specialization e.g. moving from mixed production such as tillage and pastoral to one enterprise (Tscharniske *et al.* 2005).

Alternative systems of classification that take into account a large number of attributes may be derived using multivariate statistical methods such as

cluster analysis, factor analysis and PCA (Köbrich *et al.* 2003; Riveiro *et al.* 2008). For example cluster analysis (Alvarez *et al.* 2008) and PCA (Haskell *et al.* 2007) have been used to classify dairy farms by level of intensification. In Ireland, classification using PCA of sheep farms showed 4 categories of management within the Iveragh peninsula (O'Rourke *et al.* 2012).

Indicators and surrogates for farm-scale management can also be derived using these methods, e.g. a farm scale indicator for livestock farms in Ireland has recently been proposed (Louwagie *et al.* 2012).

Intensification at the landscape scale, may be evidenced by larger field sizes, specialisation rather than mixed farming across the landscape, loss of traditional, low-intensity land use, reduction in grassland habitat, lowering of water tables (Tscharntke *et al.* 2005). However (Herzog *et al.* 2006) and (Roschewitz *et al.* 2005) found that area of grassland, field size and crop diversity within a landscape were not consistently associated with increasing intensification in terms of levels of nitrogenous fertiliser input, livestock density and pesticide applications and should therefore not be used as landscape scale measures of agricultural intensification. For details of the approach taken in this study to measuring agricultural management intensity at the landscape scale, see Chapter 4.

Regardless of whether a qualitative or quantitative approach is used to summarise farm and field management, it is recommended that the classification used must be derived from thorough analysis of both qualitative and quantitative data (Köbrich *et al.* 2003; Righi *et al.* 2011). This is the type of analytical approach taken in this section to derive variables that summarise field and farm level management.

7. 2. METHODS

Table 7. 1. Variables used in analyses of agricultural management at farm and field level

Agricultural management variable		Type	Explanation/units
At the farm level			
FarmSize	Total acreage of farm	continuous	Hectares, ha
LU_dens	Stocking density	continuous	Livestock units per hectare, LU/ha
EnvSch3	Participation in an environmental scheme	Nominal	1= conventional 2 = REPS 3=organic
Dairy	Farm enterprise or activity	Nominal	1= not dairying 2=dairying
At the field level			
TotN	Total N fertiliser (organic and chemical)	continuous	kg/ha
TotP	Total P fertiliser	continuous	kg/ha
TotApps	Total number of fertiliser applications	continuous	A count
GrassMan	Grazing and cutting of grass	5 categories	1 =short rotation grazing 2= 2 cuts of silage 3= 1 cut in early summer + grazing 4= 1 cut in mid-late summer +- grazing 5= not cut and extensively grazed
Reseed	Reseeding of grassland within 15 years	2 categories	1= Not reseeded 2= Reseeded
Spray	Use of chemical sprays in study field within 3 years	2 categories	1= Not sprayed 2= Sprayed
HgCut	Cutting of hedgerows around study field within 3 years	2 categories	1= Not cut 2= Cut

7.2.1. DATA COLLECTION METHODS

An interview with farmers was used to collect data describing management at the farm and field level. The interview schedule (Appendix 13) was developed with the help of a Teagasc research farm manager and was based upon one used previously, in 2003, with farmers. It gathered information regarding management at the farm and field level. The interview was conducted either face-to-face or on the telephone and also provided an opportunity to thank landowners for their contribution to the project.

At the farm level, the interview gathered information regarding overall farm size, stocking density, livestock type and whether the farm was in an

environmental scheme (Rural Environmental Protection Scheme (REPS) or certified organic).

For each study field, the following management information was sought: grazing and cutting regime, fertilizer applications, other chemical use and when the field was last reseeded. The hedgerow cutting regime around the study field was also queried.

Management Variables used in analyses

The variables derived from the interview and used in the analyses are described in Table 7.1. Details of how data describing farm stocking levels, nutrient inputs and grassland management were derived from interview responses are given in Appendix 14.

7.2.2. ANALYSIS METHODS TO DESCRIBE AGRICULTURAL MANAGEMENT

Descriptive statistics e.g. median and interquartile range and graphs were used to summarise and explore the data describing management at the farm and field level.

Examination of farm stocking density in relation to farm types

The relationship between stocking density and participation in an environmental scheme, farm size, and enterprise (ie dairying activity) was examined using graphs. Kruskal-Wallis tests, a non-parametric analogue of a one-way analysis of variance test, were used to test the effects of participation in environmental scheme or dairying activity on stocking densities. Spearman's correlations were used to examine whether there was a correlation between farm size and stocking density.

Examination of field management practices in relation to farm types

The relationship between each field management variable and participation in an environmental scheme, farm size, and enterprise (i.e. dairying activity versus nondairying) was examined using graphs. Differences, in field management, between farm types were tested for statistical significance.

Kruskal-Wallis tests was used to test for differences for continuous variables and Fisher's Exact Test and Chi-squared tests were used for nominal variables. Conditional plots were used to explore for potential interactions between farm characteristics e.g. dairying activity and participation in environmental scheme in relation to field management e.g. level of fertiliser use. For nominal variables, 'cotabplots' and 'mosaic' plots were used (Hartigan & Kleiner 1981, 1984; Friendly 1994, 1999). In these graphs the area in each bar is proportional to the observed frequency of observations in that category.

The base R package (R Core Team 2012) and the R package, *vcd*, (Meyer *et al.* 2006, 2012) were used for graphing.

Examination of associations between field management practices

Pairplots for all variables describing field management were presented and correlations among the field management variables were examined. The variables were a mixture of nominal and continuous data and so different types of graph and correlation measure were used. The distributions of the continuous variables, when examined using histograms, were not normal and nonparametric measures were used to examine their correlations with other variables. Spearman's correlations were used when both variables were continuous but not normally distributed. When one variable was nominal with more than two levels, Fisher's Exact test was used to test for a significant correlation, and Cramer's V was used as a post-test to determine the strength of the correlation for variables. For pairs of dichotomous variables, Fisher's Exact test was used to test for a significant correlation and Phi was used as the post-test.

7.2.3. ANALYSIS METHODS TO REDUCE AGRICULTURAL MANAGEMENT SET OF VARIABLES

A multivariate analysis of the management of study fields was conducted in order to summarise field management. The approaches considered were

- Using Principal Co-ordinates Analysis (PCO) axes.
- Using farm types, defined by farm characteristics (size, stocking density, enterprise and participation in an environmental scheme) to summarise field management.
- A new classification of farms to types that summarise their field management.
- Using a few field management variables that are highly correlated with the rest to summarise the entire set.

PRINCIPAL CO-ORDINATES ANALYSIS TO SUMMARISE FIELD MANAGEMENT

As the field management data (Table 7.1) was a mix of factors and continuous variables, Euclidean distances as used in PCA could not be calculated. A distance measure suitable for such mixed data is the Podani modified form of Gower's distance (Gower 1971; Legendre & Legendre 1998; Podani 1999). The *gowdis* function of R package FD (Laliberté & Legendre 2010; Laliberté & Shipley 2011) was used to calculate the distance matrix. This distance matrix was square root transformed and then analysed using Principal Co-ordinates Analysis (PCO).

As the PCO was carried out on a distance matrix, there was no 'species' data. Biplots showing how the 'species' data, or in this case field management data, influenced the ordination could not be drawn, nor could the loadings of each of the original variables on the two new axes be extracted. To aid interpretation of the PCO, I calculated correlations between each field management variable used to generate the distance matrix and the first two axes. This provided a measure of how well the ordination represented the original data. These correlations were examined using the *envfit* function of *vegan* (Oksanen *et al.* 2013). As the relationship between variable and ordination may not be linear, I also fitted a smooth response surface of the variable's predicted values over the biplot using *ordisurf* function in *vegan* (Oksanen *et al.* 2013).

Different combinations of the field management variables (Table 7.1) were used in a series of PCO analyses. Two variables that added greatly to the

total variance and reduced the percentage of total variance that the first two axes could explain were dropped (Number of fertiliser applications and hedgerow management).

The correlation between the management variables and the ordination was compared using the *envfit* function of *vegan* (Oksanen *et al.* 2013). The ordination in which the proportion of total variance explained by the first two axes of the PCO was high, correlation between management variables and ordination was high and sites were clearly separated is presented. This PCO result is based upon ordination of total application of nitrogen, total application of phosphorus, reseeding, and chemical use.

CHECKING IF FARM TYPES COULD BE USED TO SUMMARISE FIELD MANAGEMENT

The correlations of farm level data, such as dairying activity, size, stocking density and participation in an environmental scheme, with the PCO of field management were examined to determine whether farm type could be used as a summary variable to account for field management. *Envfit* correlation coefficients were calculated using the *envfit* function of *vegan* (Oksanen *et al.* 2013) to determine a goodness of fit statistic based on 1,000 random permutations of the data.

CHECKING IF A NATURAL TYPOLOGY OF FARMS EMERGED FROM THEIR FIELD MANAGEMENT

The PCO biplot was examined to see whether sites clustered into groups that could be used to summarise field management.

CHECKING IF ONE FIELD MANAGEMENT VARIABLE COULD SUMMARISE OVERALL FIELD MANAGEMENT DATA.

The correlations of field management variables with the PCO were examined to determine whether one or two could summarise much of the management information. *Envfit* correlation coefficients were calculated using the *envfit* function of *vegan* (Oksanen *et al.* 2013) to determine a goodness of fit statistic based on 1,000 random permutations of the data.

The strength and direction of correlations were visualised as arrows on the ordination plot. For continuous environmental variables, the *ordisurf* function in *vegan* (Oksanen *et al.* 2013) was used to check visually whether the correlation was a linear one. This function fits a generalised additive model (GAM) to predict the variable using the site scores on axes 1 and 2 as the predictor variables (Simpson 2011). I used the default settings, which use cross-validators selection of smoothness (GCV).

7.2.4. ANALYSIS METHODS TO SELECT THE BEST VARIABLES TO DESCRIBE AGRICULTURAL MANAGEMENT

The correlations of variables, identified as suitable to summarise farm and field management, with bee abundances and diversity and bee assemblage composition were examined. This served to check that agricultural management had been measured in a way that was relevant to bees. It was also a preliminary exploration of bee responses to farm management.

For binary variables (dairying activity and reseeding), Somers' Dxy rank correlation (Somers 1962) was used to examine the correlation with the non-normally distributed bee abundance and diversity data. The *somers2* function of Hmisc package for R (Harrell Jr 2012) was used to calculate Somer's Dxy rank correlation coefficient and its standard deviation.

For continuous variables (PCO axes scores and total nitrogenous fertiliser applications), Spearman's correlations were used to test their association with bee abundances and diversity.

7. 3. RESULTS

7.3.1. AGRICULTURAL MANAGEMENT WITHIN THE STUDY REGION

Overview of management at the farm level

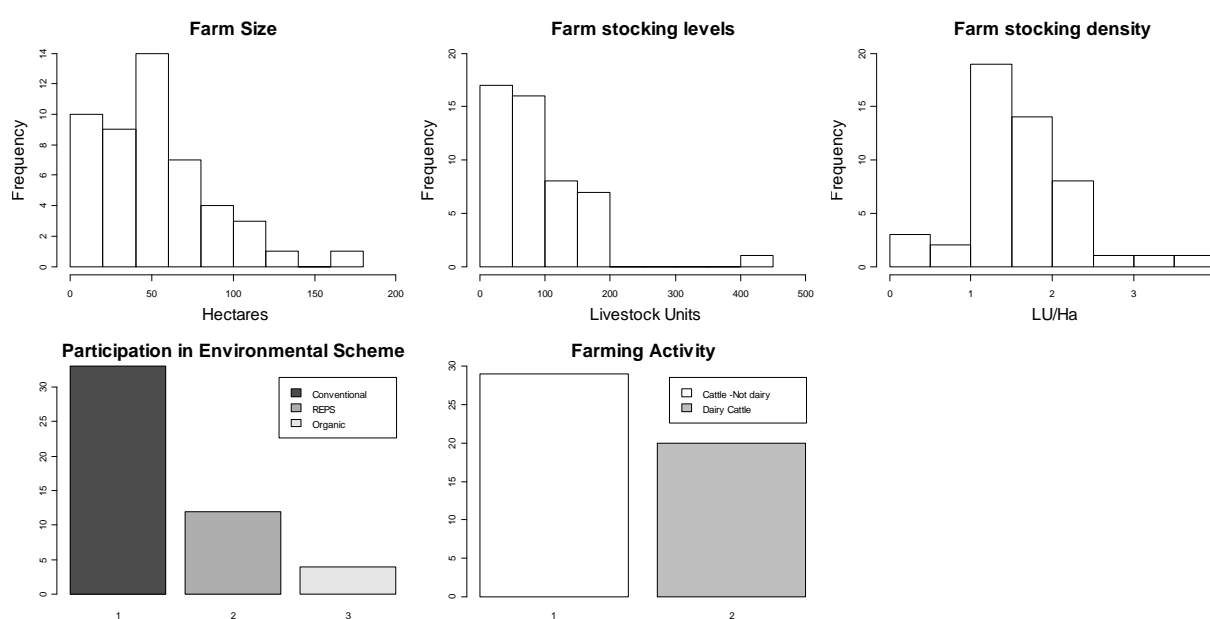


Figure 7.1. Frequency histograms showing farm size, stocking levels and stocking density, participation in environmental scheme and farming activity within sample, n=49. (NB sample was stratified to capture a range of intensities of farm management and therefore has more small and 'less intensive' farms than would have been captured by a random sample.)

Farm size

Median farm size was 47.35 ha (Mean is 48.65 ha) and interquartile range was 24.28 ha – 60.70 ha. The smallest farm sampled was 0.9 ha and the largest was 161.9 ha (Figure 7.1). The sample was biased towards smaller farms in order to capture the lower end of the spectrum of intensification. Some of the <20 ha 'farms' were a single field and were owned by people not

farming for their livelihoods but perhaps grazing horses, meadowing or letting the land. These were included in the sample as they were the examples of more traditionally managed grasslands.

Farm stocking density

The majority of farms had between 50 and 200 livestock units (Figure 7.1), with a median of 86 LU (interquartile range of 30 to 115.2 LU). Farm stocking levels ranged from zero to 3.60 livestock units per hectare. The median stocking density was 1.54 LU/Ha (interquartile range = 1.13 – 1.59 LU/ha). Stocking densities did not cluster at distinct levels but were spread along a continuum.

Farming activity

The majority of farms, 85.7%, had cattle (Figure 7.1). 41% of these farms were dairying and only three of the dairying farms did not also rear drystock. The remainder had drystock. Three of these cattle farms also had sheep. None were involved in tillage farming.

Overall horses and sheep were scarce on the farms and although their numbers were included in the calculation of farm stocking densities, they were not included in any analyses of grazing patterns. Four farms had horses only and three farms had no livestock. These smallholdings were included in the sample as their fields provided examples of semi-natural grasslands.

Farm participation in environmental scheme

A quarter (24.5%) of the farms was participating in the REPS scheme (Figure 7.1). Only 4 farms or 8% were organic.

Field management: fertiliser applications

The number of applications of fertiliser per year ranged between zero and twelve, with the majority of farms applying 2 or fewer (Figure 7.2).

The deliberate stratification of sampling is reflected in the histograms showing total nitrogen and phosphorus applications and number of fertiliser applications.

The median number of annual applications of fertiliser, either organic (manure or slurry) or chemical to the study fields was one, with an interquartile range of 0 to 2 applications. Nearly half of the fields (47%) received at least two applications of fertiliser per year. Just under a third of the fields (30%) received no nitrogenous fertiliser; 35% received 0-150kg N and 35% received more than 150kg N. The median amount of N applied was 66.7kg/ha (interquartile range of 0 – 177.9 kg /ha). The median amount of P applied was 6.7 kg/ha (Interquartile range = 0 – 24.71kg/ha).

Overview of management at the field level

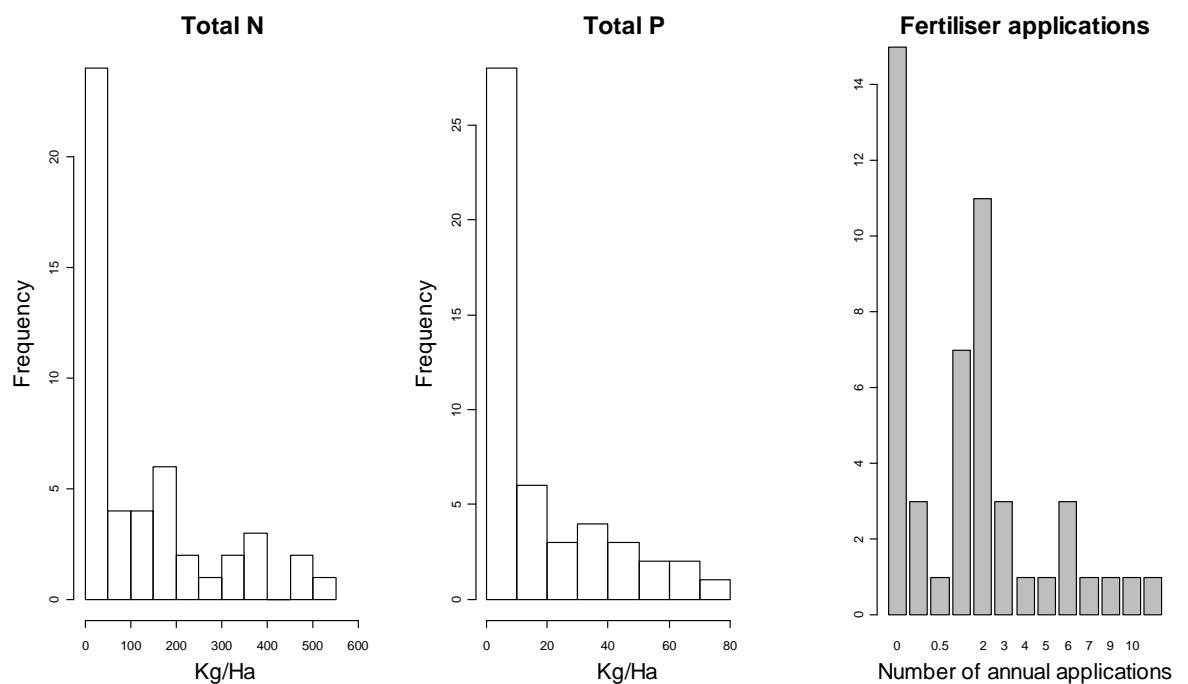


Figure 7.2. Frequency of fertiliser use upon sampled fields. (Note: fields that received a fraction of an annual application of fertiliser e.g. 0.3 or 0.5, received one application per 3 years or 2 years respectively.) (NB stratification of sample means that more small and 'less intensive' farms are included than would have been captured by a random sample.)



Figure 7.3. Frequency of different grazing and cutting regimes among sampled fields. Key: 1= rotation grazing + cut; 2= two cuts; 3 = one cut early summer and grazing; 4= one cut late summer and grazing; 5= continuous grazing, no cut.

Rotational grazing was the most frequent grazing regime in the sampled fields (Figure 7.3)

Two types of rotational grazing were described by farmers. In one form, the rotation period was 21 days, with cattle grazed in each paddock for short periods of 0.5 to 2 days. When grass growth slowed the rotation period was extended to 28 days. In the other form of rotational grazing, cattle grazed for a period of a week or longer in each paddock, followed by a fallow period of at least three weeks. These two forms were not distinguished in the analyses. In many cases rotational management was accompanied by harvesting the grass for silage or hay.

Only a small number of fields in the sample were cut twice. This was partly due to poor weather in the sampling year.

All of the fields grazed by horses or sheep were extensively grazed (i.e. they were in category 5).

The stratified nature of sampling meant that more fields were in categories 4 and 5 than would be expected in a random sample of farms in the study area.

Field management: use of chemical sprays; reseeding and hedgerow management

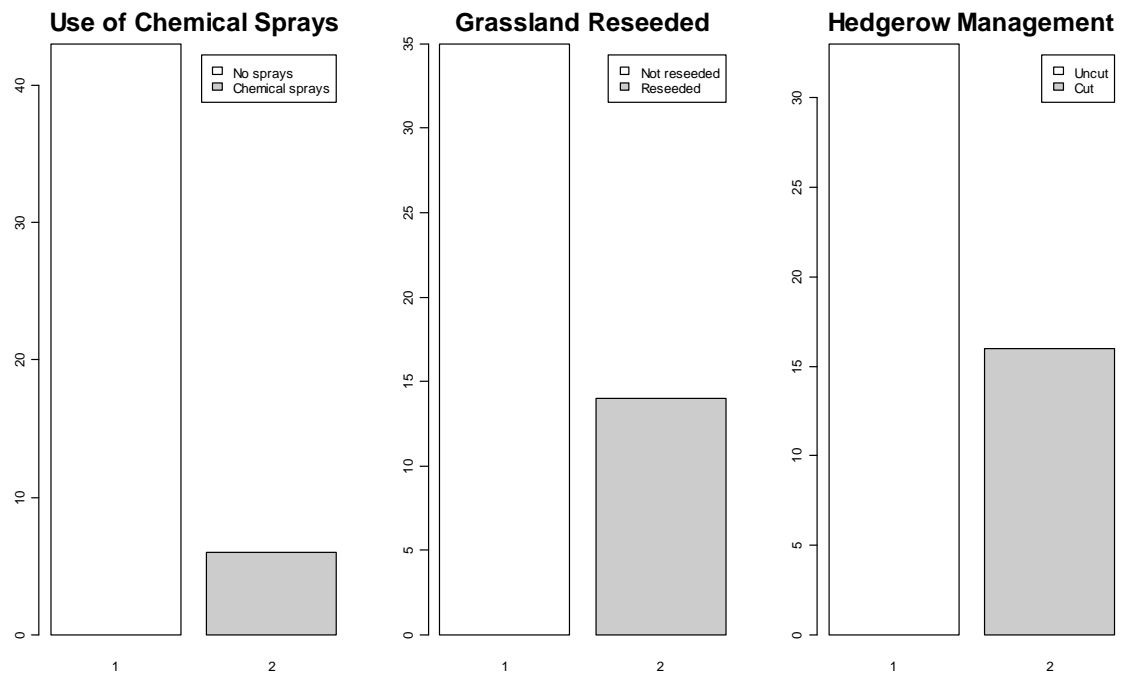


Figure 7.4. Frequency of chemical use, reseeding and hedgerow management in sampled fields. Key: 1= absence of management activity, 2 = active management

Chemical applications to grasslands were either ‘spot spraying’ of weeds such as nettles or docks or a blanket application of weedkiller followed by pesticides at the time of reseeding. 13.8% of the fields had been spot sprayed and 6.9% of fields had received blanket sprays within three years (Figure 7.4).

Spraying of field margins is not permitted on farms within REPS. However the effects of spraying were observed on farms in the scheme. 10% of REPS farmers admitted that they sprayed field margins, ‘just under the wire’ (Figure 7.4).

The level of chemical use in this sample of fields is likely to under-represent usage across pastoral landscapes as the sample was stratified to include less intensively managed fields which are uncommon.

The majority of grasslands had not been reseeded within 15 years (Figure 7.4). Less than a third of the study sites have been reseeded within the last 15 years (29%).

Approximately a third of hedgerows had been cut within the three years prior to the survey (Figure 7.4).

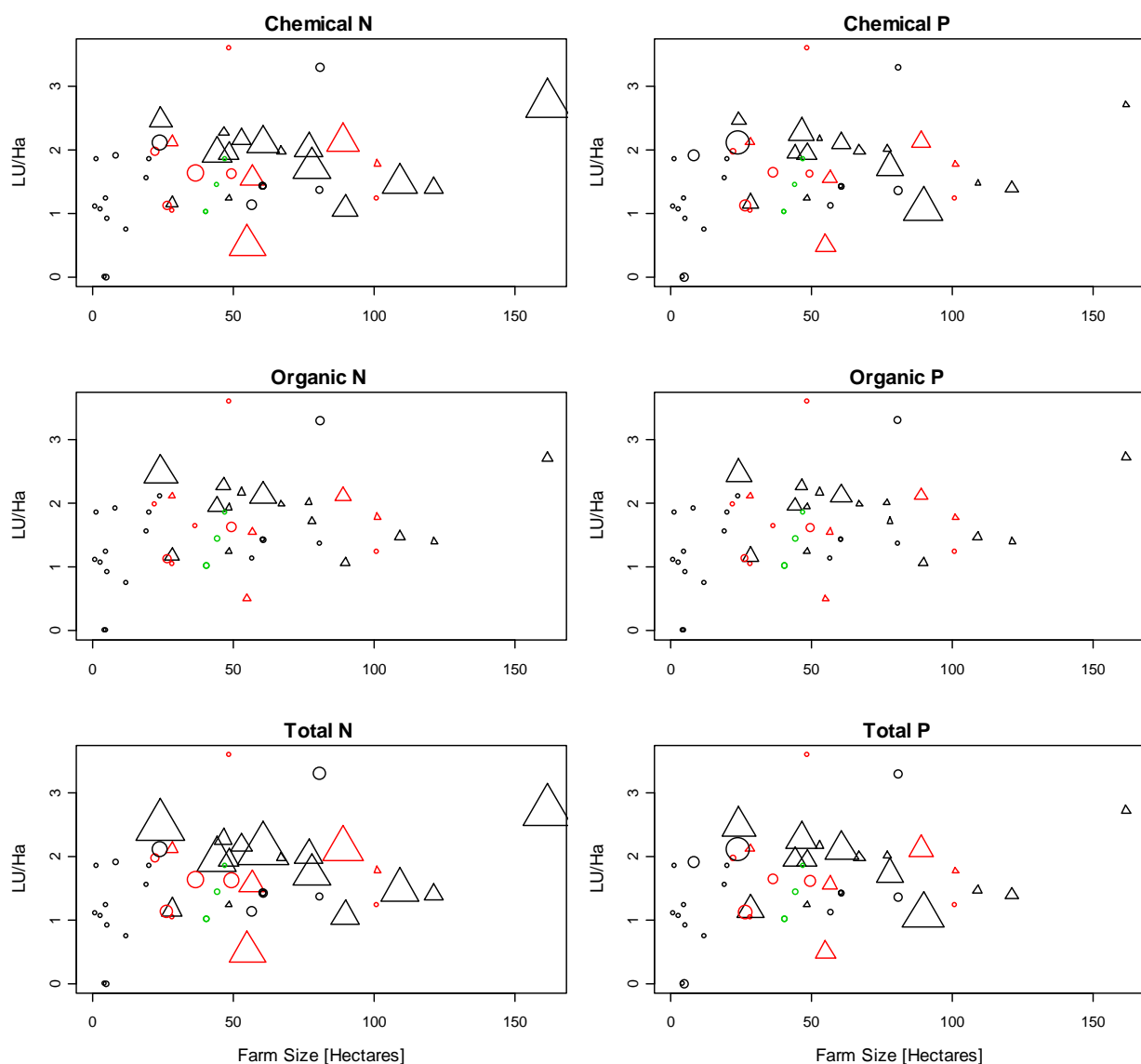
Farm stocking density in relation to farm types

Farm size had a weak correlation with stocking level (Spearman's correlation $\rho = 0.29$, $p=0.041$) (Figure 7.5).

Dairy farms, tended to be larger and to be stocked at higher levels (Figures 7.5 -7.7).

Kruskal-Wallis tests showed a statistically significant difference in size (Kruskal-Wallis chi-squared = 11.97, $df = 1$, $p\text{-value} = 0.0005$) and stocking density (Kruskal-Wallis chi-squared = 6.68, $df = 1$, $p\text{-value} = 0.01$) between farms that were dairying and those that were not.

Participation in an environmental scheme did not appear to influence livestock density on the farm, for this sample of farms (Figures 7.5 -7.7).



Legend

Symbol size is proportional to amount of nutrient applied

- Not Dairy + Not in Environmental Scheme
- Not Dairy + In REPS
- Not Dairy + Organic certification
- △ Dairy + Not in Environmental Scheme
- △ Dairy + In REPS
- △ Dairy + Organic certification

Figure 7.5. Graphs showing fertiliser applications, farming activity and stocking density (Livestock units per hectare, LU/ha) in relation to farm size.

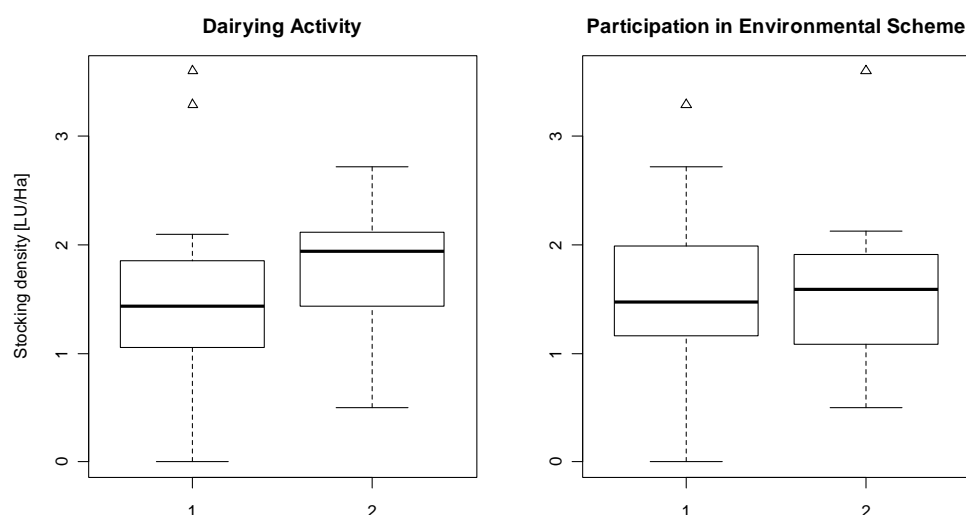


Figure 7.6. Boxplots showing stocking density (Livestock units per hectare, LU/ha) in relation to farming activity and participation in environmental scheme. Key: dairying activity: 1= nondairying, 2 = dairying; participation in environmental scheme: 1=conventional farm, 2= participant.

Examination of field management practices in relation to farm types

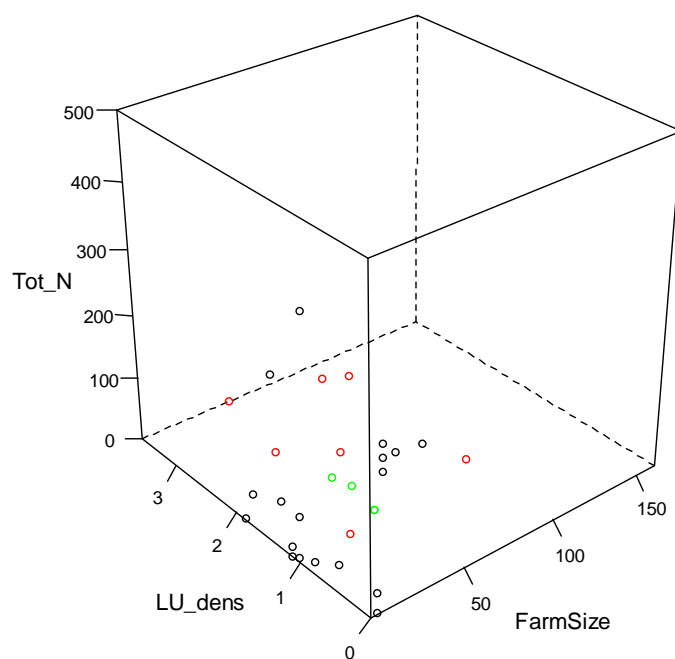
Dairy and nondairy farms

Farming activity, that is whether the farm is dairying or not, appears to be a better predictor of fertiliser inputs than stocking density, size or participation in REPS (Figures 7.5 -7.8).

There were statistically significant differences between dairy and nondairy farms in relation to fertiliser inputs (Figure 7.8: Kruskal-Wallis = 18.88, df = 1, p-value <0.001 for total Nitrogenous fertiliser and Kruskal-Wallis = 10.84, df = 1, p-value = 0.001 for total Phosphate fertiliser).

There were no significant differences between dairy and non-dairy farms in relation to grass management, reseeding, spraying and hedgerow cutting (tested using Fisher Exact Test and Chi-squared test)(Figure 7.8).

(i)



(ii)

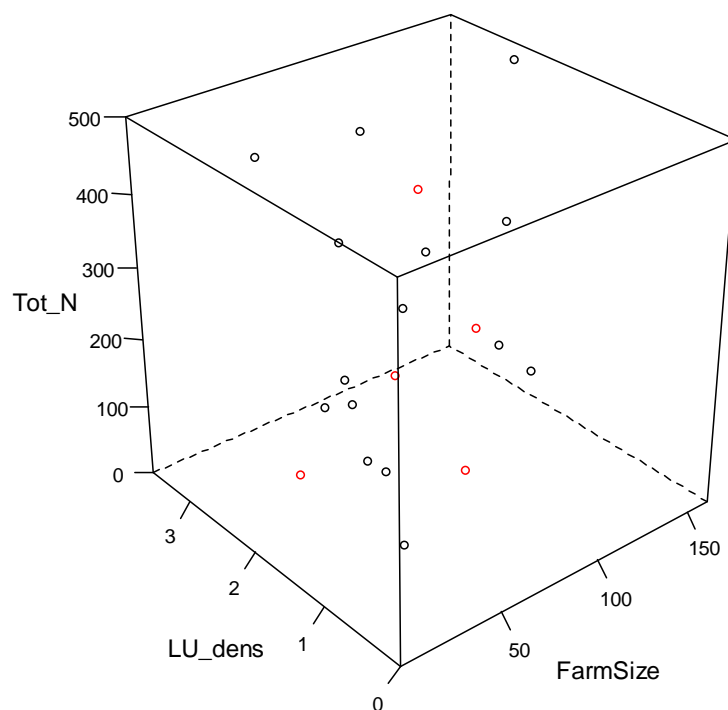


Figure 7.7. Three dimensional graph showing total nitrogen applied to sampled field [kg/ha] on (i) non-dairy farms and (ii) dairy farms showing participation in agri-environmental scheme and farm size. Key: Black = conventional farm; Red = REPS and Green = Organic.

Farms participating in an environmental scheme and conventional farms

There were no significant differences between conventional farms and farms participating in an environmental scheme (Figure 7.9) in relation to fertiliser use, grass management, reseeding, spraying and hedgerow cutting (Kruskal-Wallis, Fisher Exact and Chi-squared tests).

Farm types classified by dairying activity and participation in environmental scheme

Fertiliser use was significantly different among farm types classified by participation in environmental scheme and activity (Figure 7.10: Nitrate fertiliser: Kruskal-Wallis = 19.52, df = 3, p-value = 0.0002; phosphate: Kruskal-Wallis = 11.32, df = 3, p-value = 0.010).

There were no significant differences between farms classified by activity and participation in environmental scheme in relation to grass management, reseeding, spraying and hedgerow cutting (Fisher and Chi-squared tests and see Figure 7.10).

Further comments re field management practices and types of farm

Few farms used chemical sprays. Their use was more frequently observed on dairy farms (Figure 7.8) and on farms that were not participating in an environmental scheme (Figure 7.9). However there was no statistically significant difference in the use of sprays between these types of farms.

Reseeding of pastures was evident on all types of farms, whether they were in environmental schemes or dairying or not (Figures 7.8-7.10). Reseeded fields were more frequent on dairy farms and on farms that were not participating in an environmental scheme but these differences were not statistically significant.

Recently managed and unmanaged hedgerows were found on all types of farms. More of the recently cut hedges occurred on farms that were not in environmental schemes, particularly those that were dairying (Figure 7.10) but differences between farms were not statistically significant.

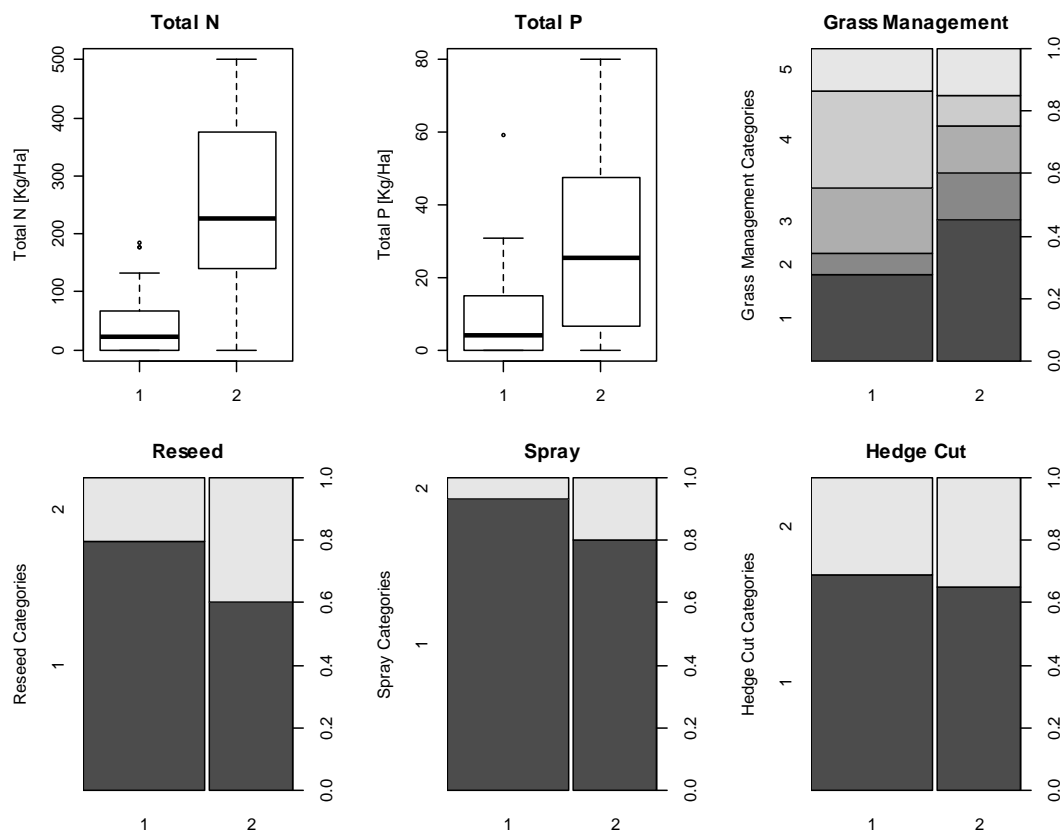


Figure 7.8. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to dairying activity. *Farm type*: 1 = nondairying; 2 = dairying farms. *Grassland management*: 1 = short rotation grazing; 2 = 2 cuts of silage; 3 = 1 cut in early summer + grazing; 4 = 1 cut in mid-late summer + grazing; 5 = not cut and extensively grazed. *Reseed*: 1 = Not reseeded, 2 = reseeded. *Spray*: 1 = Not sprayed, 2 = sprayed. *Hedge cut*: 1 = Not cut, 2 = Cut

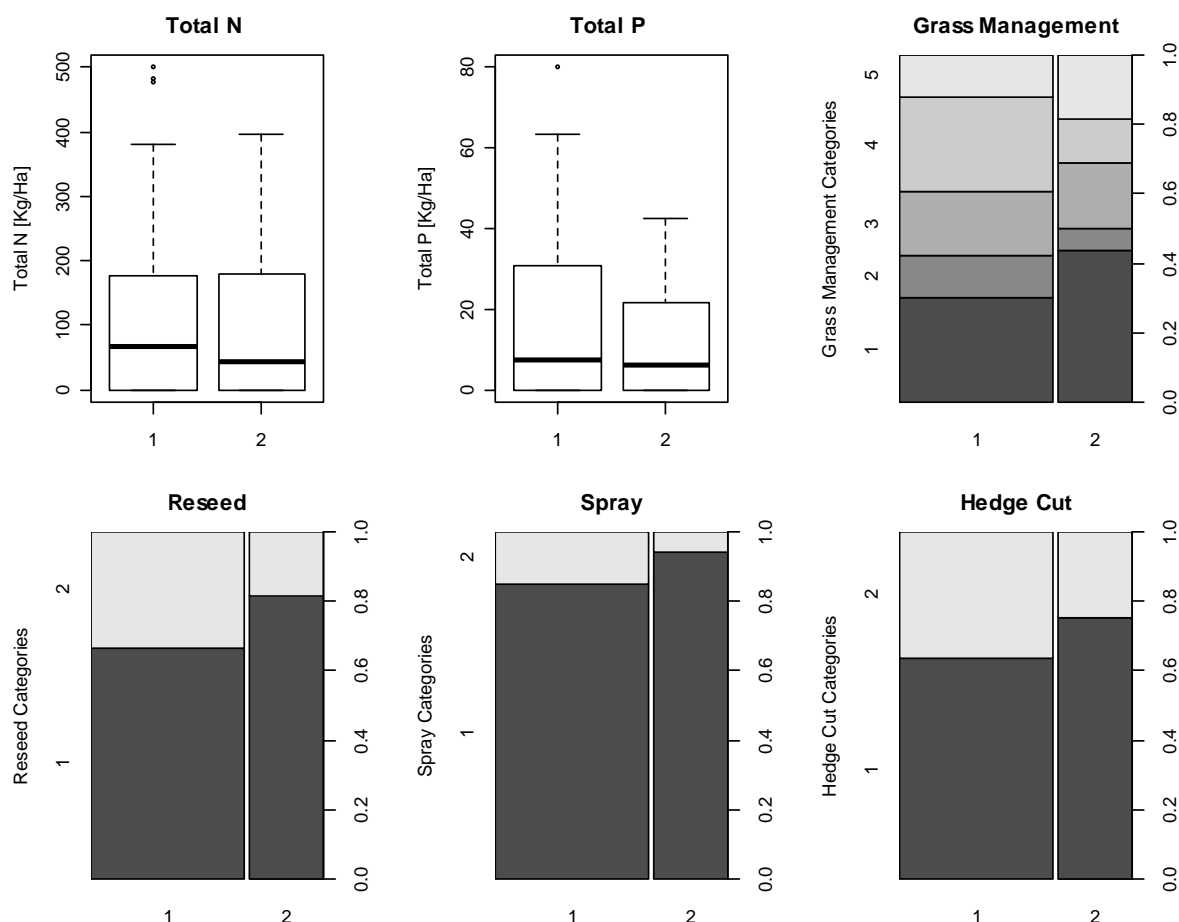
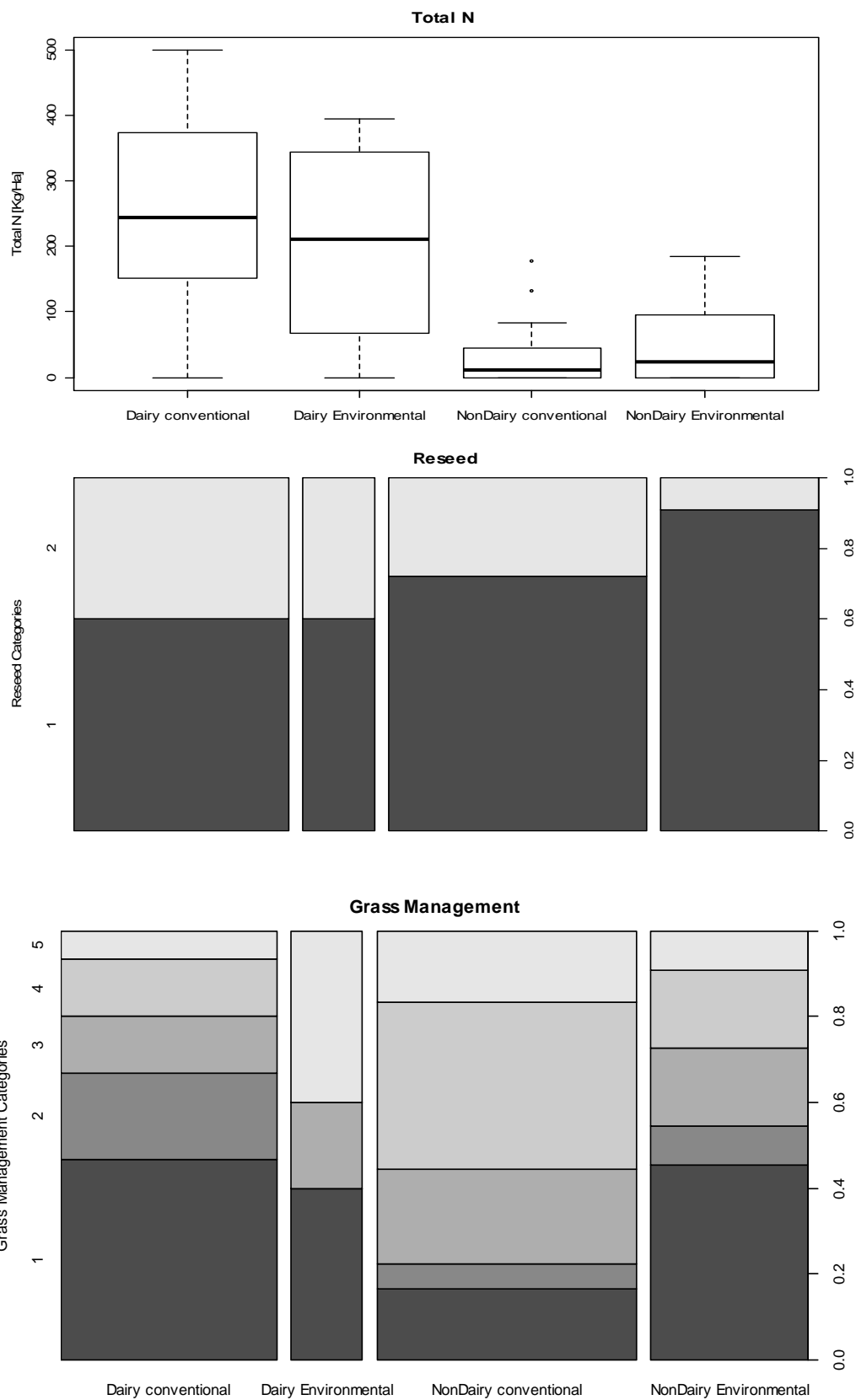


Figure 7.9. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to participation in agri-environmental scheme. Farm type: 1 = conventional; 2 = farms in REPS scheme. *Grassland management*: 1 = short rotation grazing; 2 = 2 cuts of silage; 3 = 1 cut in early summer + grazing; 4 = 1 cut in mid-late summer + grazing; 5 = not cut and extensively grazed. *Reseed*: 1 = Not reseeded, 2 = reseeded. *Spray*: 1 = Not sprayed, 2 = sprayed. *Hedge cut*: 1 = Not cut, 2 = Cut)



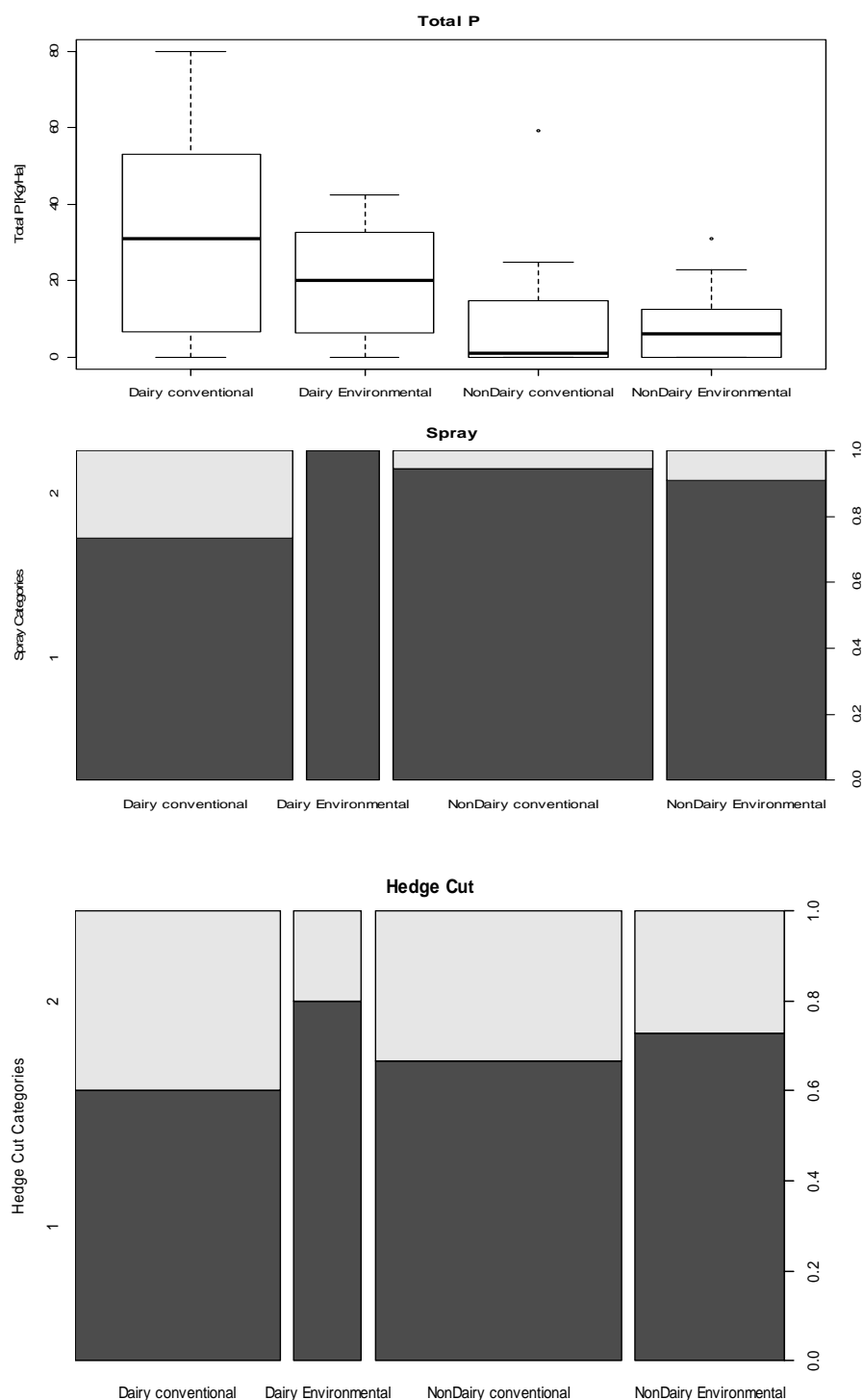


Figure 7.10. Boxplots and mosaic plots (the area in each bar is proportional to the observed frequency of observations in that category) showing field management in relation to farm type classified by participation in environmental scheme and dairying activity. *Grassland management*: 1=short rotation grazing; 2= 2 cuts of silage; 3= 1 cut in early summer + grazing; 4= 1 cut in mid-late summer + grazing; 5= not cut and extensively grazed. *Reseed*: 1= Not reseeded, 2= reseeded. *Spray*: 1= Not sprayed, 2= sprayed. *Hedge cut*: 1= Not cut, 2= Cut)

Fertiliser applications and grazing and harvesting of grass on different types of farms

Fields that were grazed on short rotation were distributed fairly evenly between dairying and non-dairying farms (Figure 7.8). However the level of Nitrogen applied to such fields was higher on dairy farms (Figure 7.11).

Fields which were cut twice for silage were uncommon (farmers reported that poor weather had prevented such management in the year of the survey) but were distributed evenly between dairying and non-dairying farms (Figure 7.8). Such fields received more nitrogen on dairy farms but the sample size was too small to ascertain whether this was a significant difference (Figure 7.11).

Fields which were managed with one cut, with or without subsequent grazing (grassland management categories 3 and 4) were more frequently observed on non-dairying farms (Figure 7.8). These fields received relatively low amounts of N fertiliser (<100kg/ha) (Figure 7.11).

Fields that were not cut at all and were extensively grazed, received low levels of fertiliser, regardless of whether they were on dairy farms or not (Figure 7.11). The relatively large number of fields that were cut late was regarded as a consequence of the sampling strategy rather than typical of a random sample. There were no completely unmanaged or abandoned fields on any type of farm.

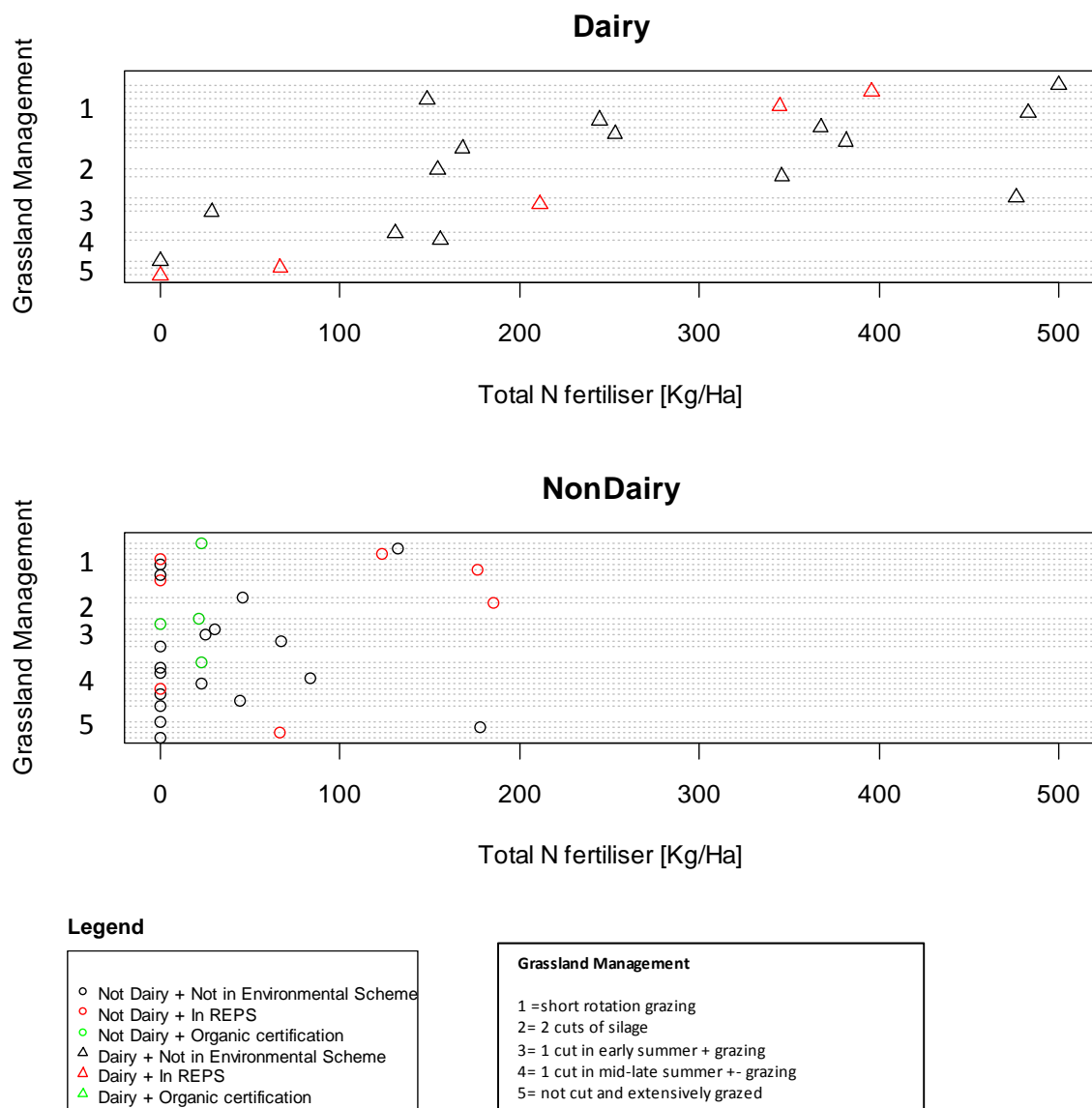


Figure 7.11. Dotplots showing levels of annual Nitrogenous fertiliser applied, broken down by type of grassland management, farm activity and participation in an environmental scheme.

Examination of associations between field management practices

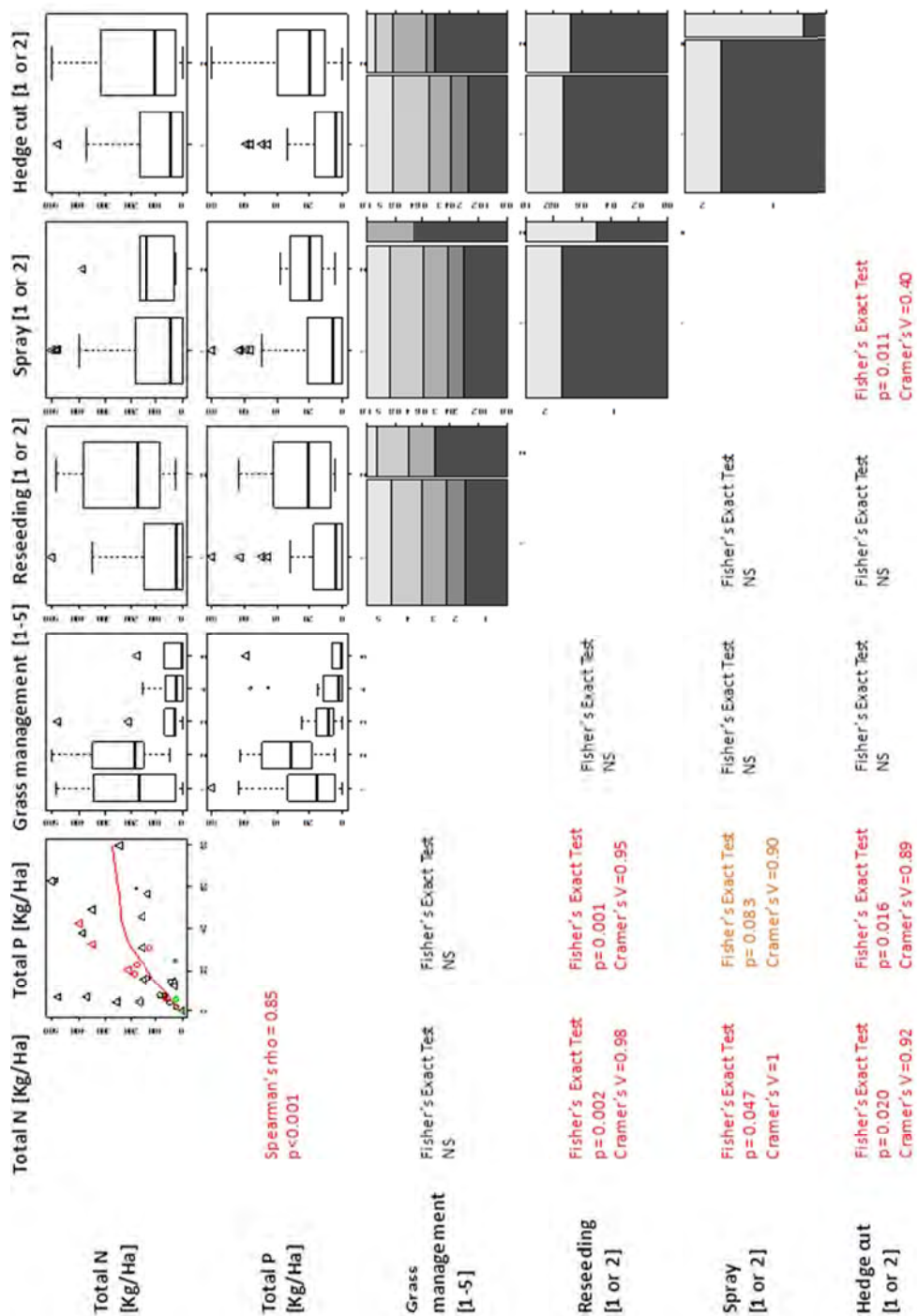


Figure 7.12. Correlation matrix and graphs visualising associations between field management practices. Farm symbols and grassland management categories as in Figure 7.11. *Reseed*: 1= Not reseeded, 2= reseeded. *Spray*: 1= Not sprayed, 2= sprayed. *Hedge cut*: 1= Not cut, 2= Cut.

Significant correlations between variables describing different aspects of field management were found (Figure 7.12). Fertiliser use was correlated with reseeding, spraying and hedge cutting. From an agricultural perspective there is no reason why hedge cutting and fertiliser applications should be associated. However rather than dismissing this as a spurious correlation I believe that it highlights farmers who were very active in their management.

No significant correlations were found between grass cutting and grazing regime and other field management practices (Figure 7.12). With a larger sample size significant associations might be detected as the following observations (statistically not significant) could be made from Figure 7.13: fields managed for 2 cuts of silage or grazed on short rotation (Grass managements 1 and 2) had higher fertiliser applications; reseeded fields were most commonly used for short rotation grazing on dairy farms.

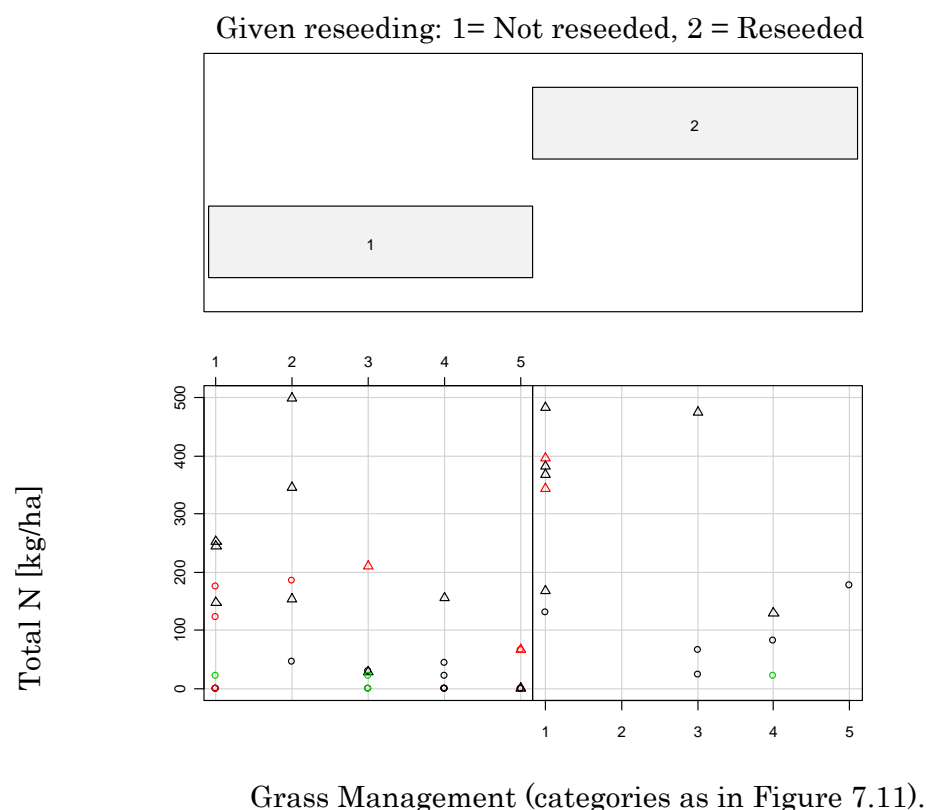


Figure 7.13. Conditional plot showing total nitrogenous fertiliser applied to fields that were reseeded and not reseeded under different grazing and harvesting regimes. (Symbols as in Figure 7.11.)

7.3.2. REDUCTION OF AGRICULTURAL MANAGEMENT DATA

Principal co-ordinates analysis of field management

The first two axes of the principal co-ordinates analysis of field management explained 63.2% of the variation in the field management as captured by the matrix of Gower distances.

Table 7.2 shows the correlations of individual field management variables with the ordination and that the PCO was effective in summarising field management.

Increasingly negative scores on the first axis were associated with high fertiliser use and reseeding (Figure 7.14). Increasingly positive scores on the second axis were associated with the use of chemical sprays (Figure 7.15).

PCO axes scores could be used to summarise field management.

Table 7. 2. Correlations of field management variables with PCO of field management

* indicates variables that were not used in the PCO.

Field management variable	Envfit r^2	p
Total N [Kg/Ha]	0.69	0.001
Total P [Kg/Ha]	0.50	0.001
Spray	0.41	0.001
Reseed	0.42	0.001
Number of fertiliser applications*	0.63	0.001
Hedgerow management*	NS	NS

A farm-level descriptor such as dairying activity, size or participation in environment scheme could not be used to summarise field management as correlations between them were weak (Table 7.3). For example, there was a significant but weak correlation between dairying activity and the ordination of field management. The significance level of the association between field management and farm size and stocking density was $p=0.06$. Participation in an environmental scheme was completely uncorrelated with field management.

Table 7. 3. Correlations between farm management variables and PCO of field management

Farm variable	Envfit r2	p
Farm size	0.11	0.060
Farm activity ie dairying or not.	0.11	0.002
Farm participation in environmental scheme	0.01	0.527
Farm stocking density	0.29	0.060

The ordination plots showed 4 separate clusters of sites (Figure 7.15). PCO separated these sites on the basis of spraying and reseeding. However within each of these four groups there was a gradient of nitrogen and phosphorus applications (Figure 7.14). Using these clusters to summarise field management would therefore omit information regarding fertiliser use.

Nitrogen application and reseeding were two variables that could be used to summarise much of the data within the complete field management dataset (Figure 7.14, Figure 7.15 and Table 7.2). Nitrogenous fertiliser application was correlated with phosphate applications and number of applications and was the variable most strongly influencing the PCO. Including reseeding captures further information associated with the first axis of the PCO. This combination of variables omits information from the second axis of the PCO, associated with chemical spray use, but only three fields were sprayed that had not also been reseeded.

The best available options for summarising field management were identified as PCO axes 1 and 2 or nitrogen application and reseeding.

At the farm level, dairying activity was selected as the best variable to summarise information on farm size, stocking density and also some information regarding field management.

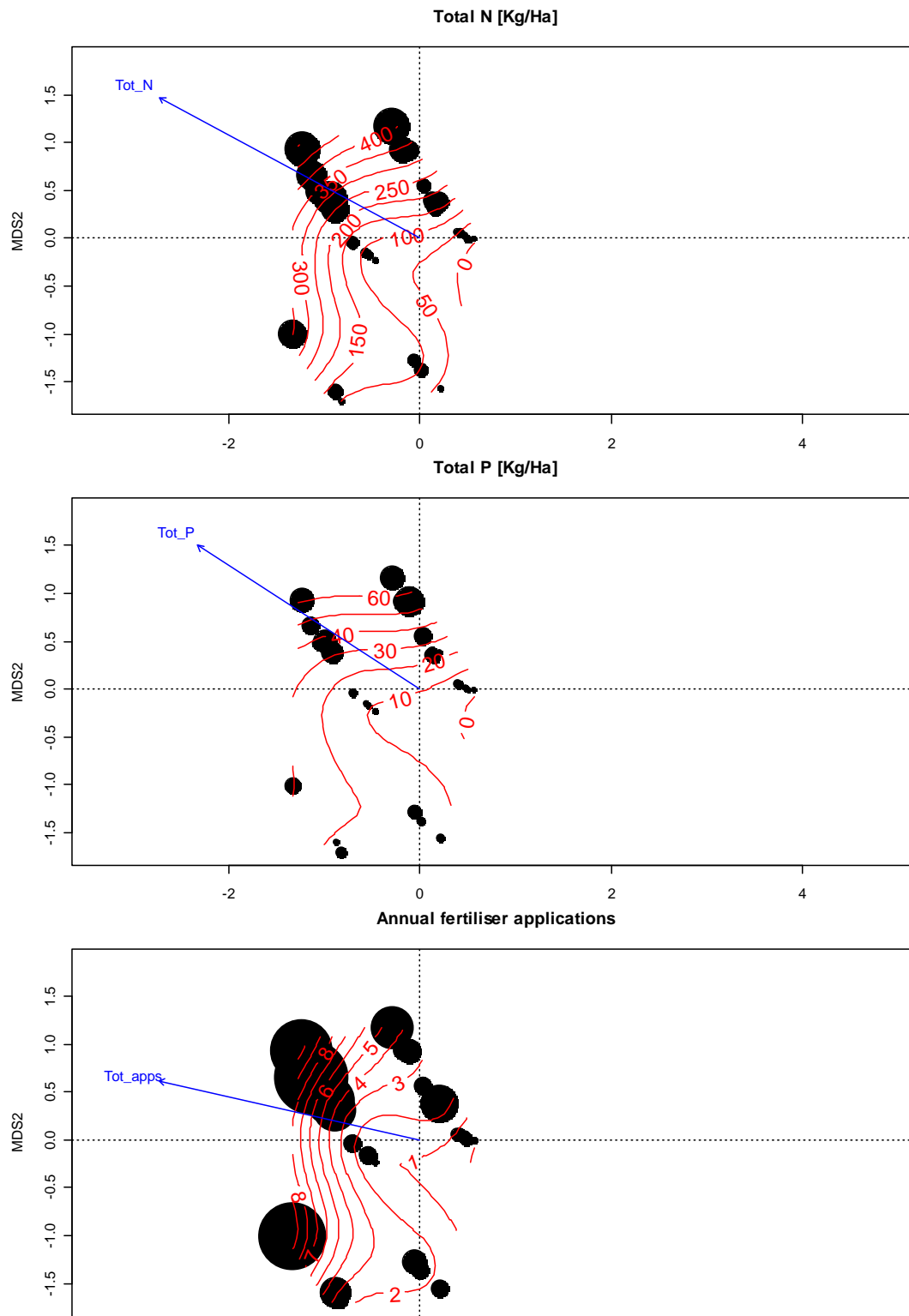


Figure 7.14. Indirect gradient analyses showing correlations of fertiliser use with PCO of field management data (using Gower's distances). Symbol size represents the value, for that site, of the fertiliser variable being illustrated. Arrows show strength and direction of correlations with fertiliser variables (all significant at $p=0.05$). Red contour lines show a smooth fitted surface for each fertiliser variable: total Nitrogenous fertiliser (Tot_N), total Phosphate fertiliser (Tot_P) and number of fertiliser applications (Tot_apps), fitted using generalized additive models using the

R function *ordisurf*.

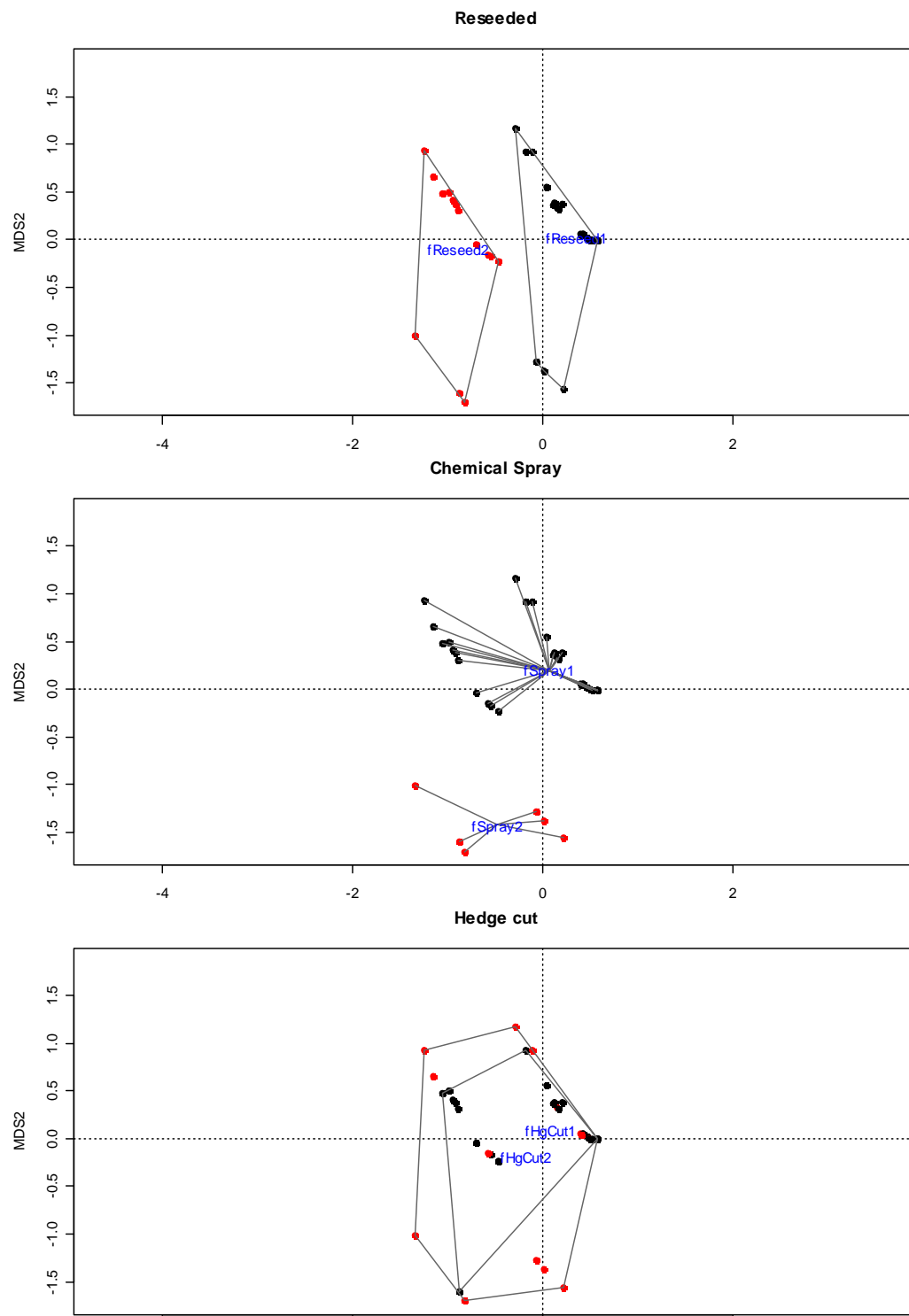


Figure 7.15. Indirect gradient analyses showing correlations between use of chemical sprays, reseeded and hedgerow management and PCO of field management data (using Gower's distances). Symbol colour represents the value, for that site, of the variable being illustrated: Black =1 (low intensity management) and Red =2 (high intensity management). Centroids (mean score of the variable on each axis) are shown by position of label.

7.3.3. BEST VARIABLES TO DESCRIBE AGRICULTURAL MANAGEMENT

Table 7. 4. Correlations between agricultural management variables and bee abundance and diversity.

LEVEL OF MANAGEMENT	FARM	FIELD	FIELD	FIELD	FIELD
	Dairying activity	PCO Axis1	PCO Axis2	Total nitrogenous fertiliser application	Reseeded
Correlation	Somer's Dxy	Spearman's	Spearman's	Spearman's	Somer's Dxy
Solitary bee abundance ($\log_{10}(\text{abundance} + 1)$)	NS	NS	NS	NS	$p < 0.01$ Dxy = -0.32
Bumblebee abundance ($\log_{10}(\text{abundance} + 1)$)	NS	NS	NS	NS	NS
Wild bee abundance	NS	$p = 0.027$ $\rho = 0.32$	NS	$p = 0.083$ $\rho = -0.25$	$p < 0.01$ Dxy = -0.41
Number of bee genera	NS	$p = 0.090$ $\rho = 0.25$	NS	NS	$p < 0.01$ Dxy = -0.45
Number of bee species	$p < 0.05$ Dxy = -0.35	$p = 0.030$ $\rho = 0.31$	NS	$p = 0.07$ $\rho = -0.25$	NS
Number of solitary bee species	NS	$p = 0.095$ $\rho = 0.24$	NS	NS	NS
Number of bumblebee species	NS	$p = 0.060$ $\rho = 0.27$	NS	$p = 0.02$ $\rho = -0.31$	NS

Wild bee abundance was correlated with field management quantified as either a score on PCO axis 1 or reseeded (Table 7.4).

The diversity of bees was also influenced by management. The number of bee genera was negatively correlated with reseeded (Figure 7.16 and Table 7.4) and the number of bee species was negatively correlated with dairying activity (Table 7.4). Numbers of bumblebee species and solitary bee species were correlated with the first PCO axis scores and number of bumblebee species was negatively correlated with level of nitrogenous fertilizer (Table 7.4).

Indirect gradient analyses showed the selected field and farm management variables not to be significantly correlated at $p=0.05$ with solitary bee or bumblebee species abundance composition.

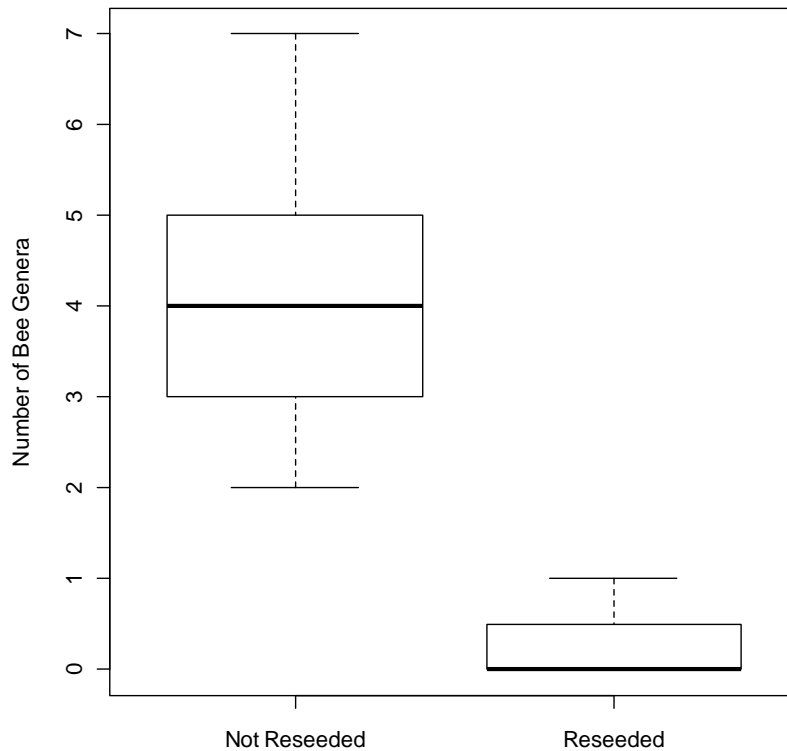


Figure 7.16. Boxplots showing number of bee genera on fields that have been reseeded and fields that have not been reseeded within previous 15 years. (Note: only 14 sites of 55 had been reseeded).

7. 4. DISCUSSION AND CONCLUSIONS

This chapter aimed to reduce a complex, multifaceted environmental influence, agricultural management at farm and field levels, to a small number of explanatory variables that could be used for analyses of bee abundances, diversity and assemblage composition.

The analyses have shown that the type of farm, defined by features such as size, activity or participation in an environmental scheme, cannot be used to conveniently summarise field management or farming intensity. There was no natural clustering of farms at particular stocking densities or sizes, for example.

The difficulty in classifying farms into particular types is a result of the high level of variation in farming practices, even amongst farms participating in an environmental scheme or producing the same product.

Participation in an environmental scheme was not correlated with any measured aspect of management. This was a surprising result. But, only one field was sampled on each farm, it is therefore possible that its management may not have been representative of management across the whole farm. Indeed, for a field that is managed under the REPS scheme, very high N values in the sampled field imply that elsewhere on the farm a field was managed with lower levels of fertiliser so that the overall farm N budget falls within the scheme's limit.

Dairying activity was the strongest contender for a worthwhile classification of farms describing their management. Dairy farms tended to be larger and had significantly higher stocking densities.

Fields on dairy farms were observed to receive more management inputs such as reseeded, spraying, fertiliser applications and frequent hedgerow cutting, although only fertiliser use was significantly correlated with dairying activity.

However there was considerable overlap in field management between dairying and non-dairying farms and the correlation between farm and field level management was weak. One could not be used to summarise the other.

PCO axis scores were shown capture information regarding field management intensity. The site scores for the first two axes from the ordination would efficiently summarise field management with regards to fertiliser use, chemical spray use and reseeded.

Only a small range of management processes were considered in this evaluation of the 'intensity of management' and farm types. For example, the proportion of semi-natural habitat on the farm or the breeds of cattle kept were ignored. This is because the aim was to identify the most relevant features that are likely to impact on bees.

Eleven variables have been reduced to three that summarise agricultural management at the field and farm level.

At the farm level, enterprise, that is whether the farm was dairying or not dairying was selected as a measure of farming intensity.

At the field level, site score on the first axis of a PCO analysis (capturing total nitrogen applied, total phosphorus applied, reseeding, and chemical use) and reseeding were selected to summarise intensity of management at this level.

CHAPTER 8: BEE- VEGETATION LINKAGES AND SPATIAL PATTERN IN PASTORAL AGRI-ECOSYSTEMS

8. 1. INTRODUCTION

It is only with an understanding of natural variability that we can detect and explain anthropogenic change. Our knowledge of the natural factors structuring bee assemblages, even on a coarse regional scale, is relatively limited (Patiny *et al.* 2009a; Grundel *et al.* 2010).

This study explores natural spatial variability and correlations with vegetation at a sub-regional scale. This is the scale at which management is most likely to impact on biodiversity (Bestelmeyer *et al.* 2003).

The majority of bee studies have tended to use abundance, species richness or a diversity index to summarise assemblage composition. Studies that consider the species composition of assemblages are also required (Winfree 2010; Winfree *et al.* 2011). This chapter takes such an approach and the bee assemblage is studied in terms of the relative abundance of its species.

VEGETATION – BEE ASSOCIATIONS

The idea that there are affiliations between plant and animal assemblages is an old one (Schaffers *et al.* 2008). Plant assemblages are likely to be a natural filter on the regional bee species pool, shaping local bee assemblages (Zobel 1997) due to the forage resources that they provide (Potts *et al.* 2003). Moron *et al.* (2008) detected a differentiation in bee assemblages of wet and dry grasslands and attributed the differences to the forage provided by the plant assemblages. Diversity within bee assemblages is associated with the diversity of forb communities (Bowers 1985; Potts *et al.* 2003; Potts *et al.* 2004; Vulliamy *et al.* 2006; Sarospataki *et al.* 2009; Fründ *et al.* 2010; Hendrix *et al.* 2010). However Grundel *et al.* (2010) points out that many bees are generalist feeders and the association between flower assemblages and bees can be a weak one and Alarcón *et al.* (2008) even finds individual bee species may change their flower affiliations between years.

Associations between plant assemblages and bee assemblages have been studied to a far less extent than associations between flowers and bees, yet may provide interesting insights into the ecology of bees (Bolotov & Kolosova 2006). The species composition of plant assemblages integrates information on environmental conditions, on vegetation structure and on site history (Schaffers *et al.* 2008). Plant assemblages reflect other environmental conditions such as soil conditions and management intensity (Tilman 1987; Ellenberg *et al.* 1991; Hill *et al.* 1999). These factors, for example, soils (Potts *et al.* 2005; Kim *et al.* 2006; Abrahamczyk *et al.* 2011), may also be influencing bee assemblage structure. I use this integrative property of plant assemblage composition to conduct an exploratory analysis of the environmental factors that may be influencing bee assemblage structure. This is a first step to identifying filters influencing bee composition which is intended to lead on to hypotheses development and future study.

Correlations between plant and bee assemblages have not been detected universally. Grundel *et al.* (2010) and Williams (2011) did not detect significant correlations between plant and bee assemblages in their studies. UK bumblebees were found to have only weak associations with plant assemblages classified to the habitat or biotope level of classification (Goulson *et al.* 2006) although Bolotov & Kolosova (2006) did find associations between bumblebees and biotopes in Russia.

A difficulty for the study of associations between plant and animal assemblages has been the lack of methods that allow the use of the plant species composition of the entire community as a predictor (Schaffers *et al.* 2008). Studies that have used species richness or diversity measures to summarise plant communities have generally had less success in finding correlations with animal assemblages than studies which used a multivariate approach (Beals 2006). I use Mantel's Test and symmetric Procrustes rotations (Mardia *et al.* 1979; Peres-Neto & Jackson 2001) to compare the plant and bee assemblages in their entirety. I investigate the strength of associations between plant communities of fields and hedgerows and bee communities in pastoral agri-ecosystems.

Ellenberg scores (Ellenberg *et al.* 1991; Hill *et al.* 1999), calculated from vegetation abundances, provide an indirect measure of soil moisture, soil nitrogen and soil pH with bee assemblage composition. I correlate these indices and other dimensions of vegetation composition, e.g. species diversity, to provide clues to the environmental filters that influence bee assemblage composition.

The succession stage of vegetation can influence bee assemblage composition via floral and nesting resources (Tschardtke *et al.* 1998). Halictidae and Andrenidae prefer the flowers of annuals (Steffan-Dewenter & Tschardtke 2001; Potts *et al.* 2003) whereas bumblebees prefer perennials (Fussell & Corbet 1991; Dramstad & Fry 1995). Ground-nesting bees require bare soil whereas trap-nesting bees require shrubs for nesting (Steffan-Dewenter & Tschardtke 2000).

Despite succession having the potential to influence the composition of bee species in various ways, assemblage changes are not always detected. Krauss *et al.* (2009) found no difference in the bee assemblages of limestone quarries in which quarrying had ceased for different lengths of time.

SPATIAL PATTERN

Plant assemblages and bee assemblages are each likely to be spatially structured, for example, aggregated in patches or forming gradients (Koenig 1999; Legendre *et al.* 2002). This spatial structure is shaped by autogenic processes such as dispersal, competition, predation (leading to spatial autocorrelation) as well as exogenous processes involving the response of the organism to environmental variables that are themselves spatially structured (causing spatial dependence)(Legendre & Fortin 1989; Legendre *et al.* 2002). The climatic zonation of vegetation across continents, for example, is associated with bumblebee assemblage composition (Hines 2008). As sites that are more distant from one another are considered, one would also expect assemblages of plants and bees to become more dissimilar (Sokal & Oden 1978a, b).

Relatively little is known about the spatial patterning of bee assemblages at a local scale, or the extent to which it is dependent on plant assemblages. Some

studies suggest a naturally high beta diversity of bees over relatively short distances so that sites that are separated by only 1-5km may have quite dissimilar assemblages (Minckley *et al.* 1999; Wilson *et al.* 2009; Grundel *et al.* 2010).

Anthropogenic impacts such as urbanisation (Sattler *et al.* 2010) and agricultural intensification (Clough *et al.* 2007; Dormann *et al.* 2007b; Quintero *et al.* 2010) have reduced differences between assemblages. The contribution of plant assemblages to such spatial patterning or the loss of spatial patterning in bee assemblages has not been studied.

In this exploratory study, I use correlograms to compare the spatial patterning of bee and plant assemblages (Sokal & Oden 1978a; b; Legendre, 1998; Legendre & Fortin 1989; Goslee & Urban 2007; Borcard & Legendre 2012). I determine the distances over which bee assemblages decline in similarity in a pastoral region in Southern Ireland. Such information facilitates the development of hypotheses regarding natural filters structuring bee assemblage composition at this geographical level. It also informs the scale which conservation measures aimed at maintaining beta diversity of bee assemblages across a region should be designed for and implemented at.

Partial Mantel analyses (Legendre & Legendre 1998; Goslee & Urban 2007) are used to identify the spatial effects on bee composition that are associated with vegetation.

Differences in the sizes and behaviour of solitary bees and bumblebees (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2003; Albrecht *et al.* 2007; Krauss *et al.* 2009; Williams *et al.* 2010) mean they forage over different distances, with smaller bees tending to forage over shorter distances and to respond to factors measured at smaller scales within the landscape (van Nieuwstadt & Ruano Iraheta 1996; Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007; Tscheulin *et al.* 2011). The associations between solitary bee and bumblebee assemblages and vegetation and space are therefore considered separately.

Space and location are regarded as two distinct influences. Space is used to describe the distance between sites whereas location refers to sampling location.

To summarise, the key questions being investigated are:

1. Are plant and bee assemblages associated?
 - a. Similarly or differently for solitary bees and bumblebees?
2. Which qualities of plant assemblages are associated with bee assemblages?
 - a. What does this suggest about natural filters influencing the composition of bee assemblages at a local level?
3. To what extent are the correlations between bees and plants driven by spatial dependence?
4. What other spatial patterning is evident within bee assemblages in the study region?
 - a. Does this offer further clues to natural filters?

8. 2. METHODS

8.2.1. DATA PREPARATION

The data used in this chapter are from surveys conducted in 2005 in Counties Limerick and Tipperary in the Southwest of Ireland. A full description of survey design and the methods used to measure explanatory and response data are provided in Chapters 3-7. Table 8.1 provides a summary of the datasets and the transformations and distances used in this chapter.

The complete dataset had 56 sampling units. Sample sizes were adjusted downwards when there was missing data or a case was not relevant to the analysis (e.g. in analyses with hedgerows if the field boundary was a wall). Sample sizes for each analysis are noted in the text.

Analyses for solitary bees and bumblebees were carried out separately to allow for the examination of hypotheses regarding the different responses of solitary bees and bumblebees to vegetation composition and geographical space.

Table 8. 1 Overview of datasets used in this chapter and the transformations and distance measures used with each.

Datasets	Transformation	Distance measure	Note
Solitary bees	converted to presence-absence	Jaccard	Counts of thirty-six species and species groups
Bumblebees	converted to presence-absence	Jaccard	Counts of ten species and one species group
Environmental			
Grassland vegetation	log10 (+1)	Bray-curtis	% cover of seventy-seven species and species groups
Hedgerow vegetation	log10 (+1)	Bray-curtis	% cover of thirty-one species and species groups
Spatial data	None	Euclidean	Treated in 2 ways as (1)Distances (m) between sites (2) 4 locations

8.2.2. REDUCTION OF DIMENSIONALITY

The analyses in this chapter used derivatives of the bee and vegetation datasets, which reduced the dimensionality of the original abundance matrices. These lower dimension derivatives were distance matrices (Table 8.1), Nonmetric Multidimensional Scaling (NMDS) solutions and Indices. The preparation of these is described below.

NMDS SOLUTIONS

For each bee dataset, an NMDS was conducted using the Jaccard distance calculated using presence-absence data. Vegetation data was square root transformed and the Wisconsin double standardization applied (these were standard transformations applied by the *metaMDS* function of *vegan* (Oksanen *et al.* 2013) when data values >50) and an NMDS based on the Bray Curtis distance was carried out. As well as using the random restarts provided by *metaMDS*, each NMDS was repeated using the best solution from the first analyses. This was to ensure the global solution was reached by preventing the NMDS becoming trapped in local optima.

Stress, a measure of agreement between the original ecological distances and configuration of the ordination, was approximately 0.2 (the borderline between a 'fair' and 'poor' fit according to Kruskal's rules of thumb (McCune & Grace 2002)) for two axes for all NMDS analyses. This was regarded as adequate and two axes configurations were used for all NMDS plots. Species were represented on ordination plots of NMDS solutions as centroids which were mapped using weighted averaging, following (Legendre & Legendre 1998).

INDICES SUMMARISING VEGETATION COMPOSITION

Indices were selected to summarise as much information as possible about vegetation composition and to summarise different aspects of that composition (see Chapters 5 and 6).

The grassland vegetation indices that were tested for correlations with bee composition were species number (SwSpNo), complement of Simpson's Index (1-D)(GrassCompSimp) and Ellenberg values for soil moisture (Sw_Ellen_Water), soil nitrogen (Sw_Ellen_N) and soil pH (Sw_Ellen_pH). Mean Ellenberg scores for each site's grassland were calculated using Turboveg (Hennekens & Schaminee 2001). Ellenberg values (Ellenberg *et al.* 1991), adapted for UK conditions (Hill *et al.* 1999), for nitrogen, soil pH and soil moisture for each observed plant species were weighted by its percentage cover in that relevé. The mean Ellenberg score for the relevé was then calculated from the Ellenberg scores of the species present.

For hedgerow vegetation, the number of woody hedgerow species (HedgeSpNo) and the Inverse Simpson's Index (1/D) (HedgeInvSimp) calculated for hedgerow woody species were used.

8.2.3. ANALYSIS METHODS

The series of analysis is listed (Figure 8.1) and then described in the following sections. Analyses were conducted using vegan (Oksanen *et al.* 2013) and ecodist (Goslee & Urban 2007) packages in R (R Core Team 2012). Sample size differed slightly between bumblebee (n=55) and solitary bee (n=53)

analyses as solitary bees were absent from some sites and Jaccard distances could not be calculated.

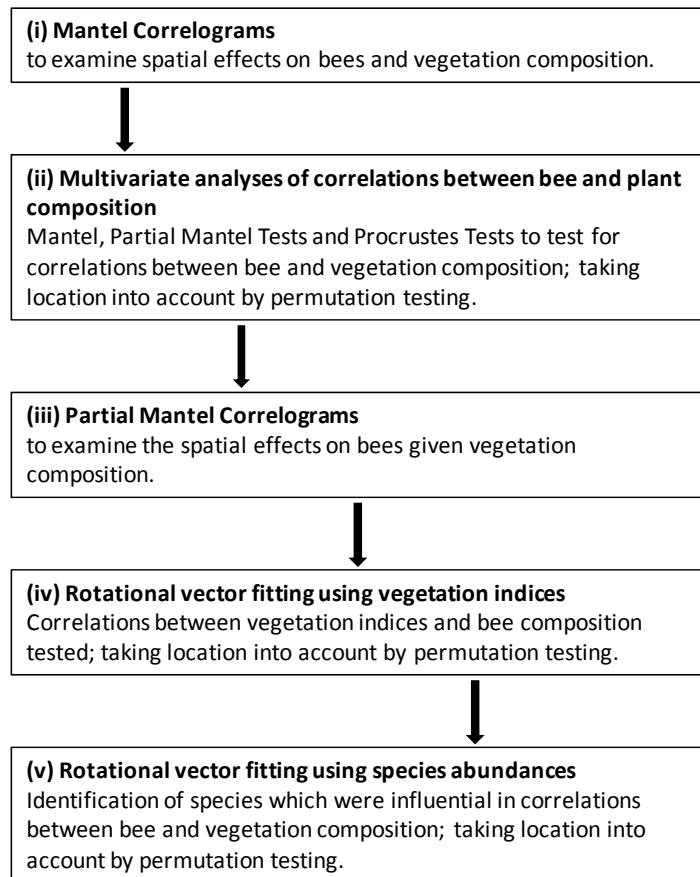


Figure 8.1. Series of analyses used in this chapter.

MANTEL CORRELOGRAMS TO EXAMINE SPATIAL EFFECTS ON BEES AND VEGETATION COMPOSITION.

Prior to carrying out Mantel correlogram analyses, plots of geographical distances between sites and compositional distances were used to visualise potential relationships between space, bee and vegetation composition. Jaccard dissimilarities were used for bees and Bray Curtis dissimilarities used for vegetation.

The following were plotted:

- dissimilarity between bee composition (solitary and bumblebees) and geographical distance between sites and

- dissimilarity between vegetation composition (hedgerow and grassland) and geographical distance between sites .

Mantel correlograms were then used to test for correlations between changing ecological dissimilarity and increasing inter-site distance over different distance intervals. This method was proposed by Oden & Sokal (1986). A full description of the method and the interpretation of Mantel correlograms is provided in Legendre & Legendre (1998). It has been confirmed as a powerful tool for ecologists to analyse spatial correlations for multivariate data (Borcard & Legendre 2012).

The Mantel correlogram procedure divides the distance between sites into intervals e.g. 0-500m, 501-1000m etc. Sturge's rule was used to determine the number of intervals (Legendre & Legendre 1998) to prevent arbitrarily inflating the explained spatial variation. A geographical distance matrix is generated for each distance interval and the correlation between it and the ecological distance matrix is then calculated using Mantel's test.

Permutation testing with 9999 permutations was used to determine the significance value of Mantel's correlation coefficients. Since there was multiple testing of correlation coefficients, one for each distance interval, Holm's test corrected probability values, at an overall type 1 error rate of 0.05, (Holm 1979; Shaffer 1995; Aickin & Gensler 1996) were used to evaluate significance.

Spearman's and Pearson's correlation coefficients were both applied within the Mantel tests and gave almost identical results. Pearson's r is presented in the results. It is plotted against geographical distance between sites in a Mantel correlogram (Legendre & Fortin 1989). Mantel correlograms were plotted using the *mgram* function of *ecodist* package (Goslee & Urban 2007) in R (R Core Team 2012).

Table 8. 2 Interpretation of p-values derived from significance testing across entire dataset and within blocks defined by spatial location in Mantel, Procrustes and envfit tests

Relative values	p_{entire}	p_{blocks}	Interpretation
$p_{\text{entire}} = \text{or } > \text{ or } < p_{\text{blocks}}$	>0.05	>0.05	No correlation between bee and plant composition at $p=0.05$
$p_{\text{entire}} = \text{or } > p_{\text{blocks}}$	$<0.05 *$	$<0.05 *$	Significant correlation between bee and plant composition and it is not dependent upon sampling location.
$p_{\text{entire}} > p_{\text{blocks}}$	>0.05	$<0.05 *$	Significant correlation between bee and plant composition and it is not dependent upon sampling location.
$p_{\text{entire}} < p_{\text{blocks}}$	$<0.05 *$	>0.05	The correlation between bee composition and vegetation composition may be due to sampling location.
$p_{\text{entire}} < p_{\text{blocks}}$	$<0.05 *$	$<0.05 *$	The correlation between bee composition and vegetation composition can be decomposed into a partial spatial effect plus an effect that is independent of location.

MANTEL TEST

Correlations between plant composition of grasslands and of hedgerows and solitary bee composition and then bumblebee composition were analysed using Mantel's test to compare their respective distance matrices. The *mantel* function of ecodist package (Goslee & Urban 2007) was used. The distribution of distances in the vegetation Bray-Curtis distance matrix and bee Jaccard distance matrices are not completely Gaussian, and so Spearman's correlation test results are presented.

The significance of the Mantel correlation statistic was evaluated by permutations of the rows and columns of the first dissimilarity matrix, which was the bee matrix in every analysis.

Permutation tests (9999 permutations) were carried out in two ways: across the entire dataset, giving p_{entire} and within 'strata' or 'blocks' giving p_{blocks} . There were four blocks corresponding to four local areas sampled: West Tipperary, West Limerick, Central Limerick and East Limerick.

The p-values derived from both permutation tests were compared and interpreted as shown in Table 8.2. This method allowed correlations between

vegetation and bee assemblage to be separated into those potentially influenced by sampling location and those that were independent of sampling location. The approach may fail to detect such effects if they occur at a finer scale than represented by the 'local area' blocks.

PROCRUSTES TEST

The solitary bee and bumblebee NMDS solutions were each compared with the grassland vegetation NMDS and hedgerow vegetation NMDS using symmetric Procrustes rotations (Mardia *et al.* 1979). This method rotates one matrix to maximum similarity with the target matrix and is at least as powerful as the Mantel test (Peres-Neto & Jackson 2001). The *protest* function of vegan (Oksanen *et al.* 2013) was used in R for these analyses.

The significance of the Procrustes correlation coefficient was evaluated by a process similar to permutation testing. The Procrustes rotation was carried out repeatedly and the correlation statistic recalculated each time to estimate its significance. This repeat testing was across the entire dataset and within blocks defined by sampling location. This allowed correlations between vegetation and bee assemblage to be separated into those potentially influenced by sampling location and those that were independent of sampling location (see Table 8.2).

8.2.4. PARTIAL MANTEL ANALYSIS

The *mantel* function of ecodist package (Goslee & Urban 2007) was used for the following Partial Mantel tests. p-values were not corrected for multiple testing in these partial tests.

PARTIALLYING OUT THE SPATIAL EFFECT FROM BEE-VEGETATION CORRELATIONS

Partial Mantel tests (Legendre & Legendre 1998) were used to partial out the contribution of distance between sites to correlations between bee composition (solitary bees, bumblebees) and vegetation (grassland, hedgerow) composition. The sizes of correlation coefficients for these partial Mantel tests were compared with the correlation between bee composition and vegetation composition when spatial location was not a conditioning variable. A

reduction in the strength of correlation between bee composition and vegetation when space was used as a conditioning matrix was interpreted to mean that the correlation with vegetation was also associated with a correlation with space.

PARTIALLING OUT THE EFFECTS OF VEGETATION FROM BEE-SPACE CORRELATIONS

Partial Mantel tests were also used to partition out the contribution of vegetation to the correlations between bee composition (solitary bees, bumblebees) and geographical distance between sites. The sizes of correlation coefficients for these partial Mantel tests were compared with the correlation between bee composition and space when vegetation was not a conditioning variable. A reduction in the strength of correlation between bee composition and space when vegetation was used as a conditioning matrix was interpreted to mean that the correlation with space was also associated with a correlation with vegetation.

PARTIAL MANTEL CORRELOGRAMS

The previous partial Mantel test conditioned upon space removed only the linear component of spatial variation from across the entire range of distances (Goslee & Urban 2007). Partial Mantel correlograms, a further extension of the Mantel test, were used to examine correlations between vegetation and bee composition taking into account *nonlinear* spatial effects (Goslee & Urban 2007; Matesanz *et al.* 2011).

In these analyses, the complete range of distances is divided into intervals using Sturge's rule (Legendre & Legendre 1998). Partial Mantel tests are conducted upon subsets of the data matrices, which are generated for each distance interval. Although the partial Mantel Correlogram may be regarded as experimental in that it has not undergone rigorous testing for statistical properties, it builds upon a well-established statistical foundation and has been peer reviewed (Feb 2012, pers. comm. Dr. Sarah Goslee, Ecologist, USDA-ARS and author of Ecodist package (Goslee & Urban 2007)). The function *pmgram* of ecodist (Goslee & Urban 2007) was used for these analyses.

PARTIALLING THE EFFECTS OF VEGETATION FROM BEE-SPACE

The dependence of spatial patterning in bee composition upon vegetation composition was analysed by treating vegetation composition as the conditional effect. The partial Mantel correlogram process involves conducting a Mantel analysis of bee composition on vegetation composition and extracting the residuals from this analysis. A correlogram is then conducted on the residuals. If the residuals showed spatial pattern, then this was the portion of the bees' spatial patterning that could not be explained by vegetation.

The resulting partial correlograms were compared with bee correlograms, with no partial effects removed, produced in (i) and differences in strength of correlation coefficients noted. If differences were found, these were regarded as being due to associations between bee and vegetation composition.

PARTIALLING THE EFFECTS OF SAMPLING LOCATION FROM BEE-SPACE

I investigated whether patches of similar bee assemblages located at particular inter-site distances and observed as peaks on correlograms were caused by sampling location or reflected other spatial patterning.

A distance matrix was generated to describe which of the four sampling locations Tipperary, West Limerick, Central Limerick and East Limerick each site was in. In the distance matrix, 'zeros' meant samples were from the same location and 'ones' meant they were from different locations. The effects of sampling location were partialled out from the correlations between bee composition (solitary bees, bumblebees) and geographical distance between sites. The Partial Mantel Correlograms for solitary bees and for bumblebees, conditioned by sampling location, were compared with the Mantel Correlograms for solitary bees and for bumblebees.

ROTATIONAL VECTOR FITTING

CORRELATIONS BETWEEN VEGETATION INDICES AND BEE COMPOSITION

Vegetation indices were related to the bee NMDS ordinations in an indirect gradient analysis (Ter Braak & Prentice 1988; Ter Braak & Prentice 2004) using rotational vector fitting (Faith & Norris 1989). The *envfit* function of

vegan (Oksanen *et al.* 2013) was used in R (R Core Team 2012). This function projected the environmental variables, in this case the vegetation indices, into the bee ordination space while ensuring that the vegetation indices had maximal correlations with the bee ordination configuration. The strength and direction of correlations were visualised by plotting them as arrows onto the ordination plots. Permutation testing, based on 1,000 random permutations of the data, was used to evaluate the significance of the correlation coefficient and determine a 'goodness of fit' statistic. Permutation testing was carried out across the entire dataset and within blocks defined by location, giving p_{entire} and p_{blocks} so that effects of sampling location upon the correlations could also be detected (see Table 8.2).

IDENTIFICATION OF SPECIES INFLUENTIAL IN BEE - PLANT CORRELATIONS

PLANT SPECIES CORRELATED WITH BEE COMPOSITION

In order to identify plant species that were significantly correlated with bee composition the abundance of individual plant species were treated as environmental variables. Plant species abundances were transformed ($\log_{10} + 1$) before they were correlated with the bee NMDS solutions. The envfit correlation coefficient was used. Permutation tests for significance values were conducted across the entire dataset and also within strata defined by sampling location, giving p_{entire} and p_{blocks} (see Table 8.2).

BEE SPECIES CORRELATED WITH PLANT COMPOSITION

To identify which bee species were associated with plant composition, each bee species was treated as an environmental variable and its correlation with the vegetation NMDS tested. Transformed counts ($\log_{10} (x+1)$) of the frequently occurring bees, which occurred at four or more sites (nineteen species of solitary bees and nine bumblebees (counting *B. lucorum* species group as one species)), were included in this analysis. These were correlated with the plant NMDS solutions using envfit correlation. Permutation tests were conducted across the entire dataset and also within strata defined by sampling location, giving p_{entire} and p_{blocks} (see Table 8.2).

8. 3. RESULTS

8.3.1. PRELIMINARY EXPLORATION

Solitary bee assemblages tended to be more dissimilar than bumblebee assemblages, regardless of the geographical distance between sites (Figure 8.2).

The relationships between assemblage dissimilarity and geographical distance between sites were weak but highly significant for solitary bees and bumblebees (solitary bees, $R^2 = 0.03$, $p < 0.001$; bumblebees, $R^2 = 0.01$, $p < 0.001$).

8.3.2. MANTEL CORRELOGRAMS TO EXAMINE SPATIAL EFFECTS ON BEES AND VEGETATION COMPOSITION.

Legendre & Legendre (1998) recommend that the correlogram is interpreted only up to distances when all study sites are included in the distance. For this dataset, this is up to 30km.

Significant spatial pattern exists in the assemblage composition of each community studied; that is bumblebees, solitary bees, grassland vegetation and hedgerow vegetation (Figure 8.3, Table 8.3).

Patches of similar solitary bee composition are indicated by the correlogram to be approximately 10km across. Patches of similar hedgerow vegetation are shown to be the same size.

The situation for grassland vegetation and bumblebee assemblages at the shortest inter-site distances (<2.9km) was unusual. At these short inter-site distances the similarity of each assemblage did not differ significantly from that of two randomly placed sites. Yet at greater distances, from 2.9-8.6km, the similarity of bumblebees or grassland was significantly different than would be expected from a random sample. Bumblebee assemblages became gradually more dissimilar as distance between sites increased. For solitary

bees, the correlogram pattern approached that of a ‘narrow wave’ (Legendre & Fortin 1989), with sites becoming rapidly dissimilar after 10km and then becoming significantly more similar again at 20km. Whereas bees and hedgerow vegetation showed strong negative autocorrelation at long inter-site distances, grassland vegetation did not. However since this difference was observed at distances beyond 30km at which all sites were not included in the analysis it requires further investigation to determine if it is a genuine pattern.

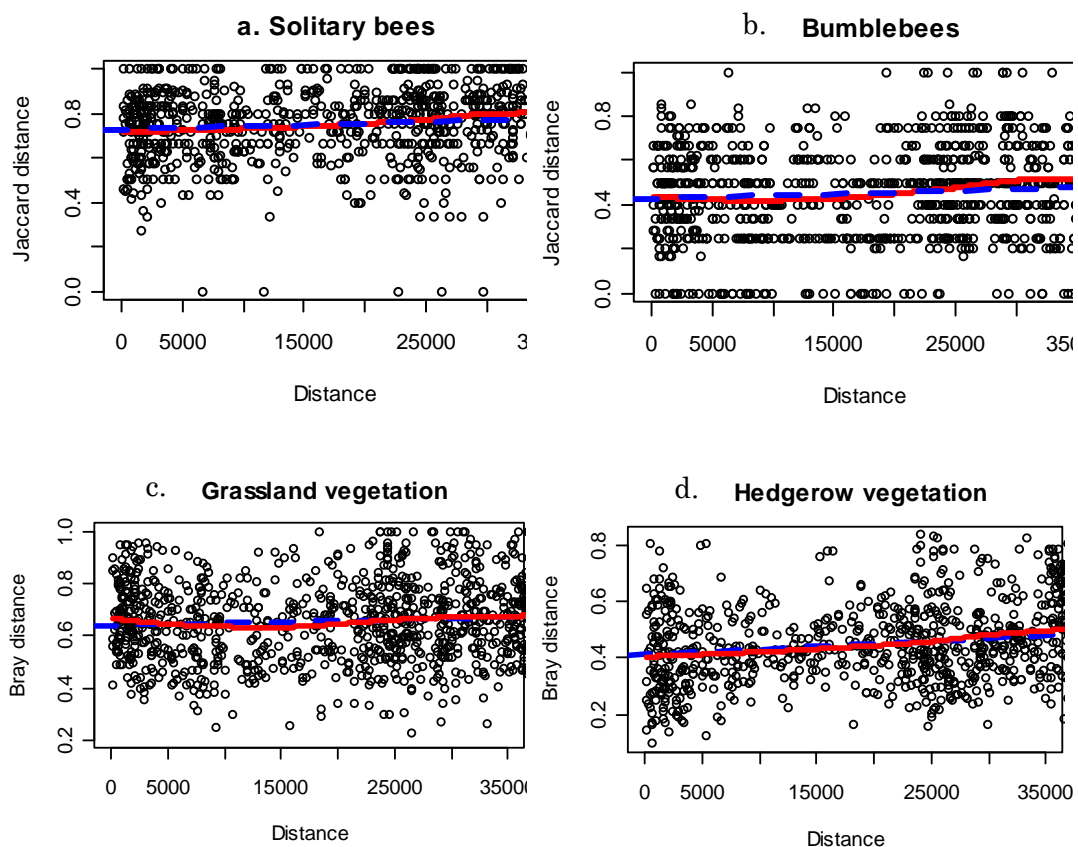


Figure 8.2. Plots showing ecological distances against geographical distance (m) for solitary bees, bumblebees, grassland and hedgerow vegetation. Smaller values of Jaccard and Bray distances indicate higher similarity between species assemblages at two sites. Blue dashed line shows simple linear regression and red line shows Loess smoother.

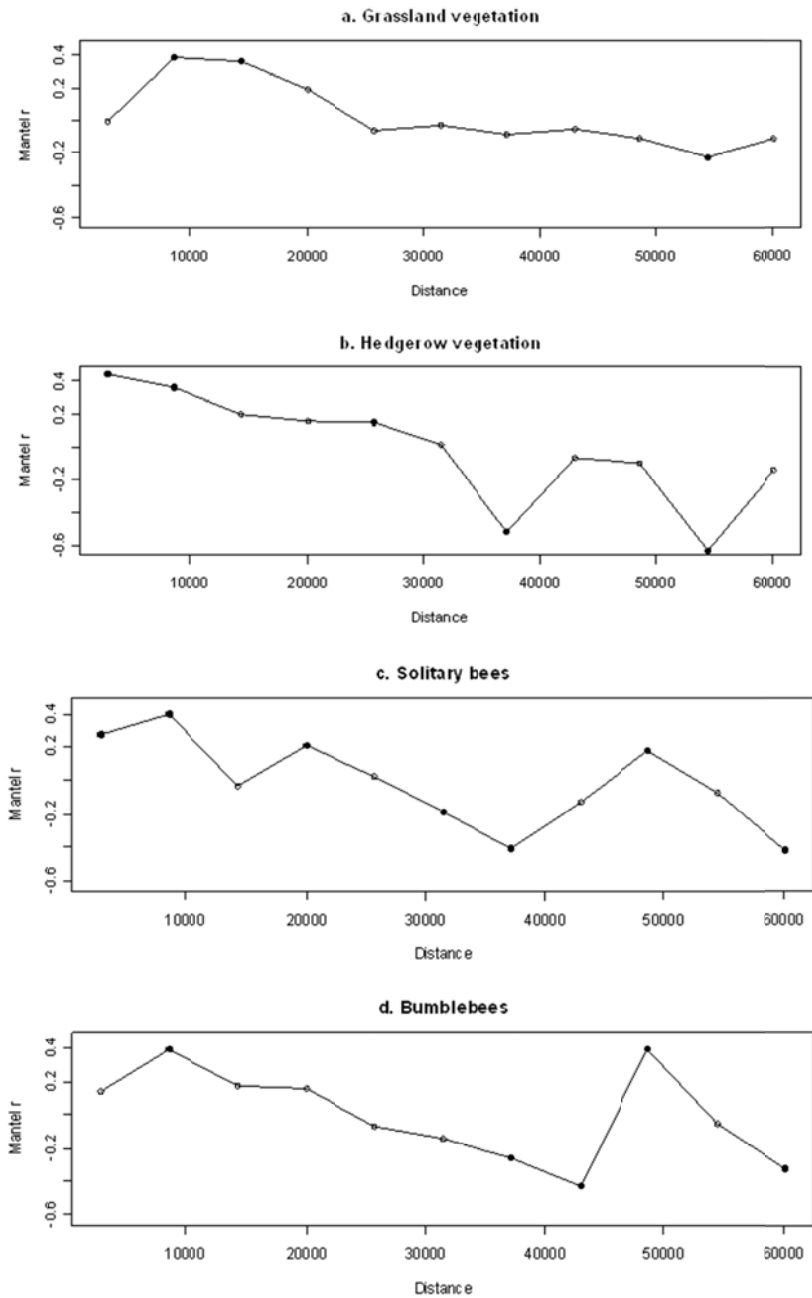


Figure 8.3. Mantel correlograms for (a) grassland vegetation, (b) hedgerow vegetation, (c) solitary bee assemblages and (d) bumblebee assemblages. Positive values of the Mantel correlation coefficient indicate that assemblages are more similar (positive autocorrelation) than expected for randomly associated pairs of observations and negative values mean that assemblages are less similar than expected for randomly associated pairs of observations (negative autocorrelation). Solid symbols indicate significant correlations between changing bee composition and geographical distance at $p=0.05$. See Table 8.3 for more detail.

Table 8. 3 Mantel coefficients and p-values for species similarity of solitary bees, bumblebees, grassland vegetation and hedgerow vegetation regressed upon geographic distance in intervals in the correlograms of Figure 8.3. P-values that were significant at $\alpha=0.05$ are highlighted in bold and those that were also significant using Holm's test are highlighted in grey.

Geographical distance		Solitary Bees			Bumblebees		
Interval	lag [km]	ngroup	Mantel r	pval	ngroup	Mantel r	pval
[1]	2.87	206	0.28	0.0002	213	0.14	0.071
[2]	8.60	108	0.40	0.0001	110	0.39	0.0001
[3]	14.33	76	-0.03	0.803	80	0.18	0.143
[4]	20.06	96	0.21	0.039	100	0.16	0.119
[5]	25.79	163	0.02	0.752	181	-0.07	0.325
[6]	31.52	132	-0.19	0.024	160	-0.14	0.060
[7]	37.25	128	-0.40	0.0001	169	-0.26	0.003
[8]	42.99	82	-0.13	0.258	85	-0.43	0.001
[9]	48.72	149	0.18	0.046	149	0.39	0.0003
[10]	54.45	105	-0.07	0.505	105	-0.05	0.679
[11]	60.18	129	-0.42	0.0001	129	-0.32	0.005

Geographical distance		Grassland vegetation			Hedgerow vegetation		
Interval	lag [km]	ngroup	Mantel r	pval	ngroup	Mantel r	pval
[1]	2.87	213	0.00	0.974	182	0.44	0.0001
[2]	8.60	110	0.38	0.0002	78	0.36	0.002
[3]	14.33	80	0.37	0.001	61	0.20	0.174
[4]	20.06	100	0.19	0.058	84	0.16	0.135
[5]	25.79	181	-0.06	0.399	155	0.15	0.043
[6]	31.52	160	-0.03	0.672	131	0.01	0.882
[7]	37.25	169	-0.08	0.297	138	-0.52	0.0001
[8]	42.99	85	-0.05	0.644	62	-0.07	0.604
[9]	48.72	149	-0.11	0.220	115	-0.10	0.377
[10]	54.45	105	-0.22	0.043	93	-0.64	0.000
[11]	60.18	129	-0.11	0.261	122	-0.15	0.168

8.3.3. CORRELATIONS BETWEEN COMPOSITION OF BEE ASSEMBLAGES AND VEGETATION

Table 8. 4 Multivariate correlations of solitary bee and bumblebee composition with the botanical composition of grassland (solitary bees, n=53; bumblebees, n=55) and hedgerow (solitary bees, n=48; bumblebees, n=50) vegetation, given sampling location and space between sampling sites, examined using Procrustes rotations and Mantel tests. Permutation tests were across the entire dataset giving **P_{entire}** and within blocks determined by sampling location giving **P_{blocks}**.

Bee Matrix	Environmental Matrix	Conditioning Matrix	Analysis	Correlation coefficient, r	P _{entire}	P _{blocks}
Solitary bees	Grassland veg.	None	Procrustes	0.28	0.034	0.184
	Grassland veg.	None	Mantel	0.10	0.063	0.219
	Grassland veg.	Space	Partial	0.07	0.110	NA
			Mantel			
	Space	Grassland veg.	Partial	0.16	0.0001	NA
			Mantel			
	Hedgerow veg.	None	Procrustes	0.35	0.006	0.073
	Hedgerow veg.	None	Mantel	0.11	0.058	0.138
	Hedgerow veg.	Space	Partial	0.07	0.180	NA
			Mantel			
	Space	Hedgerow veg.	Partial	0.14	0.0004	NA
			Mantel			
Bumblebees	Space	None	Mantel	0.17	0.0001	NA
	Location	None	Mantel	0.16	0.0001	NA
	Location	Space	Partial	0.05	0.131	NA
			Mantel			
	Space	Location	Partial	0.08	0.061	NA
			Mantel			
	Grassland veg.	None	Procrustes	0.22	0.143	0.148
	Grassland veg.	None	Mantel	0.01	0.395	0.594
	Grassland veg.	Space	Partial	-0.002	0.500	NA
			Mantel			
	Space	Grassland veg.	Partial	0.11	0.003	NA
			Mantel			
Bumblebees	Hedgerow veg.	None	Procrustes	0.35	0.009	0.043
	Hedgerow veg.	None	Mantel	0.06	0.208	0.352
	Hedgerow veg.	Space	Partial	0.02	0.380	NA
			Mantel			
	Space	Hedgerow veg.	Partial	0.12	0.002	NA
			Mantel			
	Space	None	Mantel	0.13	0.0007	NA
	Location	None	Mantel	0.09	0.004	NA
	Location	Space	Partial	0.02	0.363	NA
			Mantel			
	Space	Location	Partial	0.06	0.132	NA
			Mantel			

SOLITARY BEES AND VEGETATION, GIVEN SAMPLING LOCATION AND SPACE

Solitary bee assemblages were significantly correlated with grassland vegetation and hedgerow vegetation composition upon significance testing of the Procrustes correlation coefficient across the entire dataset (Table 8.4). However when sampling location was taken into account, with permutations in blocks, the p-values increased and were no longer significant. Mantel's test was more conservative and gave a smaller correlation coefficient and p_{entire} value just above the significance level of 0.05. Permutation testing within blocks also had the effect of increasing the p-value. The correlation between grassland plant assemblages and solitary bees was more dependent upon sampling location than that of hedgerow assemblages.

Partial Mantel tests showed correlations between solitary bee composition and grassland vegetation or hedgerow vegetation were insignificant when the effects of sampling location were 'removed'.

The strength of correlations between solitary bee composition and space were strong and highly significant. Removing the effects of grassland or hedgerow vegetation in Partial Mantel tests only slightly reduced the correlation between space and bee composition. The major part of the solitary bee-space correlation was therefore not determined by vegetation composition.

BUMBLEBEES AND VEGETATION, GIVEN SAMPLING LOCATION AND SPACE

Procrustes and Mantel tests showed no correlations between bumblebee composition and grassland vegetation (Table 8.4).

A significant correlation between bumblebee composition and hedgerow vegetation was shown by the Procrustes test. Interpretation of the two p-values from permutation tests ($p_{\text{entire}} < p_{\text{blocks}}$ and both were <0.05) (see Table 8.2), indicated that the correlation was partly associated with location.

Location (i.e. sampling location) and space (i.e. distance between sites) were both strongly correlated with bumblebee composition.

Including grassland or hedgerow vegetation as conditional effects in partial Mantel tests, reduced the correlation between bumblebee composition and space very slightly. The correlation between bumblebee composition and location was therefore not determined by vegetation composition.

8.3.4. PARTIAL MANTEL CORRELOGRAMS

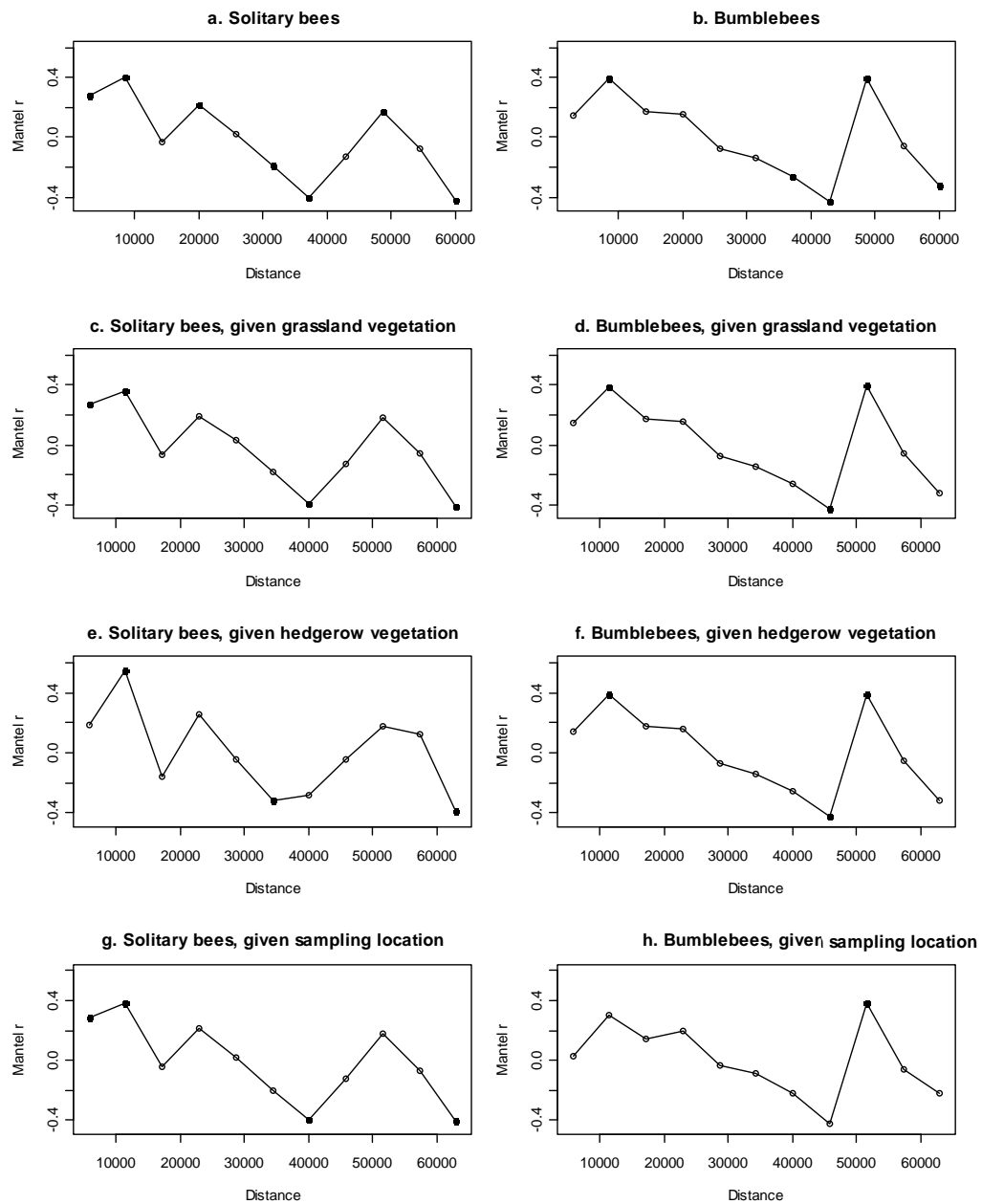


Figure 8.4. Partial Mantel Correlograms for solitary bees and bumblebees given vegetation and sampling location. Solid symbols indicate significant correlations between changing bee composition and geographical distance at $p=0.05$. See Table 8.5 for more detail.

Table 8. 5 Mantel coefficients and p-values for species similarity of (i) solitary bees and (ii) bumblebees regressed upon geographic distance, given grassland and hedgerow vegetation as in the correlograms of Figure 8.4. P-values that are significant at $\alpha=0.05$ are highlighted in bold and those that are also significant using Holm's test are highlighted in grey.

(i) Solitary bees

Geographical distance			~ Space		~ Space, given grassland vegetation		~ Space, given hedgerow vegetation		~ Space, given location	
Interval	lag (km)	ngroup	r	pval	r	pval	r	pval	r	pval
1	2.87	206	0.28	0.0001	0.27	0.010	0.19	0.122	0.00	0.939
2	8.60	108	0.40	0.0001	0.36	0.015	0.55	0.003	0.17	0.242
3	14.33	76	-0.03	0.795	-0.06	0.715	-0.16	0.409	-0.13	0.535
4	20.06	96	0.21	0.034	0.19	0.216	0.26	0.137	0.29	0.040
5	25.79	163	0.02	0.750	0.03	0.779	-0.05	0.713	0.08	0.525
6	31.52	132	-0.19	0.023	-0.18	0.172	-0.32	0.026	-0.10	0.434
7	37.25	128	-0.40	0.0001	-0.39	0.009	-0.28	0.081	-0.30	0.040
8	42.99	82	-0.13	0.257	-0.13	0.482	-0.05	0.821	-0.03	0.859
9	48.72	149	0.18	0.054	0.18	0.219	0.17	0.295	0.28	0.081
10	54.45	105	-0.07	0.496	-0.06	0.762	0.12	0.486	0.03	0.838
11	60.18	129	-0.42	0.0001	-0.41	0.010	-0.39	0.020	-0.32	0.061

(ii) Bumblebees

Geographical distance			~ Space		~ Space, given grassland vegetation		~ Space, given hedgerow vegetation		~ Space, given location	
Interval	lag (km)	ngroup	r	pval	r	pval	r	pval	r	pval
1	2.87	213	0.14	0.070	0.14	0.246	0.18	0.179	0.02	0.828
2	8.60	110	0.39	0.0003	0.39	0.029	0.39	0.064	0.30	0.111
3	14.33	80	0.18	0.141	0.17	0.406	0.19	0.407	0.14	0.475
4	20.06	100	0.16	0.122	0.16	0.383	0.16	0.399	0.20	0.313
5	25.79	181	-0.07	0.328	-0.07	0.594	-0.03	0.821	-0.03	0.778
6	31.52	160	-0.14	0.055	-0.14	0.307	-0.13	0.355	-0.09	0.535
7	37.25	169	-0.26	0.002	-0.26	0.097	-0.32	0.030	-0.22	0.162
8	42.99	85	-0.43	0.0004	-0.43	0.037	-0.40	0.065	-0.43	0.051
9	48.72	149	0.39	0.0004	0.39	0.028	0.39	0.047	0.38	0.030
10	54.45	105	-0.05	0.678	-0.05	0.812	-0.13	0.539	-0.06	0.848
11	60.18	129	-0.32	0.005	-0.32	0.100	-0.24	0.225	-0.22	0.313

The pattern of peaks in the bee correlograms remained despite removal of the variance associated with hedgerow vegetation, grassland vegetation and sampling location. This suggests that there remains spatial patterning in bee assemblages that is not accounted for by vegetation or sampling location.

A reduction in Mantel test correlation coefficients (for intervals over which bees were significantly correlated with space) occurred for solitary bees with the partialling out of the contribution of hedgerow vegetation. This indicates that hedgerow vegetation contributed to the spatial correlations of solitary bees. Grassland vegetation did not contribute to the spatial correlations of solitary bees.

Grassland and hedgerow vegetation were judged to have a negligible influence upon the spatial patterning of bumblebees. Correlation coefficients, for intervals over which bumblebees were significantly correlated with space, were unchanged by the inclusion of either vegetation's composition as a conditional effect (Figure 8.4 and Table 8.5).

The strength of correlation coefficients between bee composition and space were reduced upon the inclusion of sampling location as a partial effect. However the overall pattern of peaks in the correlograms remained similar implying that sampling location did not explain all spatial pattern and that distance between sampling points was also important.

8.3.5. ROTATIONAL VECTOR FITTING: CORRELATIONS BETWEEN VEGETATION INDICES AND BEE COMPOSITION

Grassland and hedgerow indices were significantly correlated with solitary bee composition. In contrast to the significant correlations between vegetation and solitary bee composition detected using Procrustes and Mantel's test, these correlations were scarcely dependent on spatial location ($p_{\text{blocks}} < 0.05$ and did not rise much compared to p_{entire}). The significantly correlated indices were therefore describing attributes of the vegetation composition, of importance to solitary bees, which were far less dependent on geographical location than vegetation composition considered as a species-abundance matrix.

Grassland vegetation's Complement of the Simpson's Index and Ellenberg value for soil moisture were significantly correlated with solitary bee

composition, regardless of sampling location. The Inverse Simpson's Index for hedgerow vegetation was also significantly correlated with solitary bee composition, as was the number of woody species, though less strongly. These results highlight two important dimensions of plant composition for solitary bees: species diversity and soil moisture gradients.

The majority of solitary bee species were clustered at lower values of the sward Ellenberg value for soil moisture, indicating an association with drier grasslands (Figure 8.5 [A]). However the range of Ellenberg soil moisture values was narrow, from approximately 5 to 6. A score of 5 is already considered to be a moist-site indicator (Hill *et al.* 1999). Bees that were associated with wetter conditions were *Andrena scotica*, *Sphecodes ephippius*, *Lasioglossum albipes* and *L. calceatum*. Species associated with drier conditions were *Lasioglossum leucopus*, *Nomada ruficornis* and *Andrena coitana*.

Increasing botanical diversity of both hedgerows and grasslands were associated with higher solitary bee diversity. The benefits to solitary bees may be via increased forage and nesting opportunities arising directly from this botanical diversity or may be due to an association with less intensive farm management and therefore less habitat disturbance.

The Simpson's indices for both hedgerow and grassland vegetation were more strongly correlated, than species numbers, with solitary bee composition. This suggests that *evenness* as captured by the Simpson's Index, as well as the species number of plants, is of importance to bee assemblage structure.

A more evenly structured plant community would be likely to provide a steadier progression of flowers for forage throughout the summer. This would benefit solitary bees with longer flight periods. The centroids of all observed *Nomada* species, which have relatively long flight periods, were projected to the ordination space correlated with greater botanical diversity.

Some species of solitary bee appeared to tolerate lower values of botanical diversity e.g. *Lasioglossum cupromicans*, *Andrena denticulata* suggesting that solitary bees may coexist with low vegetation diversity.

Sampling location had a greater effect upon the significance of the correlation of hedgerow Inverse Simpson's Index with solitary bee composition than the grassland Simpson's Index complement (i.e. **p_{blocks}** increased more relative to **p_{entire}** for the hedgerow index.) This difference was interpreted as reflecting a difference in the strength of association between each habitats' vegetation and spatial location. Regional distinctions in hedgerow woody composition have persisted uninfluenced by recent changes in farm management, whereas grasslands are the target of farm management. Their vegetation has become more decoupled from geographical location, with intensely managed grasslands sharing very similar composition.

There was a weak correlation between Inverse Simpson's Index for hedgerow woody vegetation (Table 8.6) and bumblebee composition. The *direction* of this correlation was unexpected (Figure 8.5 [B]) as the majority of species of bumblebee were associated with low values of the index, that is with low diversity hedgerows.

There were no further significant correlations between vegetation indices and bumblebee composition at a significance level of $p \leq 0.05$.

There may be a weak signal that bumblebees are organised along a gradient of semi-natural to heavily fertilised grasslands (the p-value for the correlation between the Ellenberg value for soil nitrogen and the bumblebee composition fell to 0.09 when the effects of sampling location were removed) but this is a tentative observation that would require further investigation.

Table 8. 6 Envfit correlations between vegetation indices and bee composition, with significance testing across entire dataset (**p_{entire}**) and within spatially defined blocks (**p_{blocks}**).

Correlations	Solitary bees			Bumblebees		
	Envfit r^2	p_{entire}	p_{blocks}	Envfit r^2	p_{entire}	p_{blocks}
Grassland Indices						
Species number	0.04	0.322	0.441	0.06	0.230	0.283
Complement of Simpson's Index (1-D)	0.12	0.046	0.048	0.01	0.780	0.770
Ellenberg value for soil moisture	0.13	0.026	0.043	0.003	0.911	0.941
Ellenberg value for soil nitrogen	0.02	0.625	0.548	0.08	0.107	0.091
Ellenberg value for soil pH	0.08	0.142	0.265	0.002	0.949	0.963
Hedgerow Indices						
Species number	0.13	0.045	0.052	0.09	0.138	0.117
Inverse Simpson's Index (1/D)	0.19	0.008	0.010	0.12	0.050	0.052

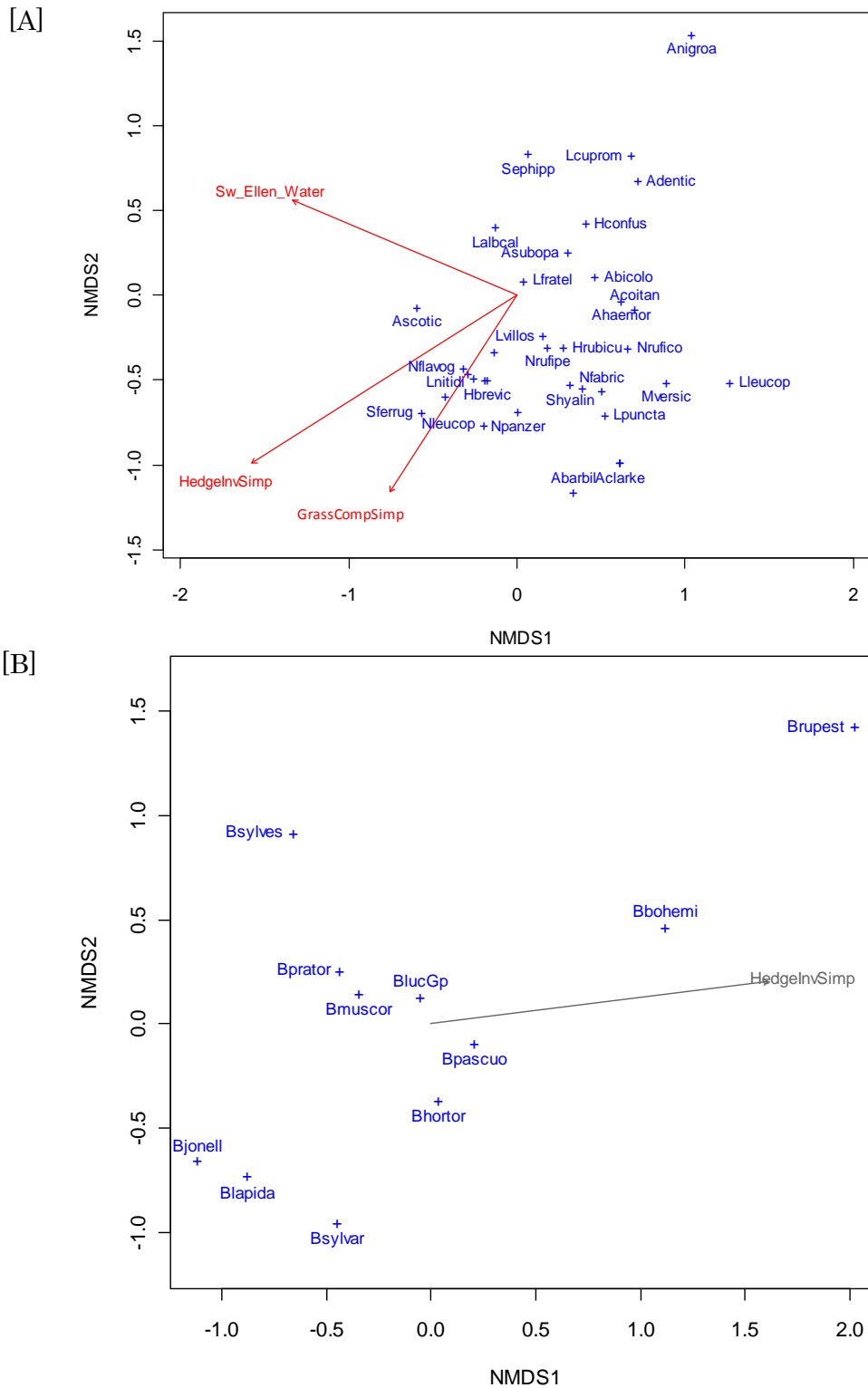


Figure 8.5. Significantly correlated vegetation indices projected onto NMDS ordinations (Jaccard distances for presence-absence data) of [A] solitary bee species (stress=0.19) and [B] bumblebee species (stress= 0.22) (See Appendix 15 for list of species abbreviations) . Arrows show direction and magnitude of significantly correlated vegetation indices (red = $p_{\text{entire}} < 0.05$, grey = $p_{\text{entire}} = 0.05$).

8.3.6. ROTATIONAL VECTOR FITTING: SPECIES INFLUENTIAL IN THE CORRELATIONS BETWEEN BEE AND PLANT ASSEMBLAGES

GRASSLAND PLANT SPECIES CORRELATIONS WITH BEE COMPOSITION

A large number of grassland plants were correlated with solitary bee and bumblebee composition (Figure 8.6 [A]-[D]) (p_{entire} and $p_{\text{blocks}} < 0.05$).

SOIL MOISTURE GRADIENT

Vectors for moisture loving plants e.g. *Ranunculus lingua*, *Cardamine pratense*, *Cirsium palustre*, projected to the left and top-left of the solitary bee ordination plot. Few solitary bee centroids were projected to this area suggesting that most solitary bees cannot tolerate such moist soil conditions. *Andrena scotica* and *Sphecodes ephippus* were an exception. Although the significance level of some moisture loving plants' correlations were reduced upon permutation testing within location blocks (Figure 8.6 [B]) e.g. *Cirsium palustre*, for others, e.g. *Cardamine pratense* and *Ranunculus lingua*, it stayed constant or increased. This shows that a soil moisture gradient was not only a reflection of sampling location but was significant even within a local sampling area.

None of the moisture loving plants were significantly correlated with bumblebee composition. A soil moisture gradient was unimportant in structuring bumblebee assemblage composition.

'SEMI-NATURALNESS' GRADIENT

The abundance of *Agrostis* grasses was significantly correlated with solitary bee composition. Significance increased upon permutation testing within location blocks, showing that the association between such grasslands and solitary bee composition was independent of sampling location. The numbers of bee species clustered at higher levels of *Agrostis* indicate the associated bee assemblage to be diverse. Species with their centroids projected in the same region of the ordination included *Sphecodes ferruginatus*, *Nomada leucophthalma*, *Nomada panzeri* and *Nomada flavoguttata* (Figure 8.6 [A],[B]). These are all parasitic upon other solitary bees and their presence

also indicates the presence of their host species. Species of solitary bee which are considered under threat in Ireland were associated with these grasslands: *S. ferruginatus* is regarded as 'Endangered' and *N. panzeri* as 'Near threatened' (Fitzpatrick *et al.* 2006a).

The opposite end of the *Agrostis* vector was also correlated with a large number of solitary bee species. In this analysis, low abundances or absence of *Agrostis* could indicate either intensely fertilised and reseeded grasslands or other types of semi-natural grassland.

Herbs associated with unimproved, drier, neutral to calcareous grasslands were significantly correlated with bumblebee composition (Figure 8.6 [C],[D]). These included *Centaurea nigra*, *Hypericum perforatum*, *Daucus carota*. Rarer bumblebees e.g. *B. muscorum*, *B. (P.) sylvestris*, *B. sylvarum*, *B. jonellus*, were associated with these plant species, whereas *B. pascuorum*, a more ubiquitous species, was positioned towards the other end of the gradient.

For the majority of plant species, their correlations with bumblebee composition became insignificant when permutation testing was carried out within geographical blocks (Figure 8.6 [D]). This reflects the restricted geographical distribution of some species of plants and bumblebees. A few remained significantly correlated with bumblebee composition and others became significantly correlated upon testing within spatial blocks (Figure 8.6 [D]), e.g. *Leontodon autumnalis*, *Rhinanthus minor*, *Cerastium holosteoides*, *Stellaria graminea* and *Potentilla anserina*. These herbs are indicative of grasslands which are not heavily managed and their correlations with bumblebee composition were not dependent on sampling location.

SUCCESSIONAL STAGE GRADIENT

Analyses suggested that a gradient in the successional stage of grasslands influenced the composition of both solitary bee and bumblebee assemblages. However the sample contained only a few sites that were managed very lightly with little grazing or cutting, to the point where ecological succession was taking place, so the following are therefore preliminary observations that would require further investigation. Plant species that suggested such a gradient were for solitary bees, *Heracleum sphondylium* and for bumblebees,

Pteridium aquilinum and *Rubus fruticosus* ag. *B. lapidarius* and *B. jonellus* appeared to be associated with a mid-stage in grassland succession to scrub.

HEDGEROW TREE AND SHRUB SPECIES CORRELATIONS WITH BEE COMPOSITION

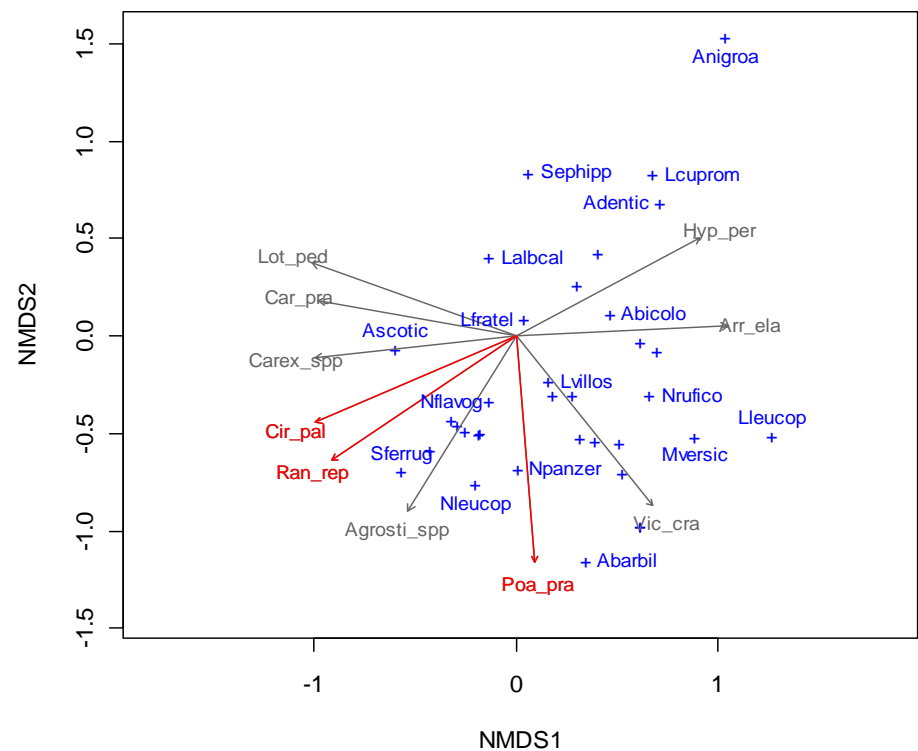
Blackthorn (*Prunus spinosa*) abundance had strong correlations with bumblebee composition (Figure 8.6 [G], Table 8.7) and solitary bee composition (Figure 8.6 [E]). For solitary bees, the correlation of Blackthorn with bee composition was influenced by sampling location ($p_{\text{blocks}} > 0.05$). However for bumblebees, the significance of Blackthorn and other hedgerow plant species' correlations with composition were not affected by sampling location (i.e. there was little difference in p-values whether permutation testing was across entire dataset or within blocks defined by spatial location, $p_{\text{entire}} \approx p_{\text{blocks}} < 0.05$, see Table 8.7).

This difference in influence of sampling location upon significance of hedgerow plant correlations with bee composition could be explained in terms of solitary bees having smaller ranges and occurring in smaller and more discrete patches than bumblebees. Only *Rubus fruticosus* ag. abundance remained significantly correlated with solitary bee composition after sampling location had been taken into account.

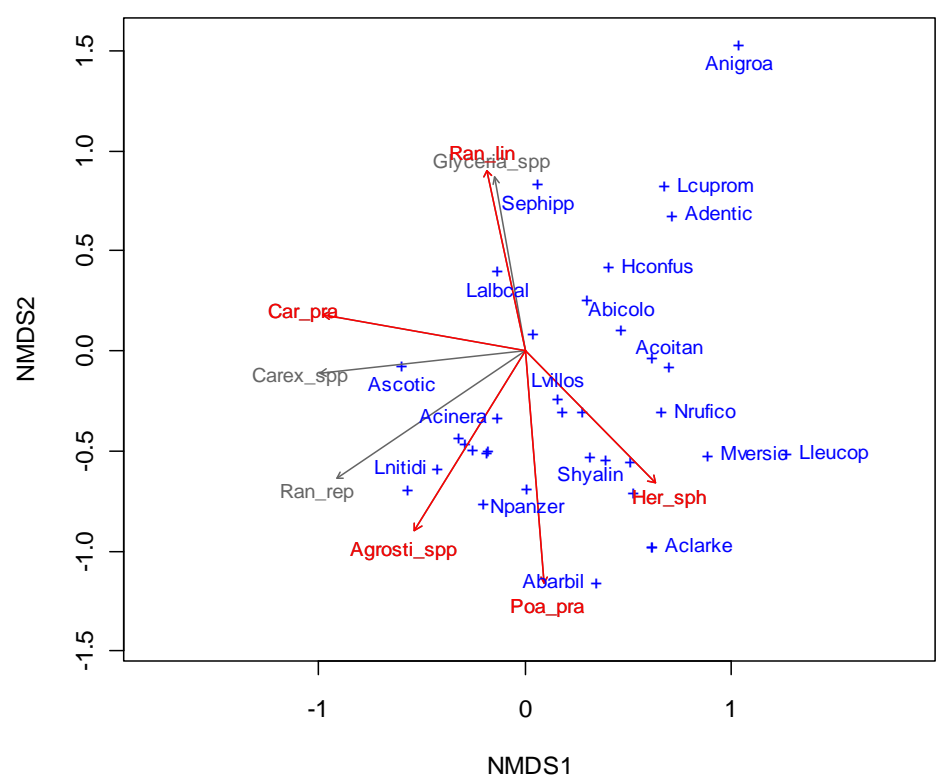
Table 8. 7 Hedgerow plant species correlations with bumblebee NMDS ordination (stress = 0.18).

Hedgerow woody species	Abbreviation	Envfit r^2	p_{entire}	p_{blocks}
<i>Acer pseudoplatanus</i>	Ace_pse	0.13	0.029 *	0.030 *
<i>Alnus glutinosa</i>	Aln_glu	0.03	0.429	0.445
<i>Betula species</i>	Betula_spp	0.01	0.699	0.728
<i>Corylus avellana</i>	Cor_ave	0.07	0.174	0.134
<i>Cotoneaster species</i>	Cotonea_spp	0.02	0.581	0.597
<i>Crataegus monogyna</i>	Cra_mon	0.17	0.019 *	0.012 *
<i>Euonymus europaeus</i>	Euo_eur	0.04	0.389	0.403
<i>Fagus sylvatica</i>	Fag_syl	0.01	0.699	0.728
<i>Fraxinus excelsior</i>	Fra_exc	0.11	0.072 .	0.071 .
<i>Hedera helix</i>	Hed_hel	0.07	0.182	0.178
<i>Ilex aquifolium</i>	Ile_aqu	0.08	0.152	0.149
<i>Ligustrum ovalifolium</i>	Lig_ova	0.08	0.143	0.166
<i>Ligustrum vulgare</i>	Lig_vul	0.09	0.137	0.124
<i>Lonicera periclymenum</i>	Lon_per	0.04	0.365	0.351
<i>Malus species</i>	Malus_spp	0.01	0.791	0.795
<i>Populus species</i>	Populus_spp	0.01	0.816	0.845
<i>Prunus avium</i>	Pru_avi	0.00	0.847	0.828
<i>Prunus domestica</i>	Pru_dom	0.04	0.333	0.320
<i>Prunus spinosa</i>	Pru_spi	0.25	0.001 ***	0.002 **
<i>Quercus species</i>	Quercus_spp	0.02	0.621	0.604
<i>Rosa canina</i>	Ros_can	0.19	0.009 **	0.010 *
<i>Rosa pimpinellifolia</i>	Ros_pim	0.14	0.042 *	0.039 *
<i>Rubus fruticosus ag.</i>	Rub_fru	0.01	0.755	0.746
<i>Rubia peregrina</i>	Rub_per	0.00	0.888	0.889
<i>Salix species</i>	Salix_spp	0.08	0.147	0.145
<i>Sambucus nigra</i>	Sam_nig	0.00	0.93	0.945
<i>Symphoricarpos albus</i>	Sym_alb	0.05	0.307	0.287
<i>Ulex species</i>	Ulex_spp	0.01	0.746	0.728
<i>Ulmus species</i>	Ulmus_spp	0.03	0.483	0.470
<i>Vaccinium myrtillus</i>	Vac_myr	0.01	0.730	0.754

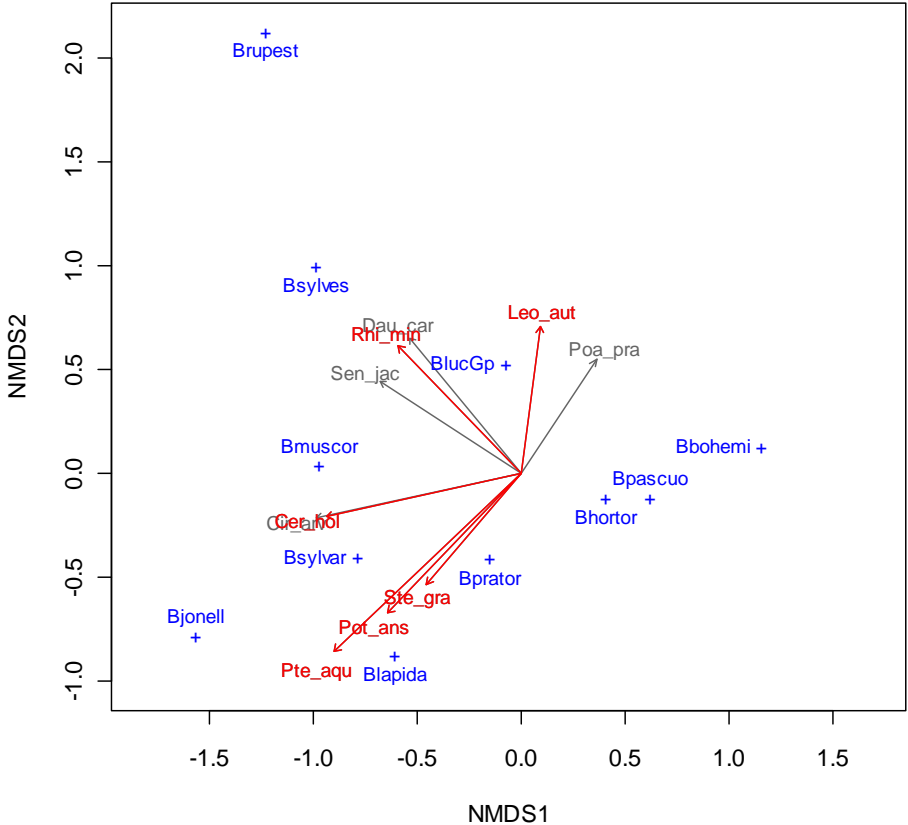
[A] Solitary bees, **p_{entire}**



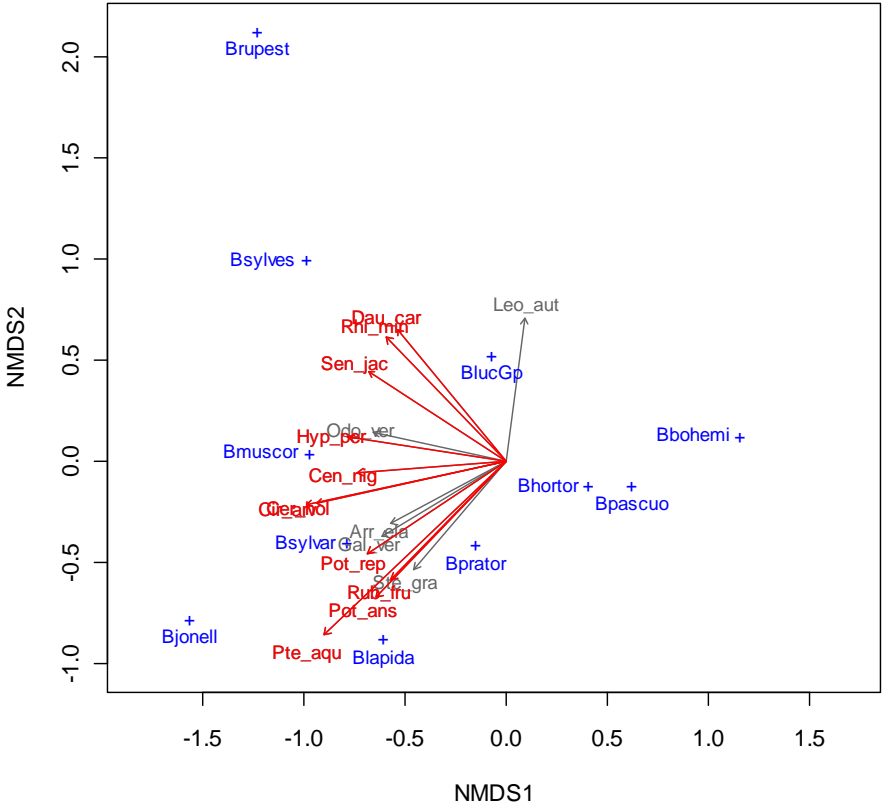
[B] Solitary bees, **p_{blocks}**



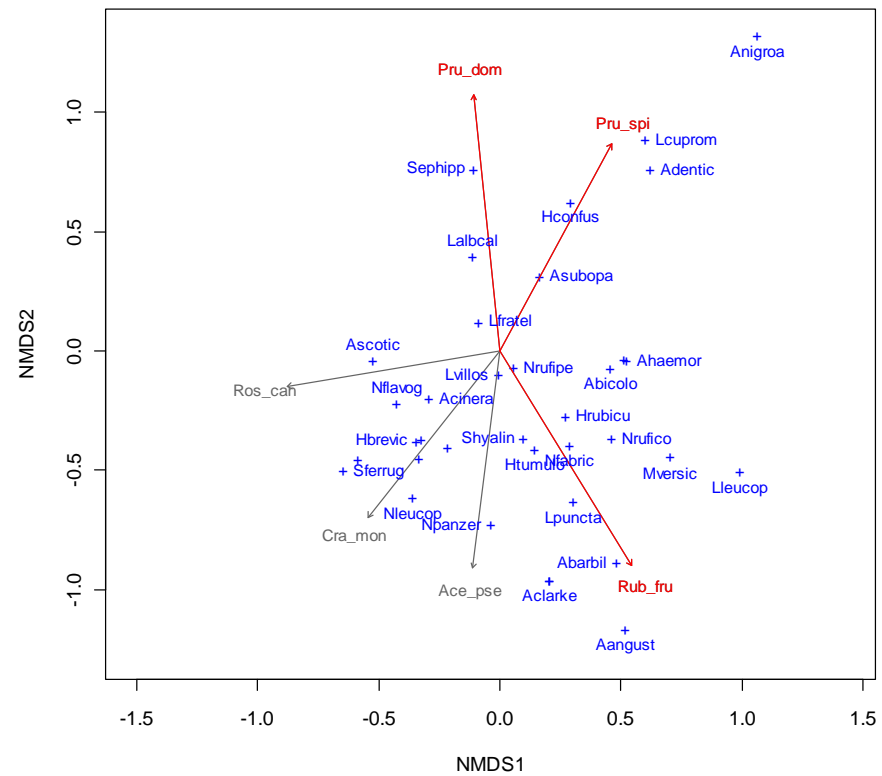
[C] Bumblebees, **p_{entire}**



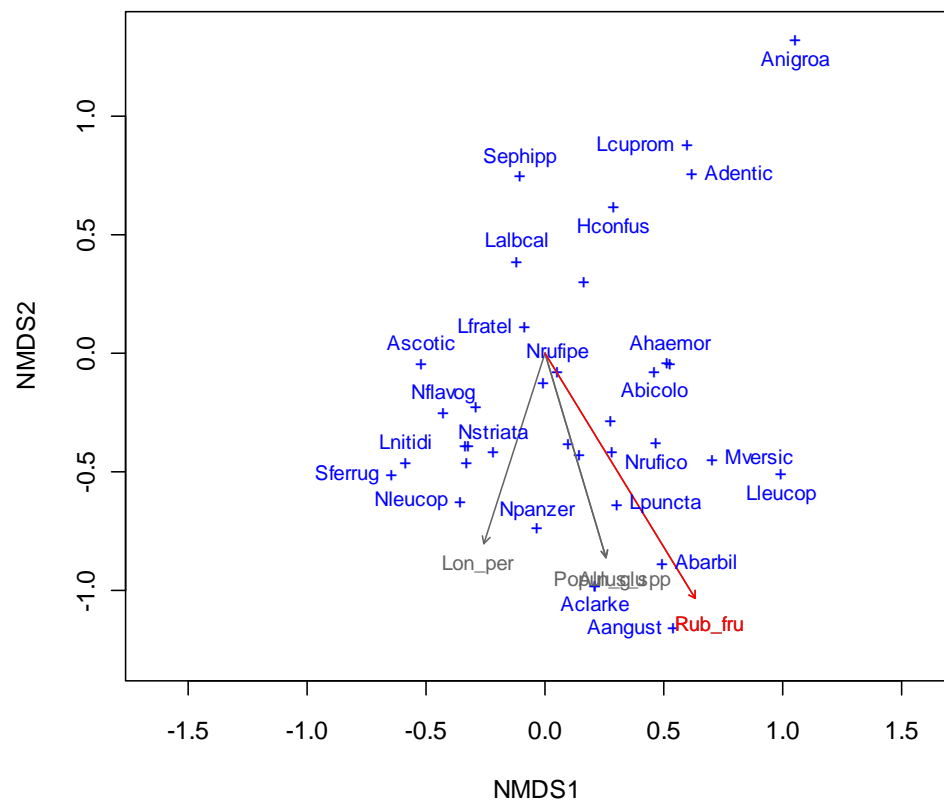
[D] Bumblebees, **p_{blocks}**



[E] Solitary bees, **p_{entire}**



[F] Solitary bees, **p_{blocks}**



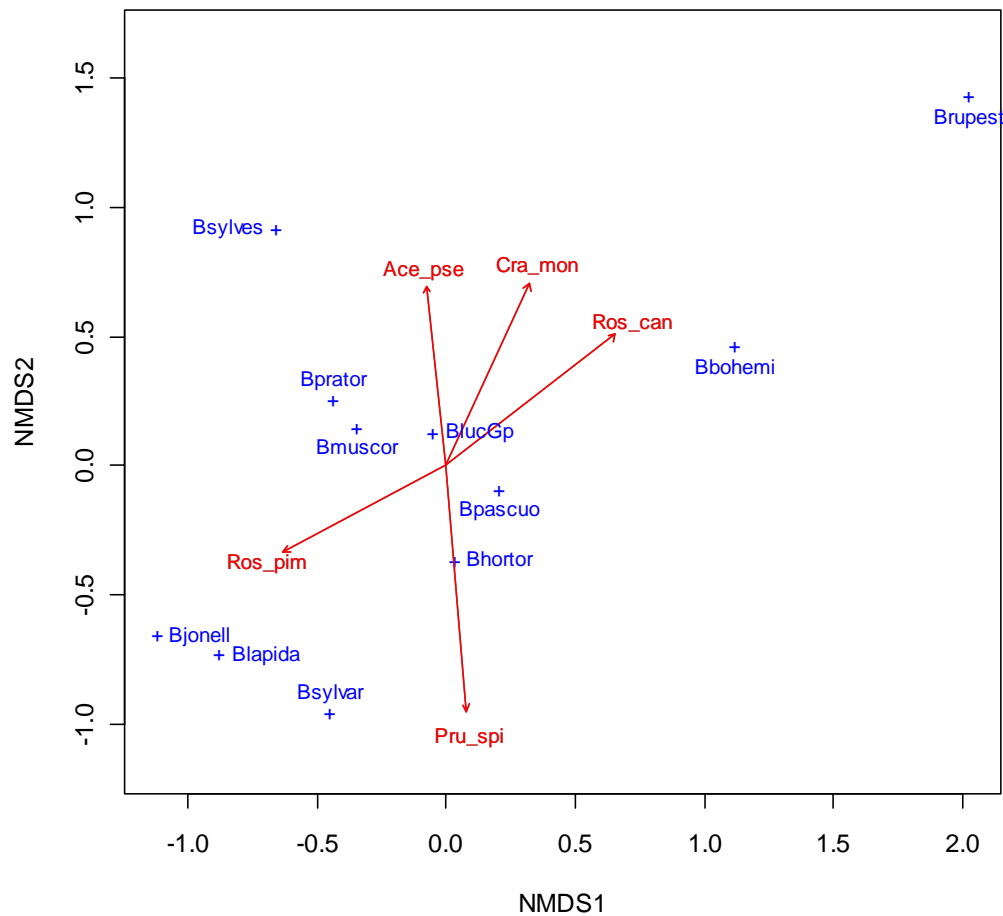


Figure 8.6. [A]-[G]. NMDS ordinations of bee species using Jaccard distances for presence-absence data (stress=0.19 for solitary bees and 0.18 for bumblebees). Arrows show direction and magnitude of correlations of plant species ($\log_{10}(\%cover+1)$) with the bee ordinations. Grey = $p < 0.09$, red = $p < 0.05$. [A]-[D] = grassland plant correlations and [E]-[G] = hedgerow plant correlations. Graph labels show significance testing method as **Pentire** for permutation testing across entire datasets and **Pblocks** for testing within blocks defined by location.

SOLITARY BEE SPECIES CORRELATIONS WITH VEGETATION

No species of solitary bee was significantly correlated with grassland vegetation composition.

Eight species of solitary bee were significantly correlated with the hedgerow plant NMDS when permutation testing was across the entire dataset. For the majority of solitary bee species that were significantly correlated with

hedgerow composition on permutation testing across the entire dataset, that statistical significance vanished when permutation testing was within spatial blocks (compare Figure 8.7 [A] and [B]). This shows the correlation to be specific to particular sampling locations.

For a minority of species: *Andrena haemorrhoa*, *Nomada panzeri*, *Nomada striata*, their correlations with hedgerow composition were significant even when tested within spatial blocks and are therefore not linked with sampling location.

A. haemorrhoa was widespread within the study region. It appears to be associated with relatively species poor hedgerows dominated by *Crataegus monogyna* with *Sambucus nigra* and *Rubus fruticosus* ag. (Figure 8.7).

Although *Nomada panzeri* and *Nomada striata*, are associated with diverse hedgerows with tall tree species, the tree species differed between the bees (Figure 8.7 [B]). *N. striata* was associated with hedgerows with rich mixtures of native tree, shrub and climber species. *Nomada panzeri* was associated with tree and shrub species typical of damp soils e.g. *Alnus glutinosa*, *Prunus avium* and non-native species e.g. *Acer pseudoplatanus*, *Ligustrum ovalifolium*. These species associations could point towards *N. panzeri* having a greater tolerance of human disturbance and damper conditions or both, than *N. striata*.

BUMBLEBEE SPECIES CORRELATIONS WITH VEGETATION

The abundances of widespread and abundant species, such as *B. pascuorum* and *B. pratorum*, were not correlated with vegetation composition.

Four bumblebee species, that are restricted in their distributions across the study region, showed significant correlations with vegetation composition: *B. lapidarius*, *B. muscorum*, *B. jonellus* and *B. sylvarum* (Table 8.8 and Figure 8.7 [C],[D]). The correlation between *B. sylvestris* and hedgerow composition was also close to $p < 0.05$.

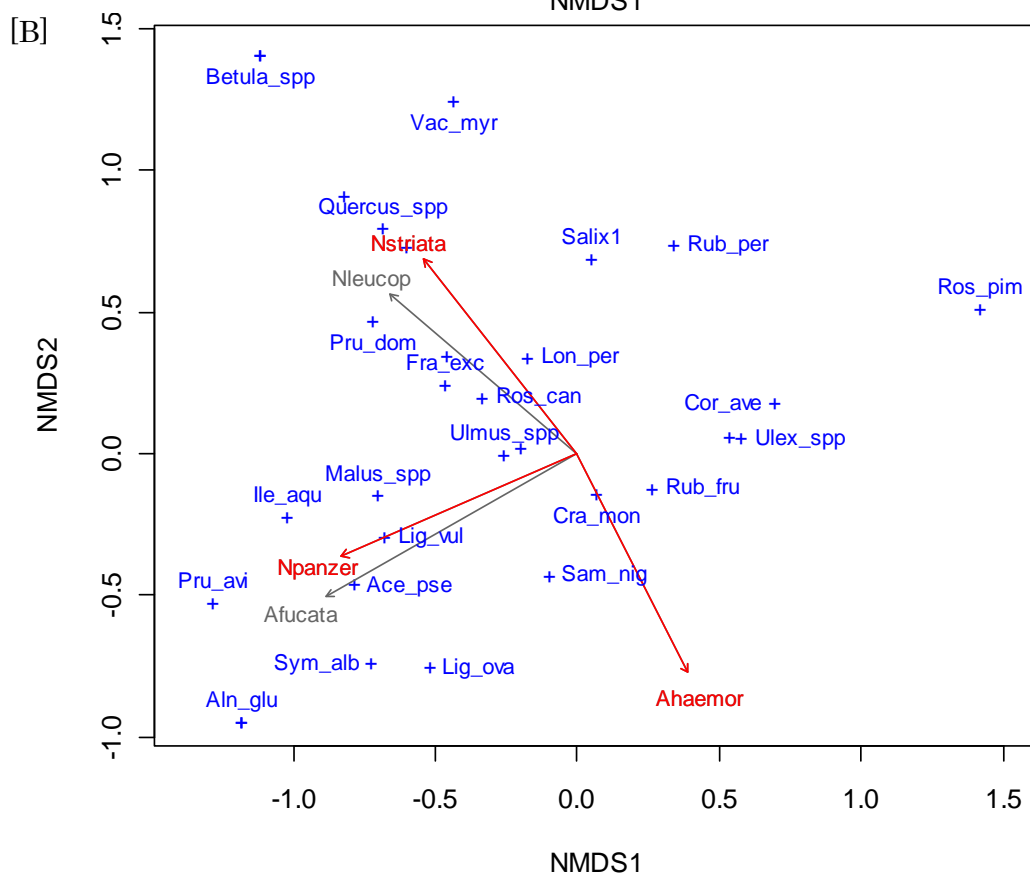
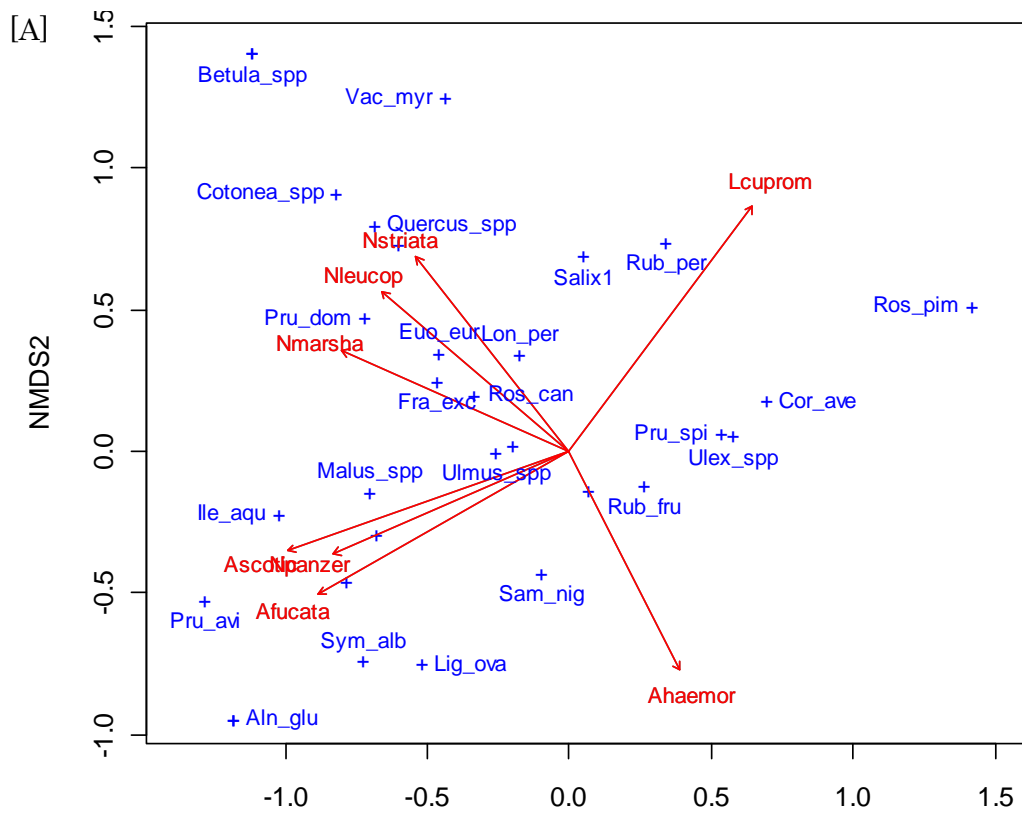
The directions of correlation vectors showed *B. jonellus*, *B. muscorum* and *B. sylvarum* were associated with calcareous unimproved grasslands that were species rich. As well as calcicolous herbs, species such as *Arrhenathrum elatius*, *Urtica dioica* and *Rubus fruticosus* were associated with *B. muscorum* and *sylvarum*. This may indicate that these bees preferred less intensively managed areas of grassland that were in early stages of succession towards scrub. However with the small number of sites at which these species occurred these associations are preliminary ideas rather than clear indications of species preferences.

Among the bumblebees, *B. jonellus*, *B. sylvarum* and *B. lapidarius* were significantly correlated with hedgerow composition (Table 8.8) and the correlation for *B. sylvestris* had a p-value close to 0.05.

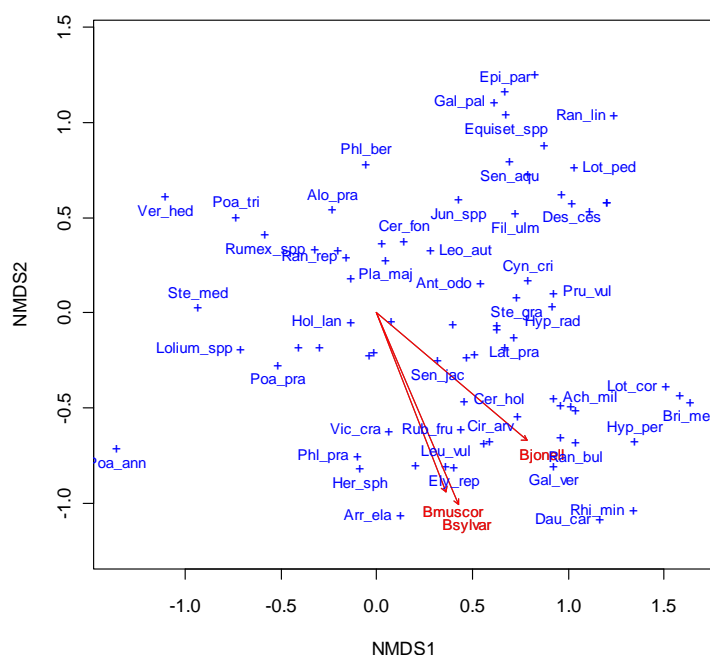
The direction of the correlations (Figure 8.7 [D]) suggested that *B. jonellus*, *B. sylvarum* and *B. lapidarius* were associated with hedgerows composed of shrubby species *Ulex* species, *Prunus spinosa*, *Corylus avellana* rather than high trees. Plant species with restricted distributions, *Rosa pimpinellifolia* and *Rubia peregrina*, also occurred.

B. sylvestris was associated with very different hedgerows, with tall tree species such as *Acer pseudoplatanus* and *Alnus glutinosa* and also with some exotic garden species, including *Ligustrum ovalifolium* and *Symphoricarpos albus*.

The significant correlations between bumblebees and grassland vegetation composition were influenced by sampling location ($p_{\text{blocks}} > 0.05$), whereas correlations with hedgerow vegetation were independent of location (Table 8.8).



[C]



[D]

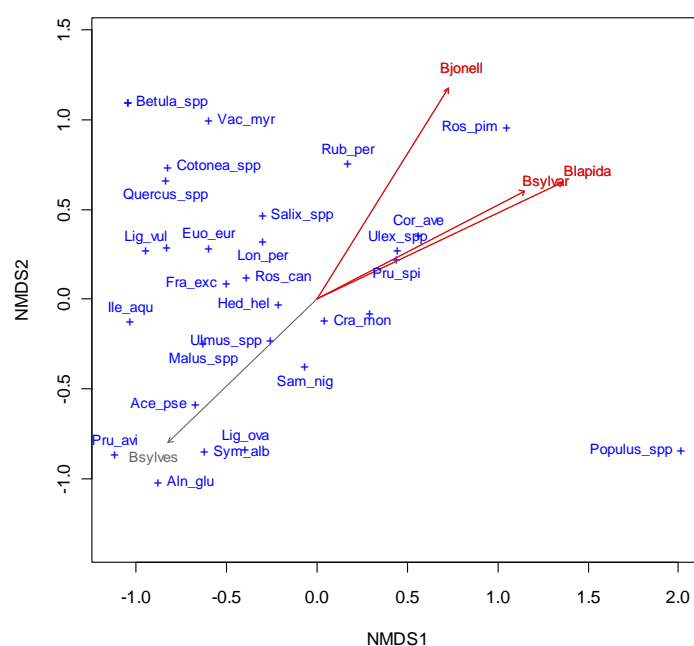


Figure 8.7. Indirect gradient analyses examining correlations of frequent bee species with vegetation composition. Arrows show direction and magnitude of correlations of frequent bee species ($\log_{10}(\text{abundance}+1)$) with the plant ordinations. NMDS ordinations of hedgerow vegetation [A], [B], [D] and grassland vegetation [C] used Bray Curtis distances with square root transformed data and Wisconsin double standardization. Stress=0.20 for hedgerow and grassland vegetation ordinations. Solitary bee correlations with hedgerow vegetation with permutation tests across entire dataset [A] and within blocks defined by location [B]. Bumblebee correlations with grassland vegetation = [C] and with hedgerow vegetation = [D], both with permutation tests across entire datasets. Grey arrows = $p > 0.09$, red arrows = $p < 0.05$.

Table 8. 8 Correlations of frequent bumblebee species ($\log_{10}(\text{abundance}+1)$) with grassland and hedgerow vegetation, with permutation tests across the entire datasets and within blocks defined by sampling location. (NA = insufficient data)

	GRASSLAND			HEDGEROW		
Bumblebee	Envfit r^2	P _{entire}	P _{blocks}	Envfit r^2	P _{entire}	P _{blocks}
<i>Bbohemi</i>	0.04	0.417	0.320	0.05	0.269	0.272
<i>Bhortor</i>	0.06	0.222	0.627	0.04	0.404	0.420
<i>Bjonell</i>	0.15	0.016 *	0.251	0.17	0.014 *	0.012 *
<i>Blapida</i>	0.04	0.330	0.636	0.20	0.006 **	0.010 **
<i>BlucGp</i>	0.00	0.898	0.870	0.01	0.772	0.740
<i>Bmuscor</i>	0.14	0.018 *	0.160	0.11	0.070 ‘	0.081 ‘
<i>Bpascuo</i>	0.00	0.870	0.851	0.05	0.330	0.330
<i>Bprator</i>	0.00	0.983	0.983	0.02	0.689	0.678
<i>Brupest</i>	NA	NA	NA	0.01	0.714	0.735
<i>Bsylvor</i>	0.17	0.013 *	0.152	0.16	0.016 *	0.020 *
<i>Bsylvor</i>	NA	NA	NA	0.11	0.080 ‘	0.064 ‘

8. 4. DISCUSSION

Solitary bees were found to be the heterogeneous element of wild bee assemblages. They showed associations with many different environmental conditions.

There are fewer species of bumblebee than solitary bee occurring in the study region. There is therefore naturally less potential variability in assemblage composition. However, the high similarity of bumblebee assemblages may also have been accentuated by recent historical losses of rarer species (Fitzpatrick *et al.* 2007; Santorum & Breen, 2005).

8.4.1. PLANT AND BEE ASSEMBLAGE ASSOCIATIONS

Significant correlations between bee and vegetation assemblages, when treated as species abundance matrices, were detected. This has rarely been reported before. The correlations were weak. The qualities of vegetation that were driving the correlations tended to reflect other environmental conditions, such as soil conditions. This may account for the difference in findings compared to some papers such as Grundel *et al.* (2010) and Williams

(2011) who described vegetation composition in terms of the flower assemblage only.

The composition of solitary bees assemblages was associated with both hedgerow and grassland vegetation. For bumblebees, when the whole assemblage was considered, a significant correlation was found with hedgerow vegetation only, though there were significant correlations between individual species of bumblebee and grassland vegetation.

PLANT ASSEMBLAGE QUALITIES DRIVING THE ASSOCIATION WITH BEE ASSEMBLAGES

Several qualities of grassland and hedgerow vegetation were associated with bee assemblages.

ASSOCIATIONS WITH GRASSLAND VEGETATION

SOIL MOISTURE

I identified a soil moisture gradient, indicated by grassland Ellenberg value and plant species correlations, as important to the composition of solitary bee assemblages. This concurs with Exeler *et al.* (2009).

Bees show distinct responses to moist conditions in different regions, presumably dependant on local climate and the bee species pool. Szczepko *et al.* (2002); Bartholomew & Prowell (2006) and Moron *et al.* (2008) report the bee assemblages of damp habitats to be less diverse than those of xeric ones, whereas Sarospataki *et al.* (2009) found small bee species to prefer wet areas in Hungary and (Hatfield & LeBuhn 2007) found bumblebees were more abundant in wet meadows in California. In Ireland, bees that are associated with wetter conditions were *A. scotica*, *S. ephippus*, *L. albicans* and *calceatum*. Species associated with drier conditions were *L. leucopus*, *N. ruficornis* and *A. coitana*.

Moron *et al.* (2008) attributed the differentiation in bee assemblages of wet and dry grasslands to food specialisation. Nesting characteristics may also determine bee species tolerance of damp conditions (Cane 1991).

The absence of an association between this moisture gradient and bumblebees, that have superior thermoregulation abilities (Heinrich & Esch 1994), together with the observation that the solitary bees associated with wetter conditions are larger, and some are hairier, than those associated with dry conditions leads me to suggest that thermoregulation capacities may be important. Species associations with soil moisture, in a cool climate such as Ireland's, may be driven by their capacities for thermoregulation. Smaller bees are recognised to face additional challenges in thermoregulation (Stone 1994; Bishop & Armbruster 1999).

GRASSLAND 'SEMI-NATURALNESS' GRADIENT

An association between bee assemblage composition and grassland vegetation considered in terms of its 'semi-naturalness' was inferred from several correlations. Since semi-natural grasslands provide rich floral resources (Morandin et al., 2007; Kwaiser and Hendrix, 2008) and nesting sites for bees (Svensson et al., 2000) a gradient in the effects of this quality of the vegetation for bees is expected.

The aspects of vegetation composition that reflected such a gradient and were associated with bee assemblage composition differed between solitary bees and bumblebees. This may be indicative of differing utilisation of grasslands by the bees, e.g. nesting versus foraging.

The Simpson's Index and abundance of *Agrostis* species, which are associated with unimproved or semi-improved grassland in Ireland (O'Sullivan 1968; Fossitt 2000), were correlated with solitary bee composition. For bumblebees, it was herbs characteristic of more semi-natural grasslands that were correlated with composition.

For solitary bees, the associations were not spatially determined but held true regardless of sampling location. For bumblebees and herbs, the correlation was spatially determined for some species e.g. *Daucus carota* but not for others e.g. *Leondoton autumnalis*.

Other studies have highlighted associations between the abundance of particular plant species and bee assemblage characteristics. For example, the

abundance of *Knautia arvensis* was positively associated with solitary bee diversity in Swedish hay meadows (Franzen & Nilsson 2008) and more generally a loss of leguminous flowers is linked with changes in bumblebee faunas (Backman & Tiainen 2002; Carvell *et al.* 2006; Dupont *et al.* 2011; Bommarco *et al.* 2012).

Surprisingly there was no correlation between grassland vegetation's Ellenberg value for soil Nitrogen and solitary bee or bumblebee composition. This characteristic of grassland vegetation is correlated with a 'semi-naturalness' gradient (see Chapter 6). It was found to be very useful to consider the same environmental factor, here grassland 'naturalness', from a number of perspectives that emphasise different dimensions of the factor.

GRASSLAND SUCCESSION GRADIENT

A number of plants that suggested abandonment and secondary succession in grasslands were associated with solitary bee and bumblebee assemblages. Others have found that the stage of succession of vegetation influences bee assemblage composition (Pawlikowski 1985; Steffan-Dewenter & Tscharntke 2001; Grixti & Packer 2006) (Steffan-Dewenter & Tscharntke 2000).

The identity of plants regarded as indicators of succession suggests that this plant-bee association may be driven by both changes in flowers and other factors associated with succession e.g. structural changes to the grassland. For example, *Heracleum sphondylium* was correlated with solitary bee composition and *Arrhenathrum elatius*, *Urtica dioica* and *Rubus fruticosus* ag. with bumblebee composition.

CALCIFUGE-CALCICOLE GRASSLAND GRADIENT

A number of herbs associated with drier and neutral to calcareous grasslands were significantly correlated with bumblebee composition e.g. *Centaurea nigra*, *Hypericum perforatum*, *Daucus carota*. Calcareous grasslands are recognised as important habitats for bees providing forage and nesting (Steffan-Dewenter & Tscharntke 1999; Goulson *et al.* 2006; Krauss *et al.* 2009; Krewenka *et al.* 2011). Rarer bumblebees e.g. *B. muscorum*, *B. sylvarum*, *B. jonellus*, were associated with these plant species. Some of these

herbs provide forage for bumblebees, e.g. *Centaurea nigra* and *Rhinanthus minor* whereas others may indicate suitable conditions for bees, such as warmer soils or greater herb diversity, without directly providing floral resources themselves.

It was surprising that a bee association with a calcifuge-calcicole gradient in vegetation was not also indicated by a correlation with grassland Ellenberg values for soil pH.

ASSOCIATIONS WITH HEDGEROW VEGETATION

HEDGEROW DIVERSITY GRADIENT

A gradient in species richness and evenness as captured by the Inverse Simpson's Index was correlated with bumblebee and solitary bee composition. More diverse assemblages of solitary bees were associated with higher diversity hedgerows.

Species-rich hedgerows may provide a surrogate woodland edge habitat for bees (Hannon & Sisk 2009). This is likely to be particularly important in Ireland where forest clearances had reduced ancient semi-natural woodland to a national landcover of approximately 2.1% by the mid-1600s and to only 0.2% by the 1830s (Rackham 1995). A small number of solitary bee species recognized as at risk of extinction in the Regional Red List of Irish Bees (Fitzpatrick *et al.* 2006a) were found to be associated with species-rich hedgerows with tall tree species.

Species-rich hedgerows may also provide more abundant and diverse nesting and foraging resources. Most of the solitary bee species recorded are ground nesters (Westrich 1996) so a nesting-related association is not likely to be due to additional nesting niches associated with trees or dead wood (as in Tscharntke *et al.* 1998; Steffan-Dewenter & Tscharntke 2000). Instead it may be associated with the earthen banks found to be more typical of botanically rich hedgerows (See Chapter 5: botanical composition and complexity of structure of hedgerows are correlated.)

In contrast, diverse bumblebee assemblages, with rare species such as *B. sylvarum* and *B. jonellus* were associated with low diversity hedgerows. These hedgerows were observed to often be ‘spontaneous’ hedgerows that developed along fence lines (Forman & Baudry 1984) on more calcareous grasslands with low levels of grazing. The correlation with low diversity hedgerows could therefore be related to the adjacent grasslands. It could also show that these rarer bumblebees are associated with ‘abandoned land covered with shrubs’ which Hirsch & Wolters (2003) report to be a very valuable habitat for bees.

INSIGHTS INTO CAUSES OF VULNERABILITY AMONG BUMBLEBEE SPECIES

Preliminary research (Santorum & Breen 2005a, see Chapter 2) that I carried out for this thesis led me to consider that the intensification of grassland management may be the main cause of declines in and differences between bumblebee assemblages in the Burren region and the East of the country.

Fitzpatrick *et al.* (2007) supported this view and opined that it is specifically the movement from hay to silage production that is responsible for bumblebee declines in Ireland and the UK, rather than declines in flowers across farm habitats as suggested by Williams (1986, 1988, 1989) and Goulson *et al.* (2006).

The view that it is the degradation of grassland habitat that is principally responsible for the decline of rare bumblebee species is lent support by this study’s findings. Only bumblebees with restricted and declining distributions in Ireland: *B. jonellus*, *B. muscorum* and *B. sylvarum* (Fitzpatrick *et al.* 2007) showed significant correlations with semi-natural grassland vegetation. The bumblebee species of highest conservation priority in the UK are also regarded as grassland specialists (Hymettus Ltd 2006).

Trying to understand why some species of bumblebees are more vulnerable than others has occupied bumblebee researchers during the last decade (Goulson 2003; Goulson & Darvill 2004; Goulson *et al.* 2005; Williams 2005a; Benton 2006; Fitzpatrick *et al.* 2007; Goulson *et al.* 2008). Studies correlating biological and ecological traits of bumblebees with their vulnerability to land-

use change (e.g. Benton 2006; Fitzpatrick *et al.* 2007) have agreed that late emergence is a trait of vulnerable species.

I posit that late emergence is an adaptation to the seasonality of semi-natural grassland habitat and other open habitats e.g. heathland, machair etc. in temperate regions. The late emergence of declining bumblebees reflects the strong association of these species with open habitats such as grassland. Early emergence in bumblebees and solitary bees coincides with vernal flowering in temperate woodlands and may reflect an association with woodland and woodland edges / hedgerows in Spring. This hypothesis is broad in its definition of habitat 'specialism' and does not contradict Goulson *et al.* (2006) who showed that bumblebees are not strict habitat specialists but are adaptable with regards to their biotope use.

A fourth bumblebee species, with a restricted and declining distribution in Ireland, *B. lapidarius*, was also associated with vegetation composition. This species is widespread and ubiquitous in the UK where it is abundant in agricultural landscapes with mass-flowering crops, such as oil seed rape. Nevertheless its rarity in Ireland poses interesting ecological questions (Fitzpatrick *et al.* 2007).

Unlike other declining bumblebee species in Ireland, *B. lapidarius* emerges early in the year (Fitzpatrick *et al.* 2007). If the idea regarding timing of emergence and open versus wooded habitat preference is correct, this would suggest *B. lapidarius* not to be a grassland habitat specialist. In this study *B. lapidarius* was found to have associations with hedgerow vegetation, composed of shrubby species rather than high trees which would support this idea.

However Murray *et al.* (2012) found *B. lapidarius* to be negatively associated with tree cover on sand dunes and positively associated with sheep grazing in semi-natural grasslands in Ireland suggesting associations with more open grassland habitat. It also shows a nesting preference for open habitats (Svensson *et al.* 2000; Kells & Goulson 2003).

It is possible that *B. lapidarius* utilises different habitats at different times in its lifecycle, perhaps becoming a grassland specialist later in the year. Its

abundance has been correlated with landscape composition at scales of up to at least 3km radius (Westphal *et al.* 2006) showing it has the capacity to forage over considerable distances and exploit different habitats. Shorter foraging distances of approximately 450m (Knight *et al.* 2005) and 750m (Carvell *et al.* 2012) have been reported in the UK. The variation in foraging distances reported may reflect a response to resource conditions in different study areas (Connop *et al.* 2011; Carvell *et al.* 2012).

The scrubby mixed hedgerows with which it is associated might provide forage early in the year when it emerges. Semi-natural grasslands may then meet other ecological requirements, such as warmer nesting sites (Kells & Goulson 2003) and forage resources later in the year. This species has been shown to have a narrow dietary breadth and forage predominantly on legumes (Connop *et al.* 2010) in summer which would restrict it to semi-natural grassland.

The idea of *B. lapidarius* having a changing habitat preference is also supported by a landscape scale analysis which showed area of woodland to have a positive impact in early summer on the number of *B. lapidarius* nests and a negative impact in late summer (Goulson *et al.* 2010). It would be interesting to study the responses of *B. lapidarius*, as well as rare species identified as grassland / 'summer flowering and open' habitat specialists and a common and widespread species such as *B. pascuorum* 's responses to spatiotemporal variation in resource availability in the landscape in the vein of Williams *et al.* (2012) study.

TO WHAT EXTENT ARE THE CORRELATIONS BETWEEN BEES AND PLANTS DRIVEN BY SPATIAL DEPENDENCE?

Sampling location contributes strongly to associations between bees and plants when entire assemblages are considered as matrices of species abundances. Dormann *et al.* (2007a) points out that such spatial dependence in correlations means that it is not possible to generalise to other regions. Instead the nature of the correlations between species abundances within assemblages of plants and bees are a local phenomenon.

This association with place was interpreted to reflect high levels of beta diversity in bee and plant assemblages. Bee and plant assemblages are distinct even when considering areas only 10km apart. Such high levels of dissimilarity between bee assemblages only a few kilometres apart has been observed in other studies (e.g. Minckley *et al.* 1999; Wilson *et al.* 2009; Grundel *et al.* 2010).

However *qualities* of vegetation that were associated with bee assemblages were not specific to sampling location and can be generalised to other locations (Dormann *et al.* 2007a).

SPATIAL PATTERN

Spatial patterns were detected for bees and vegetation.

Patches of similar hedgerow, similar solitary bee and similar bumblebee assemblages were detected. These patches are each approximately 10km in size. Grassland vegetation patches are larger and grassland vegetation remains significantly similar for sites that are up to 15km apart compared to a random pair of sites. This may be due to the homogenisation of grasslands by agricultural management (Vickery *et al.* 2001; Tallowin *et al.* 2005).

Other studies have shown bee assemblages to become dissimilar over distances of only one to five kilometres (Minckley *et al.* 1999; Wilson *et al.* 2009; Grundel *et al.* 2010). It is unclear whether this spatial patterning of bee assemblages over longer distances is natural to Ireland or whether it has been caused by human activity.

The lack of similarity of grassland vegetation and bumblebee assemblages at the shortest inter-site distances (<2.9km) was unusual and I could not find examples of a similar pattern in the literature. For grasslands it may have been caused by stratification of sites by grassland management in the sampling design.

Given the match in size of patches of similar hedgerow composition and similar bee composition, one might predict that hedgerow vegetation was

responsible for the bee spatial pattern. Hedgerow vegetation was shown to contribute to the spatial pattern in solitary bee assemblages but was not entirely responsible. The spatial patterning for solitary bees and bumblebees remained even after the effects of hedgerow composition had been partialled out. There are likely to be autogenic factors arising from the bees' biology and ecology, such as competition and dispersal processes, contributing to the spatial structure of bee assemblages (Legendre *et al.* 2002) as well as other environmental influences.

Grassland vegetation did not contribute to the spatial patterning of either solitary bees or bumblebees.

Chapter 10, in which linear regression analyses will be carried out to identify the predictors most important to bees must take into account the spatial autocorrelation in bee assemblages and the spatial patterning in explanatory variables such as vegetation. This spatial patterning causes problems for many standard statistical analyses including automated selection methods in regression analysis (Cliff & Ord 1973; Hurlbert 1984; Koenig 1999; Burnham & Anderson 2002a; Legendre *et al.* 2002; Whittingham *et al.* 2006; Mac Nally 2000; Zuur *et al.* 2010). This will be dealt with in Chapter 10.

The scale of the spatial patterning, at approximately 10km, offers a guiding scale for future bee research and for bee conservation initiatives. Studies of environmental effects that require spatial pattern to be controlled for, should sample at a distance greater than 10km. Studies investigating spatial pattern in bee assemblages are likely to find the strongest effects at distances less than 10km.

Conservation initiatives with spacing of a maximum of 10km will ensure that the range and natural variability in species abundance compositions of different bee assemblages are conserved. Agri-environmental schemes can serve as an appropriate instrument for such geographically dispersed conservation.

SUMMARY

Significant correlations between bee and vegetation assemblages, when treated as species abundance matrices, were detected. These correlations are sensitive to sampling location.

Vegetation qualities associated with bee assemblages were identified: vegetation as it reflected soil moisture and soil pH, 'naturalness' of grasslands and possibly succession stage and hedgerow species richness. These correlations are not sensitive to sampling location and can be generalised to other locations.

Species-rich hedgerows are associated with species rich assemblages of solitary bees whereas species poor hedgerows are associated with higher diversities of bumblebees.

Only bumblebees with restricted and declining distributions in Ireland: *B. jonellus*, *B. muscorum* and *B. sylvarum* (Fitzpatrick *et al.* 2007) showed significant correlations with semi-natural grassland vegetation. Late emergence by bumblebees is suggested to be an adaptation to the seasonality of semi-natural grassland habitat and other open habitats in temperate regions.

Spatial patterns were detected for bees and vegetation, particularly at distances less than 10km. Future studies must take into account these spatial correlations.

Hedgerow vegetation was shown to contribute to the spatial pattern in solitary bee assemblages.

Grassland vegetation did not contribute to the spatial patterning of either solitary bees or bumblebees.

CHAPTER 9: ENVIRONMENTAL CONDITIONS ASSOCIATED WITH BEE SPECIES COMPOSITION

9. 1. INTRODUCTION

From a conservation management perspective, it is useful to identify the most important influences on bee assemblages and to distinguish between those under human control and those that are not. Knowing the relative importance of different influences, it is possible to develop cost-effective approaches to conservation. In this chapter, I evaluate the relative importance of selected environmental influences on the composition of bee assemblages in lowland grasslands in southern Ireland.

Anthropogenic impacts are most readily observed at the level of the local assemblage and at a scale between the local and that of the regional species pool (Bestelmeyer *et al.* 2003). Natural turnover of bee species at these levels has been accelerated by anthropogenic factors (Rasmont *et al.* 1993; Biesmeijer *et al.* 2006; Potts *et al.* 2010; Bommarco *et al.* 2012). This study therefore focuses on these levels.

Some of the local filters, acting on the regional species pool of bees and structuring local bee communities (Zobel 1997) include:

- factors associated with geographical location such as soil composition (Potts *et al.* 2005; Kim *et al.* 2006; Abrahamczyk *et al.* 2011), climate (Michener 2000) and microclimate (Herrera 1995; Hendrix *et al.* 2010)
- availability and quality of habitat (e.g. Ricketts *et al.* 2008; Winfree *et al.* 2009).
- agricultural management intensity (e.g. Le Feon *et al.* 2010).
- landscape structure e.g. gradients from open to forested landscapes (Brosi *et al.* 2008; Carré *et al.* 2009)
- biotic influences such as competition (Bowers 1986; Goulson *et al.* 2002; Biesmeijer & Slaa 2006), predation (Abe *et al.* 2008; Rodriguez-Girones 2012) and parasitism (Wcislo & Cane 1996)

The gap in scientific knowledge that this study aims to address is an understanding of the relative importance and shared effects of these factors for bees in pastoral landscapes.

Environmental influences do not act independently of each other on bees (Brown & Paxton 2009). Environmental factors are likely to display spatial synchrony and vary together over geographical areas (Cliff & Ord 1973; Koenig 1999) as was shown for vegetation composition in Chapter 8. They may also be correlated. For example, farm management and vegetation are likely to be associated, due both to the effects of management on vegetation and in part due to spatial synchrony caused by the response of each to the soils and climate of the area.

Environmental factors are therefore likely to have shared effects as well as pure effects on bee assemblages. These may be distinguished using variance partitioning (Borcard *et al.* 1992; Cushman & McGarigal 2002). This approach that has been used to identify major influences on bee assemblages in other landscape types (e.g. Dauber *et al.* 2003; Sattler *et al.* 2010; Schweiger *et al.* 2005; Murray *et al.* 2012).

If an environmental effect is strongly shared with geographical location, it may not be possible to generalize to other locations (Dormann *et al.* 2007a). This study determines the extent to which factors have shared effects with place so that factors that are general can be distinguished from regional ones. This facilitates the making of management recommendations and the determination of which need to be tailored to the region (Whittingham *et al.* 2007).

The rest of this introduction will draw upon the scientific literature to explain what is known about how geographical location, landscape composition, habitat quality and farm management intensity shape local bee assemblages.

GEOGRAPHICAL LOCATION AND BEE ASSEMBLAGE COMPOSITION

The natural distribution of bee genera and species and consequent species composition of assemblages, as for other groups, has been determined by historical processes, involving events such as migration, isolation and radiation leading to speciation. Populations have been isolated by oceans, deserts, high mountain ranges and even large rivers (Michener 1979; Williams 1991; Spengler *et al.* 2011). Bee species are thought to have migrated following river valleys (Banaszak *et al.* 2006) and on rare occasion

crossed oceans, island hopping or rafting (Michener 1979; Fuller *et al.* 2005) to colonise new areas. Bees have survived in refugia (Patiny *et al.* 2009b) and recolonised areas after glaciations (Løken 1972; Franzen & Ockinger 2012) and the expansion and retraction of deserts (Michener 1979; Patiny *et al.* 2009a).

These evolutionary, topographical and climatic forces, interacting with the physiological and behavioural characteristics of individual species, have resulted in present day worldwide bee distribution patterns (Michener 1979; Michener 2000). For example, bumblebees are species of cooler climates, widespread in alpine, temperate and arctic environments of the northern hemisphere and restricted as native species to the East Indies and South America in the southern hemisphere (Williams 1994, 1996).

Climate is therefore regarded as the major determinant of bee distributions (Michener 2000), imposing finer, regional, differences in species distributions as well as broad continental differences (Minckley 2008; Abrahamczyk *et al.* 2011). At a regional scale, species distributions of Euglossine bees in the Amazon basin (Abrahamczyk *et al.* 2011) and of bumblebees in Europe (Pekkarinen *et al.* 1981; Pekkarinen & Teras 1993; Banaszak & Rasmont 1994; Banaszak 1996) have been shown to be determined by climate.

The attributes of climate that are important are likely to differ between species, for example, summer and winter temperatures are predicted to limit the northern extent and summer rainfall the western extent of the distribution of the common large carpenter bee (*Xylocopa virginica* (L., 1771)) in North America (Skandalis *et al.* 2011).

As well as the direct effects of climate on bees, some environmental variables that influence bee distribution are spatially dependent and influenced by climate themselves. These include factors such as the zonation of vegetation (Hines 2008) or risk of fungal infection within underground nests (Michener 1979).

Edaphic factors have been shown to influence species composition of bee assemblages via quality of nesting resources (Potts *et al.* 2005; Kim *et al.* 2006; Krauss *et al.* 2009). Since soils are determined by geology and

geographic processes these too are highly spatially dependent. Soil pH was identified as an influence on bee abundance in the Amazon (Abrahamczyk *et al.* 2011) and calcareous grasslands are important habitats for bees in Europe (Steffan-Dewenter & Tscharntke 1999; Goulson *et al.* 2006; Krauss *et al.* 2009; Krewenka *et al.* 2011).

Bio-geographical processes and influences have resulted in regional species pools. Local bee communities are subsets of the regional species pool, their specific composition dependent on filters, natural and anthropogenic, acting at various spatial scales (Zobel 1997).

Species pools are not static and ongoing colonisations and extinctions take place (Williams 1994) about which relatively little is known (Williams *et al.* 2001). Nevertheless, on a human timeframe, the composition of regional species pools of bees appears relatively steady. Over periods of 50 years and longer, during which there have been massive changes in landuse, a constancy in bee species composition at a regional level has been noted (e.g. Banaszak 1983; Marlin & LeBerge 2001).

Ireland's species pool consists of 102 native bee species (Fitzpatrick *et al.* 2006b). The richest bee assemblages on Irish farmland are anticipated to have less than 40 species, based on (Murray *et al.* 2012) estimate of total species richness on calcareous semi-natural grasslands within Special Areas of Conservation.

The study region of this thesis, was selected to be sufficiently small (60km x 60km) and homogeneous in altitude (range was 7m – 150m) and land-cover (dominated by agricultural grasslands), with no major geographical barriers such as large rivers or mountain ranges, that the regional species pool of bees could be assumed to be uniform throughout the study area.

The 'a priori' hypothesis was that bee assemblage composition would not be particularly influenced by climatic conditions over the short distances and small range in altitude encompassed by this particular study. Other environmental influences were expected to be the influential 'filters' that would explain the variance in species composition of bee assemblages rather than geographical location.

THE IMPORTANCE OF HABITAT QUALITY IN DETERMINING BEE ASSEMBLAGE COMPOSITION

Semi-natural habitat in the study region comprises an average of 14.3% of total farm area in Ireland, predominantly in the form of hedgerows and other field boundaries (Sheridan *et al.* 2011). These are bocage landscapes (Aalen *et al.* 1997), with grassland fields enclosed by hedgerows and banks and on occasion, walls. For the purposes of this study, I regarded agricultural grasslands as potential habitats for bees and studied the effects on bee assemblages of their habitat quality as well as that of hedgerows.

The correlations between bee assemblages and grassland and hedgerow vegetation were explored thoroughly in Chapter 8. This chapter adds to the findings of Chapter 8 by determining the relative importance of these habitats in shaping bee assemblages, compared with other environmental factors. It also assesses the extent to which the effects of vegetation on bees are shared with other factors such as agricultural management and to what extent they are pure effects.

FIELD BOUNDARY HABITAT QUALITY FOR BEES

Field boundaries and field margins are recognised to provide nesting habitat (Osborne *et al.* 2008b), permanent foraging and overwintering habitat for bees (Walther-Hellwig & Frankl 2000b; Backman & Tiainen 2002; Croxton *et al.* 2002; Hopwood 2008; Hannon & Sisk 2009). They may also facilitate bee movement through the landscape (Townsend & Levey 2005; Cranmer *et al.* 2012) or act as sinks (Krewenka *et al.* 2011; Lander *et al.* 2011) or both.

The diversity and composition of hedgerow vegetation was predicted to be an important quality for bees, due primarily to foraging opportunities. Diversity within bee assemblages has long been associated with the diversity of flowering forb communities (Bowers 1985; Potts *et al.* 2003; Potts *et al.* 2004; Vulliamy *et al.* 2006; Sarospataki *et al.* 2009; Fründ *et al.* 2010; Hendrix *et al.* 2010). Chapter 8 showed that the diversity of the woody component of hedgerows in the study region is correlated with solitary bee diversity, though not bumblebee diversity.

Bumblebee assemblage composition was found to be associated with hedgerow vegetation in Chapter 8 though the correlation was not with 'habitat quality' but rather with the type of hedgerow, classified by its dominant shrub.

It was anticipated at the start of the study that the physical structure of hedgerows may be a more important habitat quality in defining the bee assemblage than vegetation, as was found in a study of riparian areas (Williams 2011). Such an effect may be via the provision of nesting resources which are recognised as a limiting factor for bees (H. & Goodell 2011; Murray *et al.* 2012) of secondary importance after floral resources (Potts *et al.* 2003; Potts *et al.* 2005).

Hedgerows in the study region often have associated features such as earthen banks and ditches. Banks provide bare patches of soil which are suitable conditions for ground-nesting *Andrenae* (Potts & Willmer 1997; Potts *et al.* 2005) or grassy tussocks that are nesting sites for some *Bombus* species (Svensson *et al.* 2000; Kells & Goulson 2003).

Higher and wider hedgerows can provide surrogate woodland edge habitat (Forman & Baudry 1984; Hannon & Sisk 2009) e.g. for cavity nesting bees (Tscharntke *et al.* 1998).

GRASSLAND HABITAT QUALITY FOR BEES

I treated agricultural grasslands as potential habitats for bees. Certainly, semi-natural grasslands are habitat for bee populations within agricultural landscapes (Steffan-Dewenter & Tscharntke 1999; Ockinger & Smith 2007). Such grasslands offer rich floral resources (Morandin *et al.*, 2007; Kwaiser and Hendrix, 2008) and nesting sites for bees (Svensson *et al.*, 2000).

Some studies suggest that agricultural grasslands provide habitat of intermediate quality for bees between semi-natural grasslands and arable cropland, for example buffering losses of bees from semi-natural grassland sites (Hatfield & LeBuhn 2007; Sjödin *et al.* 2008). Further support for agricultural grasslands having habitat value for bees is supported by an earlier study in which numbers of bees declined more rapidly on arable land

than grassland as distance to an area of abandoned land increased (Hirsch & Wolters 2003).

However the perception of managed grasslands as a relatively benign landuse within the countryside with respect to bees has been challenged. In 2003, Dauber found that bees responded positively to increasing proportion of arable land within the landscape but not to increasing grassland area (Dauber *et al.* 2003). More recently, in a trans-European study, bees were found to be preferentially associated with areas of cropping and mixed farming rather than areas of intensive animal husbandry (Le Feon *et al.* 2010). These studies suggest that the habitat value of grasslands for bees varies considerably.

The physical structure and botanical composition of the grassland have implications for bees in terms of the consequent availability of nesting sites and forage (Hines & Hendrix 2005; Potts *et al.* 2005; Weiner *et al.* 2011). These characteristics are likely to be correlated with management (Tilman 1987).

THE IMPORTANCE OF AGRICULTURAL MANAGEMENT INTENSITY IN DETERMINING BEE ASSEMBLAGE COMPOSITION

An intensification of management of grassland production systems is associated with a decline in bee species richness (Hatfield & LeBuhn 2007; Le Feon *et al.* 2010; Power & Stout 2011; Weiner *et al.* 2011). This chapter evaluates the relative importance of agricultural management intensity compared to other environmental factors in terms of effects on bee assemblage composition.

Tscharntke *et al.* (2005) recommended that the effects of agricultural intensification on biodiversity are studied at two levels: the field and the landscape scale. I have, in this study, also included a third level, that of the farm. The farm level provides a spatial scale intermediate between that of field and landscape.

The relative importance of agricultural intensification at field, farm and landscape level on bee assemblage composition was studied. This can

determine the most appropriate level at which to direct agri-environmental measures for bee conservation.

In this chapter, the relative importance of agricultural management at the farm level on the composition of bee assemblages compared to other environmental factors is assessed. The bee assemblages of dairying and non-dairying farms are also directly compared.

AGRICULTURAL INTENSIFICATION AT THE FIELD LEVEL

Of the potential pathways by which pastoral agriculture might impact upon bees at the field scale, grazing effects have been the most studied and have been shown to be an important influence (H. & Goodell 2011). Species richness of bumblebees was associated with grazing intensity rather than level of fertilisation in semi-natural grasslands in Sweden (Soderstrom *et al.* 2001). Grazing explained 17.7% of variance in bumblebee assemblage composition on Irish semi-natural grasslands (Murray *et al.* 2012).

Variability in bee responses to grazing is a feature of the literature. For example, stocking density or grazing pressure had no effects on bee abundances and diversity in studies in Hungary, the Netherlands or Sweden (Kohler *et al.* 2007; Sjodin *et al.* 2008; Sarospataki *et al.* 2009; Batary *et al.* 2010) but did impact on bees in other Swedish studies, as well as in Scotland, Switzerland, Sichuan, the Mongolian steppe (Soderstrom *et al.* 2001; Kohler *et al.* 2007; Franzen & Nilsson 2008; Xie *et al.* 2008; Yoshihara *et al.* 2008; Albrecht *et al.* 2010; Redpath *et al.* 2010).

The diverse effects of grazing on bee abundances may be partly due to study design, for example in the definition of high intensity versus low intensity grazing (Batary *et al.* 2010) or due to the plant community studied. For example some studies focused on semi-natural grasslands and others on more modified grasslands. An interaction between landscape composition and grazing intensity may also be responsible for the differing effects observed (Batary *et al.* 2010).

Intermediate or extensive levels of grazing favour higher abundances of bees in UK semi-natural grasslands (Carvell 2002). In some situations high grazing intensities creates open patches and compacted soils that provided

nesting resources and supported greater bee abundances (Vulliamy *et al.* 2006). In general though, high grazing intensity reduces the abundance and diversity of flowers and is associated with declines in bee populations (Kruess & Tschardt 2002; Sjödin 2007; Sjödin *et al.* 2008; Xie *et al.* 2008).

The type of grazer is also important. Cattle grazing favoured higher abundances of bumblebees than sheep grazing in a study of UK semi-natural grasslands (Carvell 2002). However the rare bumblebee species, *B. sylvarum*, is positively associated with sheep grazing on Irish semi-natural grasslands (Murray *et al.* 2012).

Apart from grazing intensity there is substantial flexibility in grassland management at the field level. It may differ in timing, type and amount of fertiliser applications, reseeding, liming, drainage, stocking densities, grazing regimes and timing and frequency of mechanical harvesting (Frame 1992; Creighton *et al.* 2011).

These management actions alter the botanical composition of grasslands (O'Sullivan 1968; Tilman 1987; Crawley *et al.* 2005). The structure of the sward is determined by the grass harvesting regime, whether by grazing or cutting. Short-term rotational grazing at high stocking densities and frequent cutting or both, for example, maintain a structurally and botanically uniform sward (Vickery *et al.* 2001).

Given the range of management, a long gradient in grassland composition and structure could be expected. A structure and composition gradient of grassland has implications for bees in terms of the availability of nesting sites and forage (Hines & Hendrix 2005; Potts *et al.* 2005; Weiner *et al.* 2011). Semi-natural hay meadows, for example, have higher numbers of red-listed solitary bees than grazed semi-natural pastures (Franzen & Nilsson 2008).

However Tallwin *et al.* (2005) observed that species-poor and structurally uniform grasslands were ubiquitous in lowland England, regardless of the intensity at which they were farmed. In contrast, a recent study of Irish agricultural grasslands indicated a continuum between semi-natural and improved agricultural grasslands (Sullivan *et al.* 2010). A gradient in the

habitat quality of Irish grasslands for bees is therefore anticipated in this study.

The effects of intensification of management at the field level are also seen in the habitat quality of adjacent field boundaries, as botanical diversity and boundary structure are altered (Hegarty & Cooper 1994; Marshall & Moonen 2002; Boutin *et al.* 2008).

AGRICULTURAL INTENSIFICATION AT THE FARM LEVEL

Franzen & Nilsson (2008) regarded the farm unit to be an appropriate scale for the study of solitary bees. There is evidence that differences in management at the farm level affect bees, for example organic dairy farms support higher abundances of bees than conventionally managed dairy farms (Power & Stout 2011).

AGRICULTURAL INTENSIFICATION AT THE LANDSCAPE LEVEL

On a landscape level, intensification of farming activity is associated with a simplification of farmland as habitat patches are modified or removed to maximise the available area for farming (Robinson & Sutherland 2002; Benton *et al.* 2003; Persson *et al.* 2010).

Habitat loss within a landscape has been strongly linked with declines in bee abundances and diversity (see the meta-analyses of Winfree *et al.* 2009; Ricketts *et al.* 2008). Agricultural intensification at a landscape level, was therefore classified by habitat composition and landuse (Chapter 4).

THE IMPORTANCE OF LANDSCAPE IN DETERMINING BEE ASSEMBLAGE COMPOSITION

The primary gradient in landscape composition within the study region was associated with agricultural intensification and accompanying habitat change but other gradients in landscape composition were also uncovered in Chapter 4. The literature and preliminary analyses in Chapter 4, suggested that these secondary and tertiary gradients in landscape composition might also influence bee assemblage composition.

A gradient from traditionally unenclosed landscapes with areas of woodland, scrub or recent forestry plantations to traditionally enclosed landscapes, with

high densities of hedgerow but scarce woodland, scrub or forestry was detected in the study region. Bee assemblages in other regions have been found to be structured along a gradient from open to forested landscapes (Brosi *et al.* 2008; Carré *et al.* 2009; Diaz-Forero *et al.* 2011). The nature of the gradient in this study region reflects historical landuse as well as present day habitat availability.

The final landscape gradient included in this analysis was in the proportional area of built land, which included roads and carparks as well as housing, industrial, commercial and agricultural buildings. Various studies have shown that urban, suburban development and gardens influence bees (e.g. Cane *et al.* 2006; Hisamatsu & Yamane 2006; Ahrne *et al.* 2009; Barthel *et al.* 2010; Sattler *et al.* 2010; Bates *et al.* 2011; Samnegard *et al.* 2011; Banaszak-Cibicka & Żmihorski 2012).

The relative importance of landscape composition, as a set of variables describing agricultural intensity and the gradients from traditionally open to enclosed landscapes and rural to built land, was studied.

SUMMARY

To summarise, the key questions being investigated in this chapter are:

- What are the relative importances, pure and shared effects of geographical location, habitat quality, farm management and landscape composition for the structuring of wild bee assemblages in pastoral lowland landscapes?

Is this the same for solitary bees and bumblebees?

- At which level should agricultural management intensity be considered when studying and managing the effects on wild bee assemblages: field, farm or landscape?

Is this the same for solitary bees and bumblebees?

- Do analyses suggest trends in species composition of bee assemblages, or particularly sensitive species, associated with anthropogenic impacts, that can be investigated in subsequent studies?

9. 2. METHODS

SURVEY METHODS

Chapters 3-7 provide details of the methods used to collect bee data and measure and derive explanatory variables for this analysis. Analyses use a subset of data, from forty-five sites, at which the field boundary was a hedgerow.

Data preparation

Sampling

The data analysed is derived from the surveys described in Chapter 3. Only sites that were separated by 1km (to reduce the effects of spatial autocorrelation) and that had field boundaries with a woody component are included in this analysis. This gave a sample size of 45 farms.

Bee data

Removal of rarest species from dataset

Bee species that were recorded at only one site (Figure 9.1) were removed from the analysis to prevent very rare species having an undue large effect on the results. This left ten bumblebee and thirty solitary bee species or species groups in the analysis. Solitary bees and bumblebees were analysed both separately and together as ‘wild bees’.

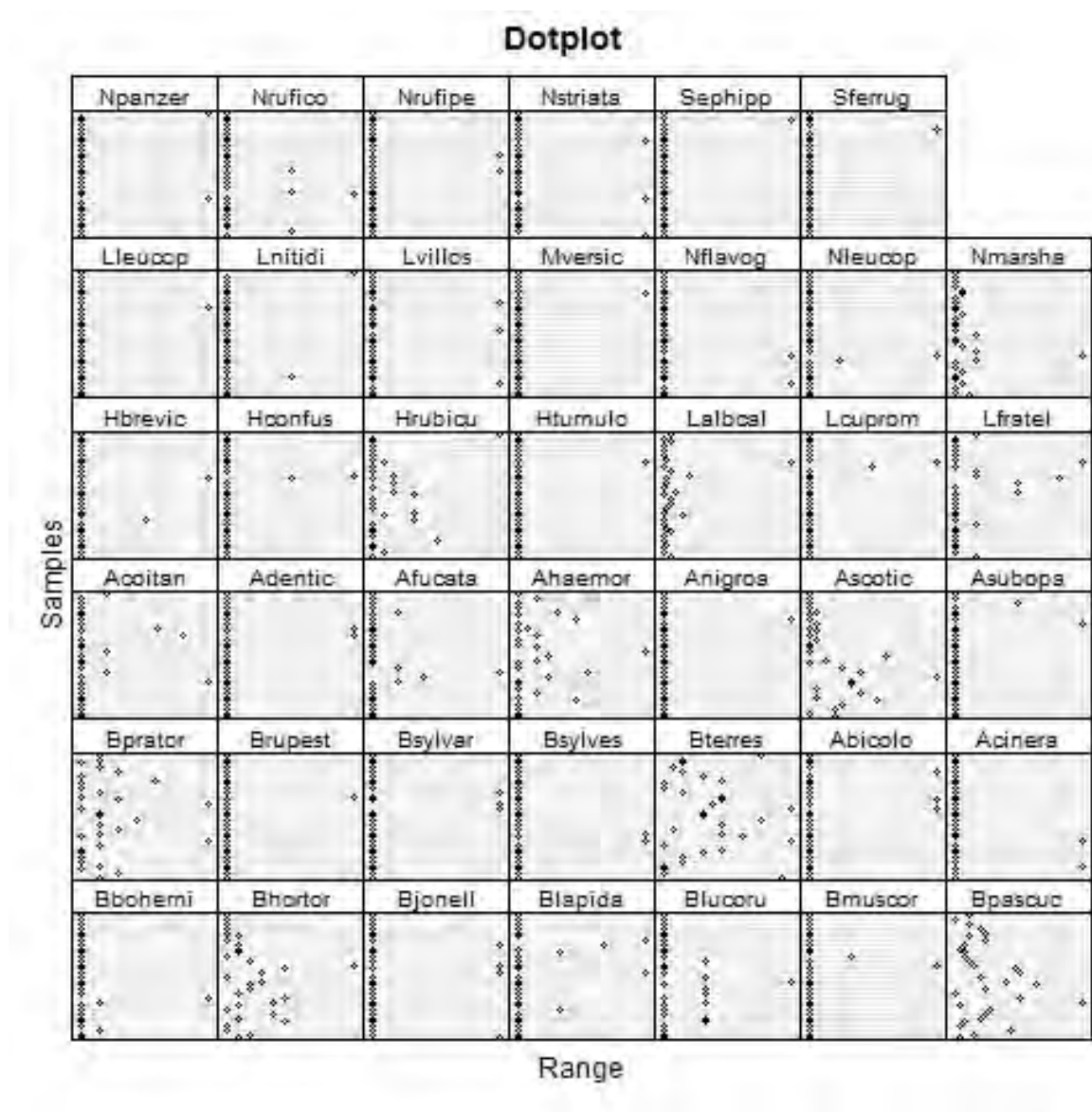


Figure 9.1. Dotplot showing abundance of each bee species across samples. The vertical axis shows samples in the same order. See Appendix 15 for species names.

Environmental data

Each environmental influence i.e. geographical location, landscape composition, habitat quality and farm management, was treated as a set of variables (Tables 4.1 to 4.4). The methods used to collect this data are described in Chapters 4-7. Collinearity within each set was kept to a minimum.

Continuous explanatory variables were centred and standardised, that is, they were scaled so that their means were equal to zero and their standard deviation equal to one. Dummy variables were generated automatically for variables that were factors by R (R Core Team 2012).

To avoid overfitting models by having too many variables relative to number of samples in the ordination; the number of predictors within each set of variables was minimised. The most influential variables within each set with regards to each bee response (i.e. solitary bee assemblage composition, bumblebee assemblage composition and all wild bees assemblage composition) were identified. Backward stepwise model selections were carried out for each bee response, using only the terms in each environmental influence's set in the starting model. Variables that did not have a significant effect were removed. This resulted in slightly different subsets of variables being used to represent each environmental influence in the models for all wild bees, solitary bees and bumblebees (Tables 4.1 to 4.4).

Geographical data

Polynomials and interactions were calculated for X and Y coordinates as recommended by Legendre (1990) and Borcard *et al.* (1992) to allow spatial pattern, in addition to linear gradients, to be extracted. However their inclusion in models did not increase the variance explained while reducing interpretability of models and so they were omitted.

Table 9.1. The set of explanatory variables used to describe the influence of geographical location on wild bee assemblages. ✓ indicates inclusion of the geographic variable in models for all bees, solitary bees or bumblebees.

Set of geographical variables used in full model	All bees	Solitary	Bumble
Easting or X co-ordinate, six figure Irish grid reference (continuous)	✓	✓	✓
Northing or Y co-ordinate, six figure Irish grid reference(continuous)	✓		✓
Geology, 2 levels- limestone or not (factor)			
Altitude (metres) (continuous)		✓	

Table 9.2. The set of explanatory variables used to describe the influence of landscape composition on wild bee assemblages. ✓ indicates inclusion of landscape variable in models for all bees, solitary bees or bumblebees.

Set of landscape composition variables used in full model	All bees	Solitary	Bumble
Area of semi-natural woodland & scrub and young forestry within 100m radius of sampling point. (continuous)	✓	✓	
Area of built environment within 100m radius of sampling point. (continuous)			
Land type(factor) Type 1= Intensive landscape (proportion of semi-natural habitat mean=21.1%, std.dev=11.8, n=26) Type 2=Intermediate landscape (proportion of semi-natural habitat1 mean =60.3%, std.dev=3.7, n=10) Type 3=Semi-natural landscape (proportion of semi-natural habitat1 mean =87.1%, std.dev=9.2, n=20) Semi-natural habitat classification included agricultural grasslands of intermediate botanical diversity, corresponding to (Sullivan <i>et al.</i> 2010)'s semi-improved grassland category.			

Table 9.3. The set of explanatory variables used to describe the influence of habitat structure and botanical composition on wild bee assemblages. ✓ indicates inclusion of habitat quality variable in models for all bees, solitary bees or bumblebees.

Set of habitat quality variables used in full model	All bees	Solitary	Bumble
Simpson's Index complement calculated for grassland vegetation (continuous). A lower score reflects higher species diversity.		✓	
Grassland vegetation's Ellenberg value for soil moisture (continuous)		✓	
Site scores on first axis of field (ie grassland) vegetation PCO (continuous). High positive scores indicate botanical composition typical of low soil fertility and higher species diversity. Low negative scores indicate plant composition typical of highly fertilised conditions and low species diversity.		✓	
Site scores on third axis of field (ie grassland) vegetation PCO (continuous). High positive scores indicate plant composition typical of more acid soils.	✓		
Structural Index, an ordinal scale(treated as continuous due to large number of categories), scoring the complexity of the hedgerow and associated features.		✓	
Inverse Simpsons index for Hedgerow woody vegetation (continuous). A higher score reflected higher species diversity and evenness.			
Site scores on first axis of field boundary (ie hedgerow) vegetation PCO (continuous). Reflect a gradient in composition from <i>Crataegus monogyna</i> (negative scores) to <i>Prunus spinosa</i> domination (positive scores). Extreme axis scores, at either end of this gradient, are species poor and dominated by the named shrub species. Intermediate axis scores, around zero, reflect the most diverse composition and are similar to ash woodland.	✓	✓	

Farming data

Chapter 7 describes the methods used to measure and describe gradients of agricultural intensification within the study region at field, farm and landscape level.

The farming influence set of predictors contained variables describing management intensity at the field and farm level. Agricultural intensification at the landscape scale was summarised by the 'land type' factor in the landscape composition set.

Table 9.4. The set of explanatory variables used to describe the influence of agricultural management on wild bee assemblages. ✓ indicates inclusion of agricultural management variable in models for all bees, solitary bees or bumblebees.

Set of farm management variables used in full model	(ii) All bees	(iii) Solitary	(iv) Bumble
Enterprise: i.e. dairying or not (factor).	✓		
Reseeding of study field (factor)			
Site scores on first axis of PCO describing management of study field (continuous). A high positive score reflects low intensity of agricultural inputs and a low negative score reflects higher inputs.	✓		

METHODS OF STATISTICAL ANALYSES

SELECTION OF DISTANCE MEASURE AND CONSTRAINED ORDINATION

METHOD

The distribution of bee abundances across sites was checked (Figure 9.1) in order to select an appropriate distance measure. The distributions were dominated by zero abundances, even after removal of the rarest species. Since zeros were considered to be due at least in part to under-sampling (see Chapter 3), a distance measure that did not give undue weight to rarity was required (Legendre and Gallagher, 2001).

Furthermore, there is a large number of 'double zeros', when a species is not recorded at two sites under comparison. Since this is again due, in part, to under-sampling, an asymmetric distance measure which does not score two

sites as more similar because they are both missing a species is required (Legendre & Legendre 1998).

Traditionally, ecologists have selected an ordination method based upon the length of environmental gradient under study (Ter Braak & Prentice 1988), typically assessed using the length of the first axis of a Detrended Correspondence Analysis (DCA) (Lepš & Šmilauer 2003). Linear methods, that is RDA, were recommended for short gradients and unimodal methods, that is canonical correspondence analysis, CCA, based upon the Chi-squared distance, for long gradients. However evidence for linear and unimodal methods each having wider applicability have been presented (e.g. Ter Braak 1986; Legendre & Gallagher 2001).

With rare species downweighted, the length of DCA axis 1 for the entire wild bee dataset was 2.2. Linear methods might therefore be recommended, that is RDA (Lepš & Šmilauer 2003). However Euclidean distance which is typically used in RDA is a symmetric distance measure and due to the large number of 'double-zeros' is therefore to be avoided. An alternative distance-based form must be used.

The Hellinger distance transformation (square root of relative abundance) was selected. This choice of asymmetric distance measure was based on its reported performance in simulation studies (it maintained distances close to the original distances in ordinations, did not give excessive importance to rare species and explained a large fraction of the variance in species data) (Legendre & Gallagher 2001; Anderson & Willis 2003).

A further useful quality of the Hellinger distance is that since it is a transformation, species data is retained. When used in Redundancy Analysis (RDA), it permits ordination biplots and triplots with species to be generated (Legendre & Anderson 1999; Legendre & Gallagher 2001) which can greatly aid interpretation.

The Hellinger transformation was applied using the *decostand* function and ordinations conducted using the *rda* function of *vegan* (Oksanen *et al.* 2013) in R (R Core Team 2012).

The *anova* function of *vegan* was used to carry out 9999 permutations to test the significance of models, axes, terms and marginal effects (Legendre *et al.* 2011), although the programme was allowed to default to fewer permutations if a stable value was reached sooner (Legendre *et al.* 2011; Oksanen *et al.* 2013).

STEPWISE MODEL SELECTION USING ALL VARIABLES TO DEVELOP A MODEL TO EXPLAIN THE VARIANCE IN COMPOSITION OF WILD BEE ASSEMBLAGES

The full model, using all sixteen variables (Tables 4.1-4.1), was established as an initial model to predict the composition of the entire wild bee assemblage. Automatic backwards stepwise model selection was used, using the *ordistep* function in *vegan* (Oksanen *et al.* 2013) to reach a model in which all explanatory terms were significant at $p=0.05$. The *anova* function of *vegan* was used to carry out 9999 permutations to test the significance of models, axes, terms and marginal effects (Legendre *et al.* 2011), although the programme was allowed to default to fewer permutations if a stable value was reached sooner (Oksanen *et al.* 2013).

The variables that were retained by backwards stepwise selection were considered to be strong influences on bee composition.

DECOMPOSING THE VARIANCE IN COMPOSITION OF WILD BEE ASSEMBLAGES

Distance measure and constrained ordination method

A series of partial RDA models (Borcard *et al.* 1992; Cushman & McGarigal 2002) were used to partition the variance in composition of assemblages of all wild bees between the major environmental influences that is: geographical location, landscape composition, intensity of farm management and habitat quality. Variance partitioning was carried out manually using the *RDA* function of *vegan* (Oksanen *et al.* 2013).

The ‘marginal’ and ‘conditional’ effects of the sets of influences were determined. Marginal effects refer to the variability explained by a given environmental influence without taking into account other environmental factors. Conditional effects describe the variability explained by a given environmental influence after the confounding effects of other environmental variables has been removed (Schweiger *et al.* 2005).

Probability values were obtained with Monte Carlo permutation testing. The *anova* function of *vegan* (Legendre *et al.* 2011; Oksanen *et al.* 2013) was used to carry out 9999 permutations to test the significance of models, axes, terms and marginal effects, although the programme was allowed to default to fewer permutations if a stable value was reached sooner .

Two levels of variance partitioning were carried out. These are described below.

First tier of decomposition

In the first level of variance partitioning, the *spatial* component of variance in bee composition was separated from the *environmental* component that could be explained by the other sets of variables. The shared effect of spatial location and other environmental variables was also estimated. To achieve this, a series of three models were run (see Table 9.5) and the variance in bee composition that each explained was calculated as the eigen value of the constrained axes divided by the total inertia . The calculations in Table 9.5 explain how the variance was then partitioned into pure and shared effects (Borcard *et al.* 1992).

The spatial and environmental models for all wild bees are presented. Correlation biplots (RDA scaling 2) showing the relationships between environmental variables and species were drawn (Ter Braak & Prentice 1988; Ter Braak 1994; Legendre & Legendre 1998).

Table 9.5. Models and calculations used in the first tier of decomposition of variance in all bees, solitary bees and bumblebees.

Model #	Summary
1	Environmental variables explanatory; no covariables
2	Environmental variables; spatial set as covariables
3	Spatial variables explanatory; all environmental sets as covariables

Calculation	Calculations for decomposition of variance	% variance explained in
A	Variation due to environmental variables	Model 2
B	Variation due to spatial variables	Model 3
C	Variation jointly explained by environmental and spatial variables	Model 1 - Model 2
	Total unexplained variance	$100 - (\text{Model 2} + \text{Model 3}) + (\text{Model 1} - \text{Model 2})$
	Total explained variance	$(\text{Model 2} + \text{Model 3}) + (\text{Model 1} - \text{Model 2})$

Second tier of decomposition

In the second tier of variance partitioning, the pure and shared effects of the sets of *environmental influences*, that is habitat quality, farm management and landscape composition, were to be analysed. However the models upon which these analyses were based were found to not be statistically significant at $p < 0.05$ and are therefore not presented.

Estimating the percentage variance in each bee species abundance explained by models

The proportion of variance in abundance of each species explained by the models was extracted using the function *inertcomp* in *vegan* (Oksanen *et al.* 2013).

DECOMPOSING THE VARIANCE IN COMPOSITION OF SOLITARY BEE ASSEMBLAGES AND BUMBLEBEE ASSEMBLAGES

The variance in solitary bee and bumblebee assemblages was decomposed separately for each group, using the models and calculations in Table 9.5. Each environmental influence in the models was represented by the variables selected as having significant effects on that guild (✓ in Tables 9.1-9.4).

A second tier of decomposition, to separate the effects of the environmental influences on the variance in bee assemblages was conducted but the models were not significant at $p < 0.05$ and the results are therefore not presented.

The decomposition of variance for solitary bees and bumblebee assemblages was compared to identify whether these guilds respond to different environmental influences.

PERMUTATIONAL MANOVA TESTING FOR DIFFERENCES BETWEEN BEE ASSEMBLAGES OF FARMS MANAGED INTENSELY AND EXTENSIVELY AND BETWEEN LANDSCAPES.

Permutational MANOVA (multivariate analysis of variance) (Anderson 2001; McArdle & Anderson 2001) was used to test whether there were significant differences between the composition of bee assemblages (all wild bees) at sites which had more intensive agricultural management compared to those with less intensive management. Farm management was considered at the field, farm and landscape level.

The composition of bee assemblages at farms which were

- Field level management intensity: reseeded grasslands were compared with old pastures
- Farm level management intensity: dairy farms were compared with those that were not dairying
- Landscape level agricultural management intensity: landscape type 1, with low proportions of semi-natural habitat and high proportions of intensively managed grasslands, were compared with landscape type 3

that had high proportions of semi-natural habitat and low proportions of intensively managed grasslands.

The *adonis* function in *vegan*, which is directly analogous to MANOVA (multivariate analysis of variance) (Oksanen *et al.* 2013) was used.

9. 3. RESULTS

9.3.1. MODEL DERIVED FOR ALL WILD BEES BY AUTOMATIC BACKWARDS STEPWISE SELECTION

The model derived by stepwise selection (starting from a model with all sixteen explanatory variables) had geographical location and grassland vegetation composition as explanatory terms. Model significance was $p=0.005$ and the first two axes were significant at $p=0.05$. The model is illustrated in Figure 9.2.

The first axis, represented a North-east to South-west gradient. It explained 9.8% of bee variance.

The second axis was determined by grassland vegetation (FieldVegAx3.sc = site scores on the 3rd axis of a PCO of field vegetation, see Chapter 6). Positive scores indicate plant composition typical of more calcareous soils. This axis explained 4.6% of bee variance. The majority of bee species were associated with neutral to calcareous conditions.

Stepwise model selection, starting with all 16 explanatory variables, did not identify agricultural management, landscape composition or any habitat quality, other than vegetation composition reflecting soil pH, as important in explaining the composition of wild bee assemblages.

9.3.2. PARTITIONING OF VARIANCE IN BEE ASSEMBLAGES

FIRST TIER OF DECOMPOSITIONS: QUANTIFYING THE RELATIVE IMPORTANCE OF SPATIAL AND ENVIRONMENTAL INFLUENCES' PURE AND SHARED EFFECTS.

DECOMPOSITION OF VARIANCE, BETWEEN SPATIAL AND ENVIRONMENTAL INFLUENCES, FOR ALL WILD BEES

24.6% of the total variance in the dataset for 'all wild bees' (total variance =0.462) was explained by environmental and spatial variables (using the three models: environmental model M1, environmental model conditioned on spatial variables M2 and spatial model M3).

12.4% of total variance was explained purely by environmental variables. 6.6% was explained by environmental variables confounded with geographical location and 9.0% purely by spatial variables (Figure 9.3).

DECOMPOSITION OF VARIANCE, BETWEEN SPATIAL AND ENVIRONMENTAL INFLUENCES, FOR SOLITARY BEES

For solitary bees, the total variance in the dataset was 0.613 of which 27.6% was explained by environmental and spatial variables (using the three models: environmental model M1, environmental model conditioned on spatial variables M2 and spatial model M3).

The pure effects of local environmental conditions were 1.4x stronger than pure spatial effects upon solitary bee composition and 1.6x stronger than the shared environmental and spatial effects (Figure 9.3). Environmental influences together explained 11.8% of the variance in solitary bee composition (Model M2 $p=0.53$) and pure spatial effects explained 8.2% variance (Model M3, $p=0.02$). The combined effect of spatial and environmental influences explained 7.6% of solitary bee variance.

DECOMPOSITION OF VARIANCE, BETWEEN SPATIAL AND ENVIRONMENTAL INFLUENCES, FOR BUMBLEBEES

The preliminary selection of variables, from each set representing an environmental influence, identified only spatial variables as having a significant effect on bumblebee composition. All other environmental influences were relatively unimportant.

The total variance in the bumblebee dataset was 0.282 of which 9.1% was explained by spatial terms alone.

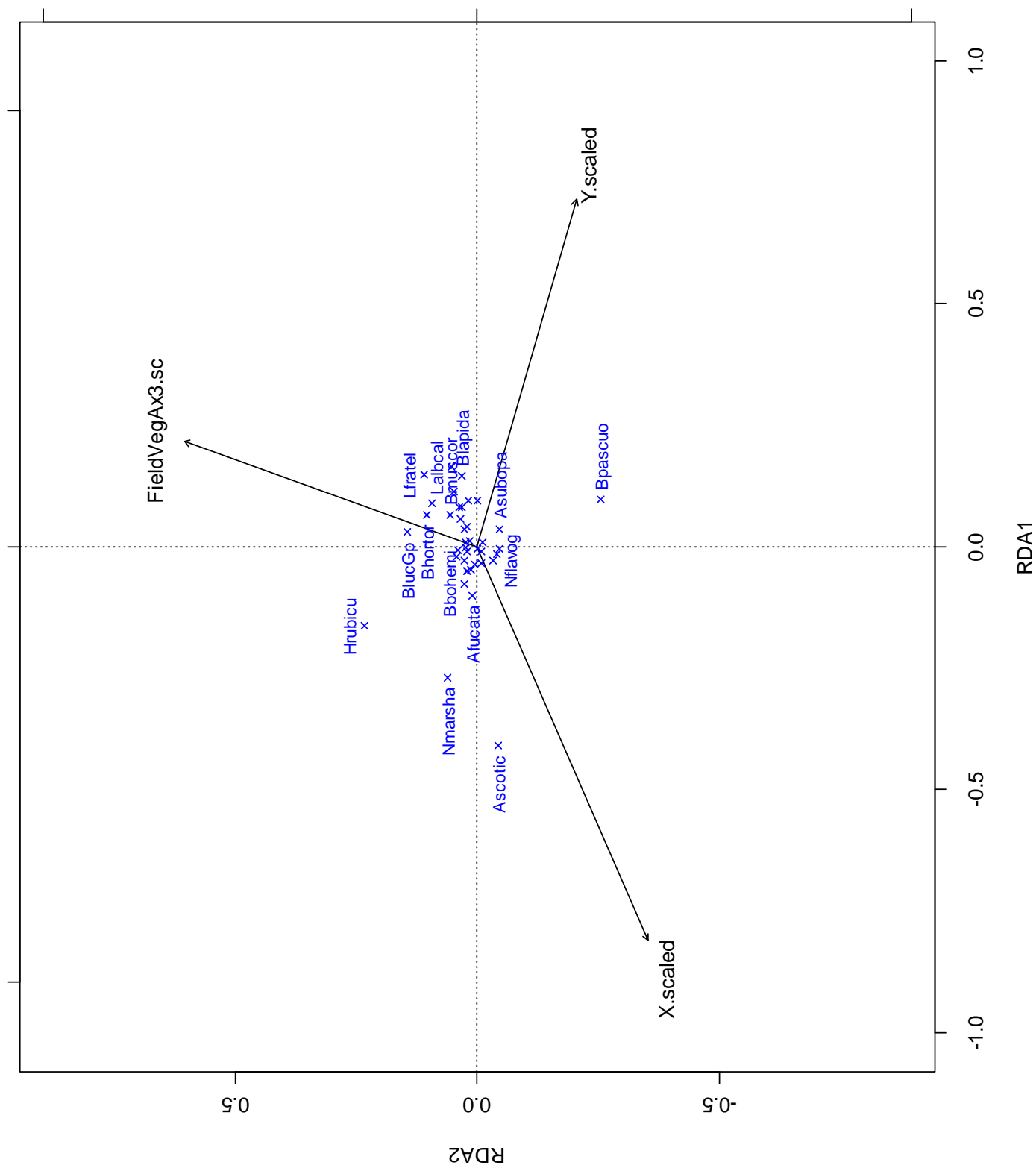


Figure 9.2. Distance-based RDA (Hellinger distance) model for all wild bees derived by stepwise selection from an initial model with all 16 explanatory variables.

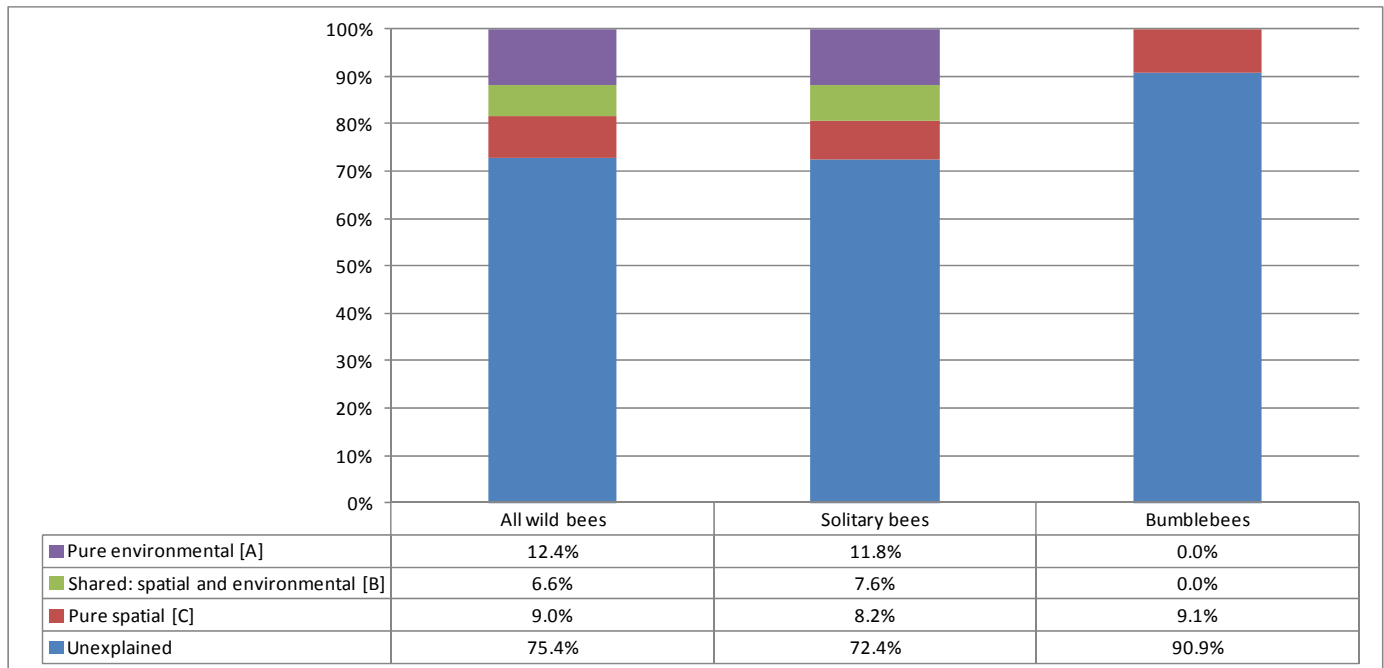


Figure 9.3. Percentages of variation of bee species abundance data matrix explained by environment and by space. The sums of canonical eigenvalues and significance of models from which these proportions of variance were derived are presented in Appendix 17.

9.3.3. IMPORTANCE OF GEOGRAPHICAL LOCATION

Decomposition of variance showed geographical location to be an important variable shaping bee assemblages. Geographical location was also identified as a significant predictor, by stepwise model selection starting with all possible predictors. The amount of variance in solitary bee and bumblebee assemblages explained purely by x and y co-ordinates was very similar at around 9%. In addition, 6.6% of the variance in all wild bee assemblages was explained by environmental variables confounded with geographical location (or 7.6% of the variance when solitary bees were considered alone).

A North-east to South-west gradient was shown to be a major environmental influence on wild bee assemblage composition by both the variance partitioning approach (Figure 9.4) and automatic stepwise model selection from a full model (Figure 9.2). This spatial effect was interpreted to be a

climatic gradient, the effects of which were accentuated by an altitudinal gradient running in the same direction.

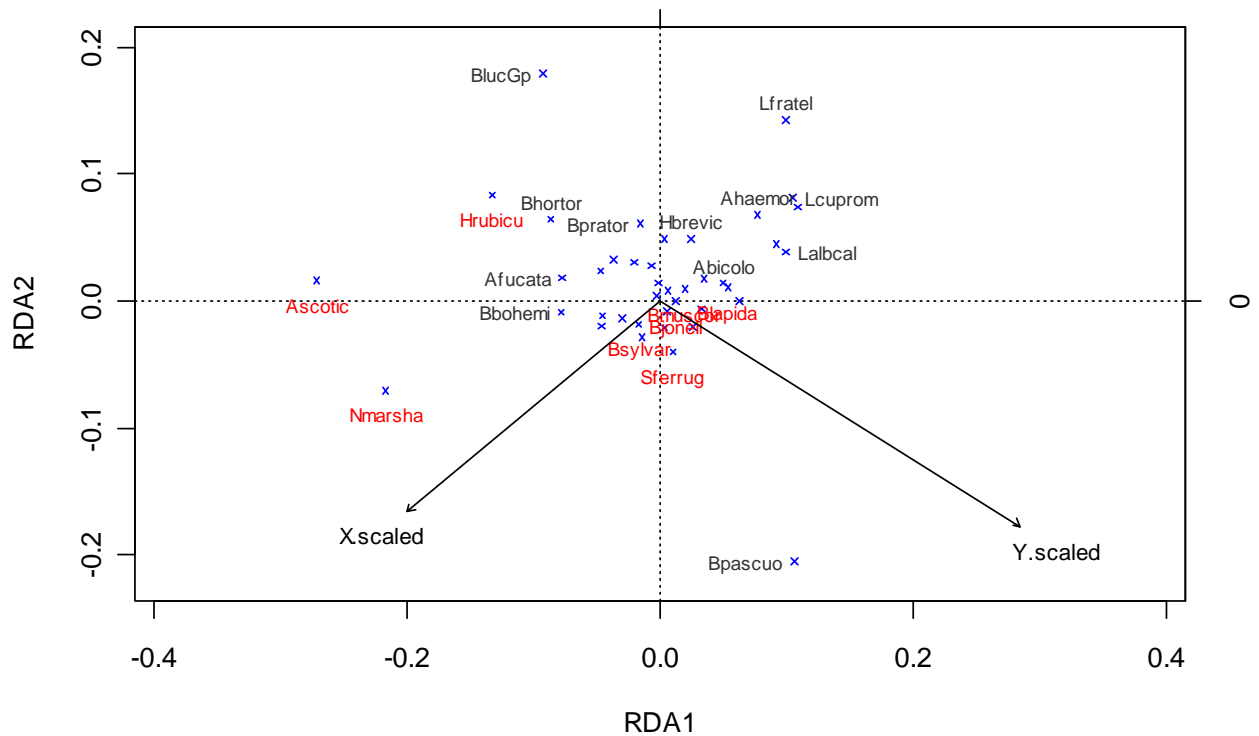


Figure 9.4. Correlation biplot (RDA scaling 2) of distance-based RDA (Hellinger distance) spatial model (M3) of wild bee assemblage composition, conditioned on environmental variables. Species shown in red are those for which the analysis explained more than 20% of the species variance.

SECOND TIER OF DECOMPOSITIONS: QUANTIFYING THE RELATIVE IMPORTANCE OF ENVIRONMENTAL INFLUENCES' PURE AND SHARED EFFECTS.

In the second tier of variance partitioning, the pure and shared effects of the sets of *environmental influences*, that is habitat quality, farm management and landscape composition, were to be quantified. However the models upon which these analyses were based were found to not be statistically significant at $p < 0.05$ for bee assemblages (all wild bees, solitary or bumblebees) and are therefore not presented. It is therefore not possible to *quantify* the pure and shared effects of habitat quality, farm management and landscape composition on bee assemblage composition using variance partitioning.

However it is possible to assess the importance of the environmental influences in terms of their effects on bee assemblages using their contribution to the environmental models for each assemblage in the first tier of decompositions.

9.3.4. IMPORTANCE OF ENVIRONMENTAL FACTORS IN INFLUENCING BEE ASSEMBLAGE STRUCTURE

No environmental influence, as measured in this study, was important in shaping bumblebee assemblage composition when bumblebees were considered separately from other wild bees. The contributions of each influence to the environmental models for solitary bee and all wild bee assemblages are reviewed below.

Agricultural management

When all wild bees were considered together, agricultural management intensity at the field level had significant and moderate effects (Table 9.6, Figure 9.5). These field management effects were independent of spatial effects.

When solitary bee and bumblebee assemblages were considered separately, no variable that directly described the intensity of agricultural management, at field, farm or landscape level, was identified as having a significant effect on composition.

Habitat quality

Grassland vegetation as it reflects soil pH had significant, moderate effects on the composition of wild bee assemblages (Table 9.6, Figure 9.5). These effects were evident even after the spatial component of variance had been partitioned out.

The p-value of the effect of botanical diversity of grassland vegetation on solitary bee assemblage structure approached statistical significance (Table 9.8). This association of botanical diversity of grassland vegetation was linked

with location (partitioning of the spatial component of variance, caused the environmental model to no longer be significant.)

Landscape composition

Before the spatial component of variance was partitioned out, landscape composition in terms of area of natural woodland, scrub and young forestry had a significant and moderate effect on the assemblage structure of solitary bees (Table 9.8 and Figure 9.6). This effect of landscape composition on solitary bees appear to be shared with location as the model was no longer significant when the spatial component of variance was partitioned out.

Table 9.6. Loadings of environmental variables onto axes of distance-based RDA (Hellinger distance) environmental model (M2) of wild bee assemblage composition, conditioned on spatial variables

All wild bees	p-value	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5
Environmental Model conditioned on spatial variables M2 , p= 0.005	axis/term	0.005	0.160	0.450	0.860	0.970
Area of semi-natural woodland & scrub and young forestry	0.52	-0.04	0.00	0.69	-0.15	0.36
Site scores on third axis of field vegetation PCO	0.05	-0.67	0.33	0.11	-0.29	-0.37
Site scores on first axis of field boundary vegetation PCO	0.52	0.16	-0.26	0.42	-0.01	-0.45
Enterprise: i.e. dairying or not	0.71	0.00	-0.37	-0.33	-0.77	-0.08
Site scores on first axis of PCO describing management of study field	0.03	-0.51	-0.46	0.24	0.52	0.41

9.3.5. SPECIES TRENDS

SPECIES RESPONSES TO SPATIAL MODEL FOR ALL WILD BEES (M3)

The abundances of a small number of bee species were strongly influenced by geographical location after the effects of other studied environmental factors were partitioned out. For example, the spatial model explained 78% of the variance in *Andrena scotica* abundances (Table 9.7). The ordination plot shows that it and its parasite, *Nomada marshamella* were very strongly associated with each other and with the North-easterly extreme of the study region. However geographical location explained much less of the variance in *Nomada marshamella* abundance (45%) than of its host.

For another group of species, although the spatial model explained a high proportion of their variance (>20%), their species centroids were near the origin of the ordination plot (species shown in red near the origin in Figure 9.4). Taking *Bombus sylvarum* as an example, 38% of this species' variance (Table 9.7) was explained by the spatial model alone but it had low scores on axes 1 and 2 (Figure 9.4). This combination for a species, of low axes scores and no association with any extreme in x and y co-ordinates was interpreted as highlighting species with restricted or patchy geographical distributions that were not associated with extremes in latitude or longitude. Supporting this interpretation, though *B. sylvarum* shows a restricted distribution nowadays, historical records (Fitzpatrick *et al.* 2007) show this species to have been more widespread in the past, indicating that its present day distribution is not restricted by geographical factors.

SPECIES RESPONSES TO ENVIRONMENTAL MODEL FOR ALL WILD BEES (M2)

The main environmental influences in the environmental model for all wild bees, after the partitioning out of spatial effects, were intensity of agricultural management at the field level and grassland vegetation composition as it reflected soil pH. Taking *Nomada marshamella* and *A. scotica* as a case study: these species were very highly correlated with each other in the ordination constrained by geographical location. However after location was partitioned out they were not correlated in the environmental

model. The parasitic species is much less tolerant of agricultural intensification at the field scale than its host species.

The ordination biplot shows that in environments with higher intensity field management and more calcareous soil conditions or both, that the bee assemblage is likely to be dominated by common bumblebees and a few solitary bee species. In environments with less intense field management and more acidic soil conditions or both, the bee assemblage will be dominated by solitary bee species. Only a few species had extreme negative scores on axis 1 indicating an association with more acidic grassland vegetation managed at low intensity e.g. *Halictus rubicundus* and *Nomada marshamella*. The majority of species had less extreme negative scores on axis 1. This was interpreted to mean that the majority of bee species were associated with more neutral to calcareous grasslands, managed at relatively low intensities.

Species sensitive to intensity of agricultural management at the field level and grassland vegetation composition as it reflected soil pH were regarded as those with negative scores on the first axis. Species with positive scores were regarded as tolerant of these conditions.

These analyses did not distinguish between agricultural management at the field level and grassland vegetation composition as it reflected soil pH. However for the bumblebees with positive scores, identified as 'tolerant species', it is likely that the widespread and common species; *B. pascuorum*, *B. hortorum*, *B. pratorum* and *B. lucorum* group are tolerant of higher intensity field management. For *B. sylvarum*, which was restricted to one area within the study region, its position in the ordination was due to an association with calcareous grasslands.

A suitable indicator species for shifts in bee assemblages in response to the environmental gradient described would be a species with an extreme score along the first axis, for which the environmental model explained a large proportion of its variance (meaning that other environmental variables would not confuse interpretation of its response) and for which the spatial model explained a negligible amount (meaning that it is widespread). No species meets these criteria (Table 9.7).

Table 9.7. Proportion of variance in abundance of each species explained by spatial (M3) and environmental (M2) models

Bee Species	Spatial model with environmental set as covariables (M3) (p=0.005)	Environmental model, with spatial set as covariables (M2) (p=0.005)
Bbohemi	9.39	9.79
Bhortor	5.26	1.75
Bjonell	18.28	17.14
Blapida	21.72	20.26
BlucGp	22.04	10.20
Bmuscor	21.97	17.59
Bpascuo	20.33	7.80
Bprator	21.68	0.56
Brupest	27.14	4.65
Bsylvr	38.00	22.93
Bsylvr	12.93	11.39
Aangust	5.74	7.30
Abarbil	10.84	3.92
Abicolo	24.80	7.99
Acinera	4.04	1.72
Aclarke	11.74	3.04
Acoitan	4.02	12.44
Adentic	19.61	28.28
Afucata	22.07	21.21
Ahaemor	11.60	6.88
Anigroa	17.27	0.19
Ascotic	78.35	74.72
Asubopa	14.24	5.14
Hbrevic	10.27	2.02
Hconfus	10.08	9.61
Hrubicu	23.91	4.64
Htumulo	14.89	2.91
Lalbccl	2.89	15.85
Lcuprom	18.22	37.85
Lfratel	19.60	38.95
Lleucop	5.72	2.66
Lnitidi	6.94	3.91
Lpuncta	18.19	6.59
Lvillos	19.79	1.16
Mversic	18.55	6.73
Nflavog	18.24	6.01
Nfabric	9.99	3.69
Nleucop	7.83	5.95
Nmarsha	44.77	26.17
Npanzer	7.26	20.59
Nrufico	5.24	4.73
Nrufipe	17.32	4.87
Nstriata	18.80	13.24
Sephipp	8.17	0.98
Sferrug	17.13	18.48
Sgeoffr	11.74	3.04
Shyalin	13.44	6.77

SPECIES RESPONSES TO ENVIRONMENTAL MODEL FOR SOLITARY BEES

(M1)

The environmental model (M1) without removal of confounding spatial effects is presented. When spatial effects were removed, the environmental model was no longer significant at $p < 0.05$. This shows that the environmental effects described in this section are correlated with place.

The assemblage of solitary bees was mainly structured by their response to landscape composition in terms of area of natural woodland, scrub and young forestry plantations. This gradient described landscapes with fields enclosed by hedgerows progressing to landscapes that were historically unenclosed or open and now have areas of semi-natural woodland, scrub or young forestry. Species associated with open landscapes with developing scrub, woodland or young forestry were *Andrena bicolor*, *Lasioglossum albipes/calceatum* group, *Lasioglossum cupromicans* and *Nomada ruficornis*. Species associated with an enclosed landscape were *N. marshamella* and *A. scotica*.

Table 9.8. Loadings of environmental variables onto axes of distance-based RDA (Hellinger distance) environmental model, with no constraints (M1), for solitary bee composition.

Solitary bees	p-value	RDA1
Environmental Model with no constraints, M1, $p=0.02$	axis/term	0.005
Area of natural woodland, scrub and young forestry plantations (scaled)	0.03	-0.56
Sward vegetations' Inverse Simpson Index (scaled)	0.08	-0.44
Sward vegetations' Ellenberg for soil moisture (scaled)	0.48	0.34
Site scores on 1st axis of grassland vegetation PCO (scaled)	0.16	0.08
Hedgerow structural index (scaled)	0.29	0.63
Site scores on 1st axis of hedgerow vegetation axis PCO (scaled)	0.27	-0.69

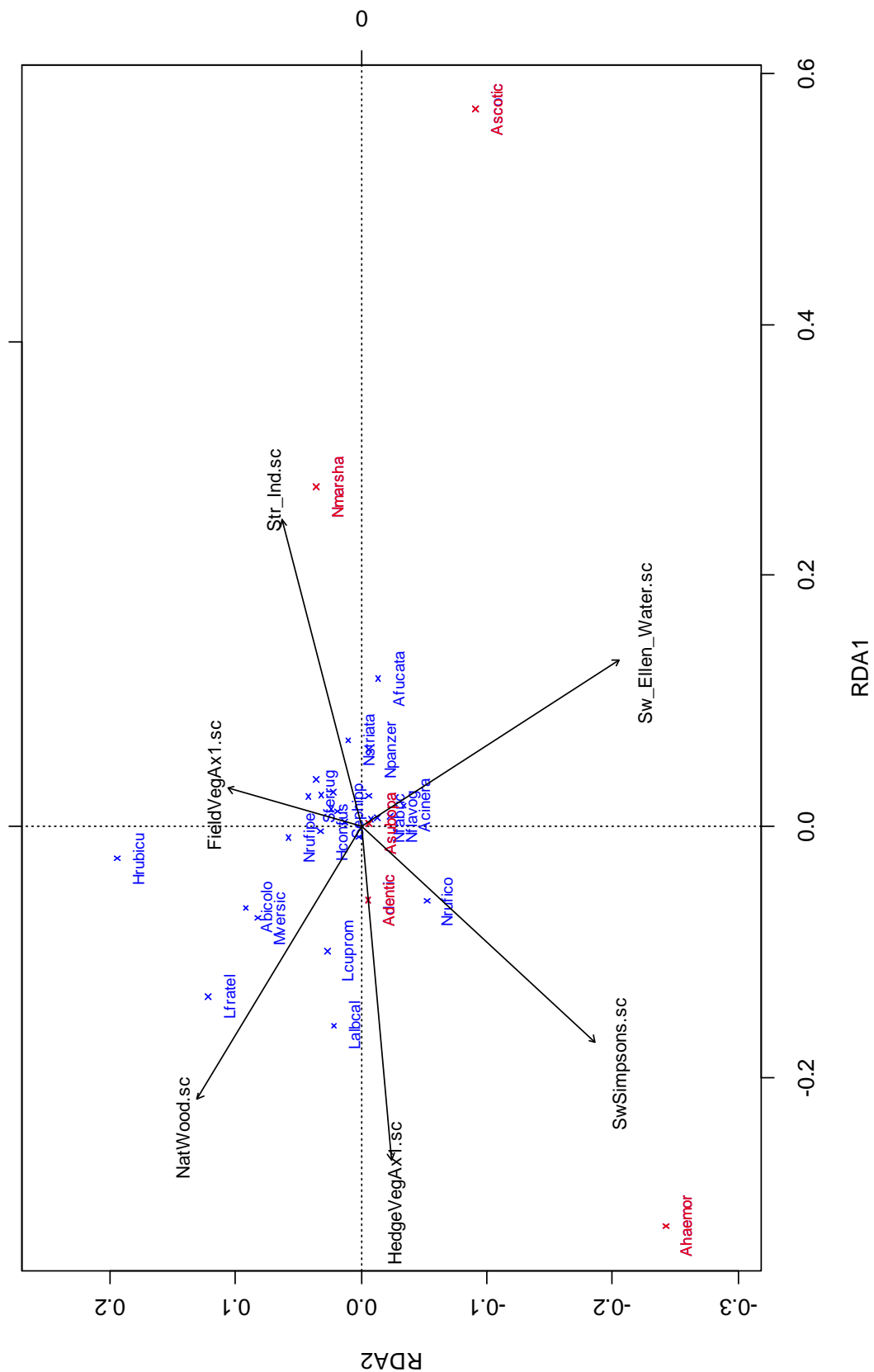


Figure 9.6. Hellinger distance-based RDA Model M1 (Environmental variables explanatory; no covariables) for solitary bees only. Only axis 1 is significant at $p=0.05$. Species shown in red are those for which the ordination explained >20% of their variance.

9.3.6. PERMUTATIONAL MANOVA TESTING FOR DIFFERENCES BETWEEN BEE ASSEMBLAGES OF FARMS MANAGED INTENSELY AND EXTENSIVELY AND BETWEEN LANDSCAPES.

AGRICULTURAL INTENSITY AT THE FIELD LEVEL

Testing with permutational MANOVA showed there to be no significant differences between the composition of wild bee assemblages at sites which had more intensive agricultural management compared to those with less intensive management when considered at the field level (reseeded field compared to old pasture).

AGRICULTURAL INTENSITY AT THE FARM LEVEL

Testing with permutational MANOVA showed there to be no significant differences between the composition of wild bee assemblages at sites which had more intensive agricultural management compared to those with less intensive management when considered at the farm level (dairy farm was compared to non-dairying farm).

AGRICULTURAL INTENSITY AT THE LANDSCAPE LEVEL

Testing with permutational MANOVA showed there to be no significant differences between the composition of wild bee assemblages at sites which had more intensive agricultural management compared to those with less intensive management when considered at the landscape level (landscape type 1, with low proportions of semi-natural habitat and high proportion of intensively managed grasslands was compared with landscape type 3 with high proportions of semi-natural habitat and low proportion of intensively managed grasslands).

9. 4. DISCUSSION

The assemblage structure of bees was shown to be shaped mainly by natural or bio-geographic factors. Change in assemblage composition due to agricultural intensification in recent decades was detected as a subtle shift in the relative proportions within the assemblage made up by common bumblebees and diverse solitary bees.

9.4.1. SPATIAL EFFECTS ON BEE ASSEMBLAGE COMPOSITION IN LOWLAND PASTORAL LANDSCAPES

RELATIVE IMPORTANCE OF SPATIAL INFLUENCES

Spatial effects explained, on their own, approximately 9% of the variance in species composition of wild bee assemblages. A further 7% of solitary bee or all wild bee variance was explained by the shared effects of location with other environmental variables.

Spatial effects were the most important influence on bumblebee assemblage detected (no other effects were distinguished).

For solitary bees, pure spatial effects were not as strong an influence as the pure effects of local environmental conditions which explained 1.4x more variance. Associations between spatial variables and landscape composition and habitat qualities had a shared effect that explained 7.6% of solitary bee variance.

The spatial effect on bee assemblage composition was much greater than the contribution detected in cities (Sattler *et al.* 2010) and very similar to that reported for bees in Special Areas of Conservation in Ireland (8.8%) (Murray *et al.* 2012, Supplementary Information).

Sattler *et al.* (2010) interpreted the near absence of spatial structure to suggest that processes such as dispersal and competition between species

play a minor part in the structuring of the assemblage and that instead it is human pressures and the capacity to cope with them that determines species composition.

The strength of spatial effects detected in this study may be an indicator that bee communities on pastoral farmland in the study region are still being structured by natural processes.

SPATIAL GRADIENTS INFLUENCING BEE ASSEMBLAGE COMPOSITION

This study focused on identifying spatial structure in bee assemblages arising from bee responses to environmental variables that are themselves spatially structured i.e. exogenous sources of spatial structure or spatial dependence (Legendre *et al.* 2002).

A large part of the spatial structure in bee assemblage composition is associated with a North-east to South-west gradient. This gradient was associated with an altitudinal gradient (from sea level to 170m) and gradient in rainfall (range in 1981-2010 mean annual rainfall from 1000mm to 1400mm) (Met Éireann 2013).

Climate is recognised as the main bio-geographical influence structuring bee assemblages (Michener 2000; Patiny *et al.* 2009a; Minckley 2008; Abrahamczyk *et al.* 2011). Dormann *et al.* (2008) has predicted that climate change is more important than changing land-use intensity in terms of influencing future species richness of bees in Europe. Flux in bee communities has been reported in the Arctic in response to climate change (Franzen & Ockinger 2012). The simulation models of Kuhlmann *et al.* (2012) for bees responses to climate change in Africa indicated that bee species will differ greatly in their responses to climate change. Climatic specialization has been identified as a risk factor for bumblebee species decline (Williams 2005a). Given the less developed thermoregulation capabilities of solitary bees (Heinrich & Esch 1994; Bishop & Armbruster 1999) these are likely to be particularly at risk.

It was not possible, in this study, to distinguish between the relative effects of climatic and other variables associated with altitude on bees. However the strength of these biogeographical effects on some species, such as *Andrena*

scotica , associated with the North-eastern edge of the study region, and its parasite *Nomada marshamella*, may indicate a sensitivity to climate and climate change.

9.4.2. ENVIRONMENTAL INFLUENCES ON BEE ASSEMBLAGE COMPOSITION IN LOWLAND PASTORAL LANDSCAPES

Environmental variables, together, explained 12.4% of total variance in wild bee assemblages as a pure effect and a further 6.6% was confounded with geographical influences. The amount of variance explained is lower than in Murray *et al.* (2012) (nesting resources explained 23.6% of the total variance in bee assemblage composition on semi-natural grasslands) but comparable with Schweiger *et al.* (2005).

For bumblebees, no other environmental influence apart from spatial effects was found to have a significant effect on assemblage composition. This contrasts with Murray *et al.* (2012) who explained 17.8% of the variance in bumblebee community data with the effects of site management of semi-natural grasslands and found bumblebees to be more sensitive to site management than solitary bees. On the typical farmland in this study region, environmental influences acted primarily on the solitary bee component of wild bee assemblages, rather than on bumblebees. The heterogeneity in wild bee assemblages was shown to be chiefly due to solitary bees.

The failure to detect environmental effects on bumblebee species composition in this study in comparison with Murray *et al.* (2012) is interpreted to be due to the reduction in habitat quality of grasslands studied and bumblebee species sensitive to grassland management having already been exterminated from most farmland. Dormann *et al.* (2008) put forward a similar hypothesis for the predicted lack of diversity response of bees across Europe to future land-use change compared to climate change.

The relative importance and pure and shared effects of the sets of environmental influences, that is habitat quality, farm management and landscape composition, on bee assemblages were to have been determined using a second tier of variance partitioning. This was not possible as the

Page 299 of 464

models upon which analyses were based were not statistically significant. Although the relative effects of environmental influences could not be *quantified* using variance partitioning, useful information was extracted about their importance for the structuring of bee assemblages from their contributions to the models in the first tier of decompositions. The following sections describe these influences.

EFFECTS OF LANDSCAPE COMPOSITION ON BEE ASSEMBLAGE COMPOSITION

Landscape composition influenced solitary bee composition but not bumblebee composition. The effects of this gradient were shared with spatial effects.

Murray *et al.* (2012), Bommarco *et al.* (2010) and Holzschuh *et al.* (2008) also found the solitary bee component to be more sensitive than bumblebees to surrounding land-use. This sensitivity was interpreted by these authors to be due to the reduced dispersal distances of solitary bees compared to bumblebees making them more dependent on nearby habitat patches whereas larger and more mobile bees were better able to tolerate habitat loss from the local landscape.

The element of landscape composition that solitary bees were sensitive to in this study was a gradient describing the organization of trees and shrub cover in the landscape. Bee composition has also been associated with tree cover in other studies (e.g. Munyuli *et al.* 2013; Tscharntke *et al.* 1998; Artz & Waddington 2006 and Carré *et al.* 2009).

However though the spatial organization of tree cover varied, the total area of tree cover was relatively constant along the gradient (Chapter 4). Solitary bee assemblage composition was therefore not sensitive to the area of tree and shrub cover per se. The explanation of an effect for solitary bees but not bumblebees therefore needed to be reconsidered. The hypothesis put forward by Murray *et al.* (2012), Bommarco *et al.* (2010) and Holzschuh *et al.* (2008) could not apply to this landscape gradient as the availability of habitat remained constant along it.

The gradient described landscapes with fields enclosed by hedgerows progressing to landscapes that were historically unenclosed or open and now have areas of semi-natural woodland, scrub or young forestry. Enclosure of the landscape with hedgerows reflects a longer history of more productive agriculture and indicates a greater level of disturbance in the landscape, possibly since the eighteenth century (Hall 1994). The gradient is therefore associated with past and present land-use intensity as well as today's pattern of tree cover. Historical landuse intensity may be responsible for the differences in solitary bee composition.

Microclimate may provide an alternative explanation for the association of solitary bee composition and not bumblebees with this landscape gradient. Hedgerows slow air flux and influence sunlight levels, humidity and other dimensions of microclimate as well as soil desiccation (Forman & Baudry 1984; Burel 1996). These are factors to which bees are sensitive (Potts & Willmer 1997; Cane 1991; Stone 1994; Herrera 1995). Solitary bees are likely to be more responsive to the microclimates fostered by a hedgerow enclosed landscape than bumblebees due to their weaker thermoregulation (Michener 1979; Bishop & Armbruster 1999) and flight capacities (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007).

EFFECTS OF HABITAT QUALITY ON BEE ASSEMBLAGE COMPOSITION

Indirect analyses (Ter Braak 1987) in Chapter 8 showed a number of habitat quality variables describing the vegetation of hedgerows and grasslands to be correlated with bee assemblage composition.

However this chapter's direct analyses (Ter Braak 1987) identified only grassland vegetation as it reflects soil pH to have significant effects on the composition of wild bee assemblages. The habitat quality variables identified as correlated with bee assemblage composition in indirect analyses were therefore collinear.

Grassland composition as it reflects soil pH is the most important 'habitat quality' predictor of bee assemblage structure. Murray *et al.* (2012) found calcareous grasslands, of all semi-natural habitats in Ireland, to support the highest levels of bee diversity. This association of bee diversity with

calcareous soils is a general one, having been observed across Europe (Steffan-Dewenter & Tscharntke 1999; Goulson *et al.* 2006; Krauss *et al.* 2009; Krewenka *et al.* 2011).

EFFECTS OF AGRICULTURAL MANAGEMENT ON BEE ASSEMBLAGE COMPOSITION

The effects of agricultural management on the composition of wild bee assemblages were not apparent in this study region when only bumblebees were considered. This is probably because the species that are particularly sensitive to agricultural management are already extinct from local areas of farmland in the East of the country (Santorum & Breen 2005a; Fitzpatrick *et al.* 2007). Others have found bumblebees to be sensitive to field level management (Soderstrom *et al.* 2001; Murray *et al.* 2012) and shifts in bumblebee assemblage composition in response to landscape scale land-use change have also been reported (Sepp *et al.* 2004; Dupont *et al.* 2011; Bommarco *et al.* 2012).

However when the entire bee assemblage was considered together, a shift in composition from assemblages dominated by diverse solitary bees to assemblages dominated by common bumblebees and a few solitary bee species was noted as field management became more intense. This finding supports the assertion by Carré *et al.* (2009) that agricultural intensification does not lead to the extinction of all bees in agricultural systems but changes the structure of the bee assemblage so that resilient species come to dominate and vulnerable species are lost. (Note that the effects of this field management gradient on bee assemblage composition were shared with the effects of grassland vegetation varying in response to soil pH. It was not possible to separate the effects of these two variables on bee assemblages in this study.)

Le Feon *et al.* (2010) reported that in areas of high intensity of agricultural management in four Western European countries, (Belgium, France, the Netherlands and Switzerland), that bumblebees became more abundant relative to solitary bees. This study suggests a similar change may be occurring in Ireland, though analyses of abundance are required to verify this. This analysis will follow in Chapter 10.

This is one of the first studies to consider whether shifts in solitary bee assemblage accompany changes in bumblebee assemblages. Certainly declines among bumblebees have led to a few common species dominating bumblebee assemblages in the UK (Williams 1982) and Ireland (Santorum & Breen 2005a; Fitzpatrick *et al.* 2007).

Although shifts in assemblage composition along a gradient of intensifying field management were discernible they were not so great that they resulted in assemblages that were significantly different on MANOVA testing for fields, farms or landscapes managed at the high and low extremes of agricultural intensification in the region.

It is possible that changes in bee assemblage composition in response to agricultural intensification are not always in the same direction and are therefore difficult to detect with ordination methods. Alternatively, species may be lost in a highly predictable order and impacted assemblages are subsets, or nested within the original, intact assemblage (Atmar & Patterson 1993). This would obscure differences between assemblages from methods such as Permutational MANOVA. The combination of methods used in this study is an attempt to overcome these problems.

Such issues, together with high variability in bee assemblages that is unconnected with the environmental factors being studied but caused by spatial and temporal fluctuations as well as the large proportion of rare species in bee assemblages (Williams *et al.* 2001; Oertli *et al.* 2005) are thought to have led to the poor performance of environmental models in explaining variance in bee assemblages.

To overcome this common problem, Cane *et al.* (2006) and Williams *et al.* (2010) suggest that the use of guild and functional groups may reveal patterns that are not visible when the entire assemblage is studied. This approach is taken in Chapter 10 to determine whether wild bees are responding to environmental factors in the pastoral landscape in ways that are not revealed by analyses of species composition.

Despite the challenges, there is a need for studies of species composition and relative abundance so that the responses of individual species to land-use

change can be identified (Winfree 2010; Winfree *et al.* 2011). This study shows the value of this approach and successfully highlighted a number of species that showed sensitivity or resilience to environmental factors.

In terms of using these responsive species as biotic indicators, only those that have a widespread geographic distribution can be used generally as indicators (Pearson 1994). This study has shown that most solitary bee species have geographically restricted distributions and are therefore unsuitable as indicators. Bumblebees offer greater possibilities as biotic indicators as more bumblebee species are either widely distributed now or were historically.

SUMMARY

Spatial effects were very important in influencing the species abundance composition of wild bee assemblages in the farmland studied. Their strength was similar to that reported for bees in Special Areas of Conservation in Ireland (Murray *et al.* 2012) and may therefore indicate that bee assemblages on farmland are still structured predominantly by natural processes. A Northeast to Southwest gradient, contributed to these spatial effects. Species of solitary bees were identified that are very sensitive to this gradient.

No environmental effects, apart from the spatial effects, were identified that shaped the bumblebee component of the wild bee assemblage. This is likely to be because species of bumblebees sensitive to land-use change have already been lost from most farmland in the study region.

A landscape composition gradient describing landscapes enclosed by hedgerows grading into open landscapes with patches of woodland, scrub and young forestry plantations was identified as an influence on solitary bee assemblage structure. This is not regarded as a habitat availability effect. Instead the spatial configuration of woody habitat, or another predictor correlated with it such as historical land-use, is important to solitary bee composition.

In Chapter 8, indirect analyses identified a list of habitat qualities that were correlated with bee assemblage structure. However constrained analyses in this chapter showed only grassland vegetation as it reflected soil pH to have a significant effect. The other habitat quality variables correlated with bee assemblage structure are therefore also correlated with each other and this predictor.

Agricultural intensification at the field level is associated with a shift in the assemblage composition of wild bees. Common bumblebees come to dominate and solitary bee diversity declines. This environmental gradient was shared with the effects of vegetation as it reflected soil pH.

The shift in wild bee assemblages in response to agricultural intensification was not large enough to be statistically significant on testing with MANOVA.

Bee species were identified that are particularly sensitive or tolerant of agricultural intensification, though this was gradient could not be separated from the effects of grassland vegetation as it reflected soil pH.

Solitary bee species identified as particularly sensitive or tolerant were not geographically widespread and are therefore not suitable as general biotic indicators. Bumblebees offer more possibilities.

CHAPTER 10: ENVIRONMENTAL CONDITIONS ASSOCIATED WITH BEE ABUNDANCE AND DIVERSITY

10. 1. INTRODUCTION

In Chapter 9, patterns in species composition of bee assemblages in relation to environmental factors in pastoral landscapes were analysed. Williams *et al.* (2010) suggests that the use of guilds and functional groups may reveal patterns that are not visible when the entire assemblage's species composition is studied. This chapter takes such an approach and uses abundance and diversity as alternative measures of bee responses and studies their association with the environmental conditions evaluated in Chapter 9, looking for further ecological patterns.

10.1.1. LITERATURE REVIEW

Chapters 1-9 have reviewed the literature and explained current knowledge about bee responses to landscape composition; agricultural management; local habitat quality and geographical location.

Challenges for analysis

Spatial autocorrelation in bee assemblages, that is a spatial structuring of the response variable due to its own behaviour and response to the environment (Legendre *et al.* 2002), was detected over distances less than 10km (Chapter 8). Further spatial pattern in bee assemblages arose from explanatory variables being spatially structured (Chapter 8 and 9) (spatial dependence (Legendre *et al.* 2002)). This also causes collinearity or spatial synchrony between explanatory variables (Cliff & Ord 1973; Koenig 1999).

Spatial autocorrelation means that *data points are not independent* and there is a strong risk of pseudoreplication (Hurlbert 1984).

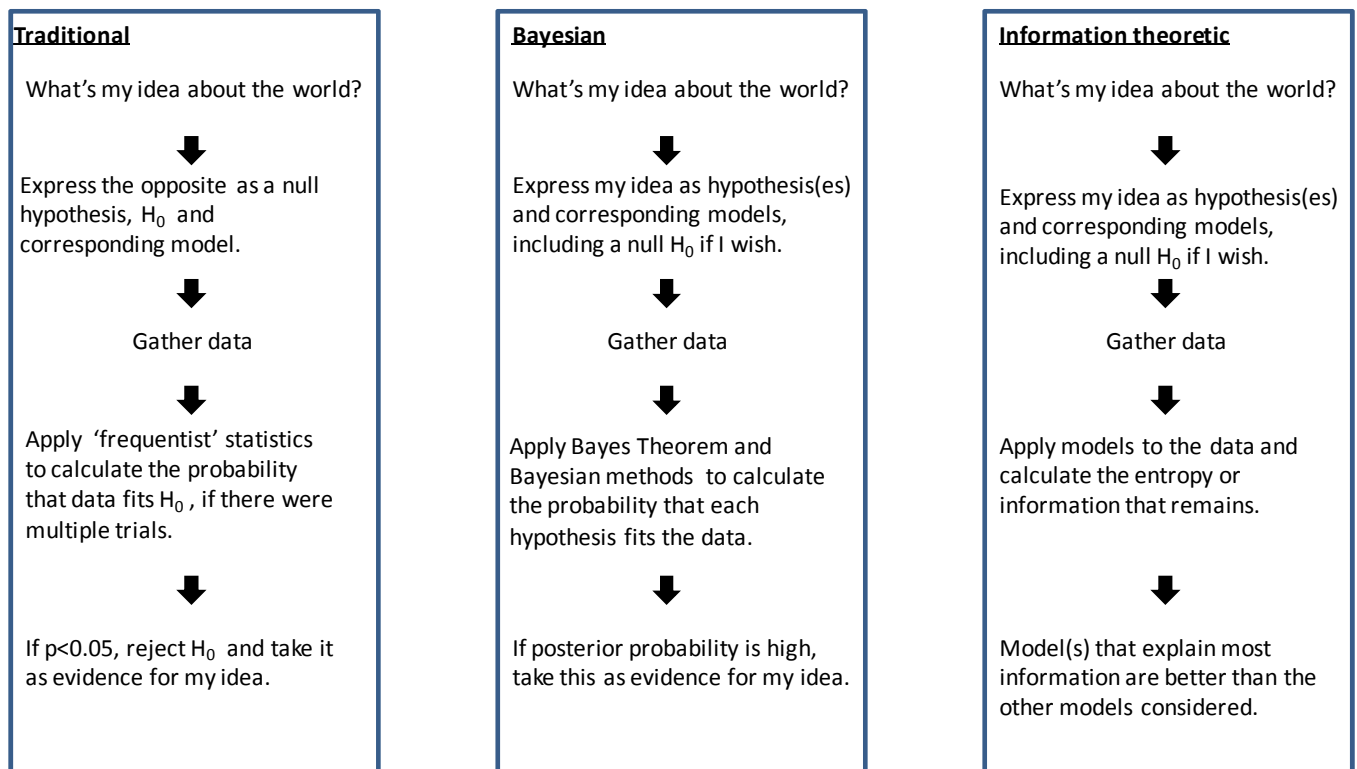
Spatial dependence and correlations between explanatory variables cause problems for automated selection methods (e.g. backwards elimination, forwards selection) in regression analysis (Burnham & Anderson 2002a; Whittingham *et al.* 2006). Models with different combinations of explanatory variables will be reached depending on the automatic selection method used and order of variables (Dormann 2007). I seek to identify which predictors are

most important to bees. This is precisely the situation in which collinearity is most problematic (Mac Nally 2000; Zuur *et al.* 2010).

Bayesian and Information theoretic approaches and model averaging are considered preferable to stepwise regression methods as these reduce the risk of omitting important terms and giving biased parameters when collinearity is present (Johnson & Omland 2004; Hobbs & Hilborn 2006; Link & Barker 2006).

I used several different statistical approaches to judge the importance of predictor variables influence on bee abundances and diversity: frequentist methods, information theoretic methods and Bayesian methods. The statistical methods differ so fundamentally in their approach to scientific problems that they can be considered different statistical paradigms (Anderson *et al.* 2001) (Figure 10.1). Each statistical approach provides different outputs, which together enhance understanding of the problem. If the results reached using different statistical methods agree, this gives additional confidence to the findings and if the results disagree then assumptions can be isolated (Mac Nally 2000; Stephens *et al.* 2005).

Figure 10.1. Overview of three statistical paradigms used in analyses



Bayesian methods calculate the posterior probabilities of the ideas based on the evidence in the data. Posterior probabilities are very different to traditional p-values.

A traditional p-value gives the probability that the data would fit the null hypothesis if the study were repeated many times; that is, $P(D/H)$ = probability of the data, D, given the hypothesis, H.

Whereas Bayesian posterior probability = $P(H/D)$ = probability of the hypothesis, H, given the data, D. (Ellison 1996).

I used this combination of methods partly to overcome some of the limitations of stepwise multiple regression which have been summarised as bias in estimation of model parameters, a focus on a single best model and inconsistencies among model selection algorithms (Whittingham *et al.* 2006). A further reason was that Information theoretic and Bayesian methods are particularly useful in exploratory observational studies such as this one (Anderson 2008).

In a situation where only one model fits the data well, traditional stepwise regression methods would be adequate to identify the influential terms and estimate model parameters. However, if several models fit the data well, then stepwise regression methods would omit important terms and give biased parameters. Bayesian and Information theoretic approaches and model averaging would then be preferable (Johnson & Omland 2004; Hobbs & Hilborn 2006; Link & Barker 2006).

Bayesian methods were used to determine whether one or multiple models fit the data and to give a measure of model certainty.

Predictions using Bayesian averaged models were used for illustrative purposes, to facilitate understanding of the models, rather than for management or policy decision making.

The importance of variables was judged using the posterior probabilities of their coefficients in the averaged model (Bayesian approach) and their sums of Akaike weights (Information theoretic approach). Evidence ratios of sums

of Akaike weights allowed for direct comparison of predictors' importance (Burnham & Anderson 2002b). All possible models, using every variable but excluding interactions, were used in the analyses. Such an approach normally draws criticism for being unthinking in terms of scientific hypotheses but is regarded as a valid method for the evaluation of the relative importance of variables when equal treatment of each variable is required (Anderson 2008).

Factors affecting bees do not act independently (Brown & Paxton 2009). For example, landscape composition, farm management, location and the agricultural potential of the region in terms of its climate and soils may be correlated with each other and interact in their effects on bees. Variance partitioning (Legendre & Legendre 1998) was used to separate between the effects of those variables identified as most important and the effects of location. Location and factors associated with it are likely to be resilient to manipulation and are therefore likely to be unsuitable targets for environmental measures and policy.

Levels at which diversity in bee assemblages was considered

The diversity of bees was studied at two taxonomic levels, those of species and genera.

Species richness is the most commonly used as a measure of diversity (Magurran 2004). Studies using higher taxonomic levels are infrequent but have been used as a surrogate for species richness to reduce sampling effort in diversity studies (e.g. Cardoso *et al.* 2004; Biaggini *et al.* 2007; Rosser & Eggleton 2012). In this study, the number of genera was used as a correlate with functional diversity rather than as a surrogate for the number of species.

Studying change in functional diversity along environmental gradients can develop insights into bee community responses to environmental change (Biesmeijer & Slaa 2006; Cane *et al.* 2006; Hoehn *et al.* 2008; Moretti *et al.* 2009) and identify traits that make species vulnerable or able to colonise new conditions (Bommarco *et al.* 2010; Williams *et al.* 2010; Banaszak-Cibicka & Żmihorski 2012). Some authors have cautioned that genera may behave as

random groups of species rather than species with similar ecological traits (Bevilacqua *et al.* 2012) and data above the species level may not be sufficiently sensitive to detect environmental change (Grimbacher *et al.* 2008). Bees might be an exception to this limitation given the high degree of differentiation in functional traits between genera. Bee genera show different functional traits in terms of parasitism, social behaviour, nesting behaviour, foraging, size and flight period (Michener 2000; O'Toole & Raw 2004).

In Ireland, where there are only eleven bee genera (plus *Apis*) (Fitzpatrick *et al.* 2006a), it was anticipated that number of genera might provide a quick and easy surrogate measure of functional diversity. *Psithyrus* were counted as an additional unit of diversity although they are classified as a subgenus of *Bombus*. Being parasitic, *Psithyrus* species are functionally very different from *Bombus* species.

Bee diversity and abundance were also studied at the guild level. Bumblebees and solitary bees were predicted to differ in their relative vulnerabilities to environmental factors (see Chapter 1) and were analysed separately. The hypotheses, based upon differences in mobility and reported vulnerability in other agri-ecosystems (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2003; Albrecht *et al.* 2007; Krauss *et al.* 2009; Williams *et al.* 2010) were:

Solitary bees will be more sensitive to small scale factors i.e. habitat structure, botanical composition and field and farm management at the study site rather than to landscape composition.

Bumblebees will be more sensitive to landscape composition than to field and farm management.

Different conservation approaches may be required if bumblebees and solitary bees are sensitive to different influences.

Summary

This study is chiefly exploratory with some testing of hypotheses developed from the literature. Its aim is to determine the relative importance of geographical location, landscape composition, vegetation of grasslands and

hedgerows, hedgerow structure and agricultural management on the abundances and diversity of bees in simple pastoral landscapes.

The effects of the most influential of these factors on bees will be filtered from location effects to give a clearer understanding of the factors which may be easily managed for bee conservation and those which are likely to be resilient to change.

Landscape was considered at a relatively small scale and agricultural management along a gradient rather than extremes.

As well as effects on abundance and species richness of bees, effects on bee functional diversity were studied, using number of genera as a surrogate for functional diversity.

Several complimentary analytical approaches were used to strengthen confidence in findings and promote further thinking if a mismatch in results is found.

Predictions of how bee abundances and diversity vary for a number of scenarios typical of Irish farming were made using averaged models. These predictions are for illustrative purposes only. The main purpose of this study is to identify the most important influences that can be managed for bee conservation in pastoral landscapes.

10. 2. METHODS

10.2.1. PREPARATION AND PRELIMINARY EXPLORATION OF DATA

Response variables, their distribution, outliers and transformations

The responses of five measures of bee abundance and diversity to environmental predictors were investigated. The response variables: bumblebee abundance; solitary bee abundance; bumblebee species number; solitary bee species number and number of wild bee genera, were totals

observed over a standard sampling period of 6 weeks of pan-traps at each site (see Chapter 3 for details of survey methods).

Data from 45 sites, for which complete management data was available, were analysed.

Chapters 4-7 describe how the explanatory variables, which described landscape composition; agricultural management; local habitat quality and geographical location, were measured and reduced to the representative set (Table 10.1) used in these analyses.

The distributions of response and explanatory variables were checked using simple graphing methods (histograms, QQ plots (theoretical quantile against sample quantile plots), dotplots and boxplots).

Response variables were transformed to reduce heteroscedasticity, the effects of outliers and skew in distribution so that the data approximated to a Gaussian distribution (see Appendix 18 for QQ plots of transformed data). This allowed parametric methods to be used.

The transformations applied were:

[A] To bumblebee abundance : $\text{Ln}(\text{Bumblebee abundance} + 4)$;

[B] To solitary bee abundance: $\text{Ln}(\text{Solitary bee abundance} + 1)$;

[C] To number of bumblebee species: Square-root (Number of bumblebee species);

[D] To number of solitary bee species: $\text{Ln}(\text{Number of solitary bee species} + 1)$;

[E] To number of genera of wild bees: $\text{Ln}(\text{Number of genera of wild bees} + 1)$

One site, a sandpit that had been reclaimed as farmland, had very high abundances of solitary bees. Analyses for solitary bees were run with and without this site. It was found not to be overly influential in the models and the case was retained in the dataset.

Continuous explanatory variables were z-transformed, that is, mean-centred and scaled by their standard deviation. This has the effect of minimising correlations among the predictor variables making analyses more robust.

Factors were polychotomised (e.g. if 3 categories, converted to two variables with 1s and 0s that captures all the information of the 3 original categories). Histograms of the distributions of standardised explanatory variables were plotted and the spread of values was judged sufficiently normal for the use of parametric analytical methods (Appendix 18).

Table 10.1 Explanatory variables used in analyses of bee abundances and diversity. See Chapters 4-7 for methods.

Environmental influence	Variable	Summary
Geographical location	Xeast	Six figure Irish grid reference easting. Range = 127360 - 190120
	Ynorth	Six figure Irish grid reference northing. Range = 116940 - 158890
Landscape composition	impgrass	Area of improved grassland within 100m radius of sampling point. Range = 0.00 – 2.85ha (highly correlated with first axis of landscape PCO)
	wood	Area of woodland, scrub and young forestry within 100m radius of sampling point. Range = 0.00 – 1.74ha (highly correlated with 2 nd axis of landscape PCO)
Grassland vegetation	sward1	Sites scores on grassland vegetation PCO axis 1. Reflective of soil fertility. High positive scores indicate botanical composition typical of low soil fertility with higher species diversity. Low negative scores indicate plant composition typical of highly fertilised conditions with low species diversity. Range = -1.47 – 0.95
	sward2	Sites scores on grassland vegetation PCO axis 3. Reflective of soil pH and calcium and magnesium content. High positive scores indicate plant composition typical of more acid soils. Range = -2.00 – 1.30
Hedgerow structure and vegetation	hgSimp	Simpsons index. A higher score reflected higher species diversity and evenness. Range = 1.38 – 7.28
	index	Structural Index, an ordinal scale, scoring the complexity of the hedgerow and associated features. The variable was treated as continuous due to large number of categories, i.e. ten. Range = 3 - 13
	hedge1	Site scores on the first axis of a PCO of field boundary vegetation. Reflects a gradient in composition from <i>Crataegus monogyna</i> (negative scores) to <i>Prunus spinosa</i> domination (positive scores). Extreme axis scores, at either end of this gradient, are species poor and dominated by the named shrub species. Intermediate axis scores, around zero, reflect the most diverse composition and are similar to ash woodland. Range = -1.12 – 1.57
Agricultural management	dairy	A nominal, binary variable describing if farm is dairying = 0, or not = 1.
	reseed	A nominal, binary variable describing whether the field on which sampling was centred was reseeded = 1 or not = 0.
	manage	Site scores on the first axis of a PCO describing management of study field. A high positive score reflects low intensity of agricultural inputs and a low negative score reflects higher inputs. Range = -1.33 – 0.57

A check for collinearity between the standardised explanatory variables was conducted, using graphs, Spearman's correlations between standardised explanatory variables and the Variance Inflation Factor of each variable within the set (Zuur *et al.* 2010). Although moderate correlations (Spearman's $\rho > 0.40$) were noted between some pairs of explanatory variables the variance inflation factors were generally low (< 4), suggesting that the level of multicollinearity present would not be a major problem for the modelling. Two variables, manage and reseed had higher vifs (16.46 and 11.19 respectively) but were still both used in the regression analyses. In a preliminary exploration of relationships between response and explanatory variables, they were graphed together and Spearman correlation coefficients between them calculated. (See Appendices 5.B-5.D for the results of these preliminary analyses).

10.2.2. IDENTIFICATION OF MAJOR ENVIRONMENTAL PREDICTORS USING STEPWISE MULTIPLE REGRESSION

The strongest predictors, with Spearman's correlation coefficients > 0.20 , were identified from the preliminary analyses and used to build initial models for each response variable. An automatic model search that started with this model and had as its upper limits, the inclusion of all variables and one-way interactions, and as its lower limits, a model with no variables was conducted. This model search was based on stepwise regression using AIC values. Forward and backward selections were used. The significance of the terms in the model, suggested by automatic selection, was tested using analysis of deviance (Chi-square tests) comparing models with and without the variables of interest. Backwards stepwise selection was continued manually until all terms in the model were significant at $p \leq 0.05$. The model was checked using a post-hoc residual analysis (the distribution of residuals was checked for normality, homogeneity of variance and the effects of outliers).

The terms contained within the final model accepted after residual analysis were regarded as those identified as most important to the bee response variable. Models are presented, not as optimum models or predictive models but simply to identify important influences.

The stepwise selection process, since it included one-way interactions, also suggested potential interactions between explanatory variables. These interactions were graphed using conditional plots and evaluated in terms of whether or not they made sense ecologically and whether there was sufficient data to include their effects in models.

These analyses were conducted using the base package of R (R Development Core Team 2011).

10.2.3. RANKING OF PREDICTOR VARIABLES USING BAYESIAN METHODS

For each of the five bee response variables, a set of models, from one with no explanatory variables to the global model with all explanatory variables, were established. Interactions were not considered. Since there were 12 explanatory variables, there were $2^{12} = 4096$ models in each set.

The models' fit to the data was evaluated using the Bayesian information criterion, BIC (Schwarz 1978). This measure quantifies how much information in the dataset had been explained by each model.

Model certainty was evaluated for the first five models in terms of their cumulative posterior probability (Table 10.2). These cumulative posterior probabilities were low indicating considerable model uncertainty and that no single model was the best to predict any of the five response variables. A model averaging approach was therefore particularly appropriate for this study's datasets.

For the model averaging, the best models, within each set of 4096 models, were identified using (Furnival & Wilson 1974) leaps and bounds algorithm and refined further by two further criteria, as applied by the bicreg function of BMA package (Raftery *et al.* 2012). This identified a set of best models that

are referred to as belonging to “Occam’s window” (Raftery 1995) (Table 10.2 and Figure 10.4).

The frequency of each explanatory term’s presence in these best models was displayed to provide a quick visual assessment of each term’s relative importance. The models in Occam’s window were averaged and the distributions of the posterior probabilities of the averaged coefficients in these averaged models were used as a measure of importance for each explanatory variable. Posterior probabilities of greater than 50% (that an averaged model coefficient did not equal zero) were regarded as indicating that a variable was influential on bees.

Table 10.2 Level of model uncertainty shown as cumulative posterior probability of the best five models ranked using BIC, together with the number of models in Occam’s window over which model averaging was conducted.

Response variable	Cumulative posterior probabilities for best five models	Number of models in Occam’s window
Bumblebee abundances	0.32	53
Solitary bee abundances	0.46	31
Bumblebee species number	0.30	46
Solitary bee species number	0.25	62
Number of wild bee genera	0.52	25

10.2.4. RANKING OF PREDICTOR VARIABLES USING INFORMATION-THEORETIC METHODS

The importance of each explanatory variable was evaluated using an information-theoretic approach.

The full set of 4096 models for each response variable was used. The Akaike information criterion (AIC) value was calculated for each model (Akaike 1974). Each models’ AIC value was then weighted relative to all the other models in the set’s AIC values to give the models’ Akaike weights. The importance of each variable was calculated by summing the Akaike weights for all the models in which the variable featured as a predictor. This allowed direct comparison of predictors’ abilities to explain the information contained within the bee data, using ratios called ‘evidence ratios’ (Anderson 2008).

10.2.5. POST-HOC MODEL CHECKS

A post-hoc residual analysis of the Bayesian averaged models was carried out to check that no major influence had been omitted from the models. Many Bayesians do not typically carry out post-hoc model checks (Gelman & Shalizi 2012). However, there is no reason not to and the process is regarded as useful by some authors (e.g. Stephens *et al.* 2005; Gelman 2011; Gelman & Shalizi 2012).

In the post-hoc analysis, standardised residuals were plotted against fitted values to assess homogeneity. A QQ plot of residuals was plotted to evaluate normality. The residuals were plotted against each explanatory variable to determine if there was any residual pattern which would imply that the assumption of independence (i.e. that values of y at one x do not affect values of y at another x) had been violated (Zuur *et al.* 2010).

Spatial independence among the residuals was checked with spline correlograms using the R-package, *ncf* (Bjornstad 2009). The values of standardised residuals were checked and if their value $> \pm 2$ they were regarded as outliers.

10.2.6. PREDICTING ABUNDANCE AND DIVERSITY OF BEES IN THREE SCENARIOS USING AVERAGED MODELS

The Bayesian averaged models were used to make inferences about bumblebee and solitary bee abundances and diversity for three scenarios in pastoral agri-ecosystems of the SouthWest of Ireland.

To facilitate the interpretation of the BMA results, the standardization of explanatory variables was reversed and the predicted mean values back-transformed. Back-transformations of the mean values gave the predicted geometric mean rather than the arithmetic mean for the bee variables. The standard deviations derived from the averaged models' predictions are in the context of the predicted transformed means. Once these means have been back-transformed the standard deviations or more precisely, confidence

intervals set at plus and minus 2 times the standard deviation, become multiplicative. To circumvent this problem in interpretation, the predicted standard deviations were converted to percentages of variation relative to the predicted mean or coefficients of variation (CV). CV is a proportion and has no units and therefore also provides a measure of the variance of the back-transformed geometric means. High levels of variance may signal ecological instability (Tilman 1996). Trends in the predicted coefficients of variance with different scenarios were also reported.

Scenario 1: investigating the predicted effects on bee abundances and diversity of moving south by 100- 300km.

Bee abundances and diversity were predicted along a north-south gradient. A new dataset was constructed in which latitude (Ynorth) was varied along the range of the original data and all other explanatory variables were held constant at their means in the original data.

Scenario 2: comparing the predicted effects on bees on two farms in the same locality but with differing management intensity

Bee abundances and diversity were predicted for two farms that differed in their management only. The farms differed in variables: sward1, reseed, dairy, manage. For farm 1, these variables were given values that reflected maximum agricultural management intensity within the study's original dataset (i.e. reseeded, dairying, minimum score on sward1 and manage). Farm 2 was not reseeded, not dairying and had maximum scores for sward1 and manage which represented minimum management intensity and high grassland sward diversity typical of lower soil fertility. Both farms had values averaged (mean) from this study's original dataset for variables Xeast and Ynorth, sward2, hgSimp, index, hedge1, impgrass and wood, describing location, grassland composition in relation to soil pH and calcium content, hedgerow structure and vegetation and landscape composition.

Scenario 3: the predicted effects on bee abundances and diversity for similar farms located in landscapes that differ in their proportion of intensively managed grassland.

Bee abundances and diversity were predicted for farms under identical management, with similar grasslands and hedgerows, but located in landscapes with differing proportions of intensive grassland. A new dataset was created in which the only variable that varied was *impgrass*, the area of intensive grassland within 100m of the sampling point. This was allowed to vary along the range observed in the sample. All other variables were held at their mean values in the original sample.

10.2.7. EXAMINING THE EXTENT TO WHICH THE EFFECTS OF INFLUENTIAL ENVIRONMENTAL VARIABLES WERE SHARED WITH LOCATION

Part of the variance explained by each explanatory variable was expected to be associated with sampling location. Partial linear regression was used to distinguish between pure and shared effects of important variables and location.

The variance in each response variable explained by the most influential variables (as identified using methods described in Sections 10.2.2 – 10.2.4) was decomposed to filter the effect of location from the effects of these variables. Legendre and Legendre's algorithm for the decomposition of variance was used (Legendre & Legendre 1998). For each response variable, a set of three models per influential predictor were run, with and without location (*Xeast* and *Ynorth*). The form of these models is detailed in Table 10.3. R^2 of each model was determined (adjusted R^2 for abundances and R^2 for diversities as adjusted R^2 was found to give excessively high values) and algorithms (Table 10.3) used to calculate the variance explained by location and each influential variable and their shared effects as illustrated in Figure 10.2. When the shared effect [b] was found to be negative, it was treated as zero in subsequent calculations of the pure effects. Legendre and Legendre

suggested that negative values for shared effects indicated collinearity between variables (Legendre & Legendre 1998).

Table 10.3 Models and calculations used to decompose the variance explained by influential variable V_x and location.

Model	R^2 = algorithm component
$x = X_{east} \beta_1 + Y_{north} \beta_2 + V_x \beta_3 + \epsilon$	$[a+b+c]$
$x = X_{east} \beta_1 + Y_{north} \beta_2 + \epsilon$	$[a+b]$
$x = V_x \beta_3 + \epsilon$	$[b+c]$
Calculations	
Effect	Algorithm using R^2 values
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$
Pure X_{east} and Y_{north} effect, a	$= [a+b] - b$
Pure V_x effect, c	$= [b+c] - b$

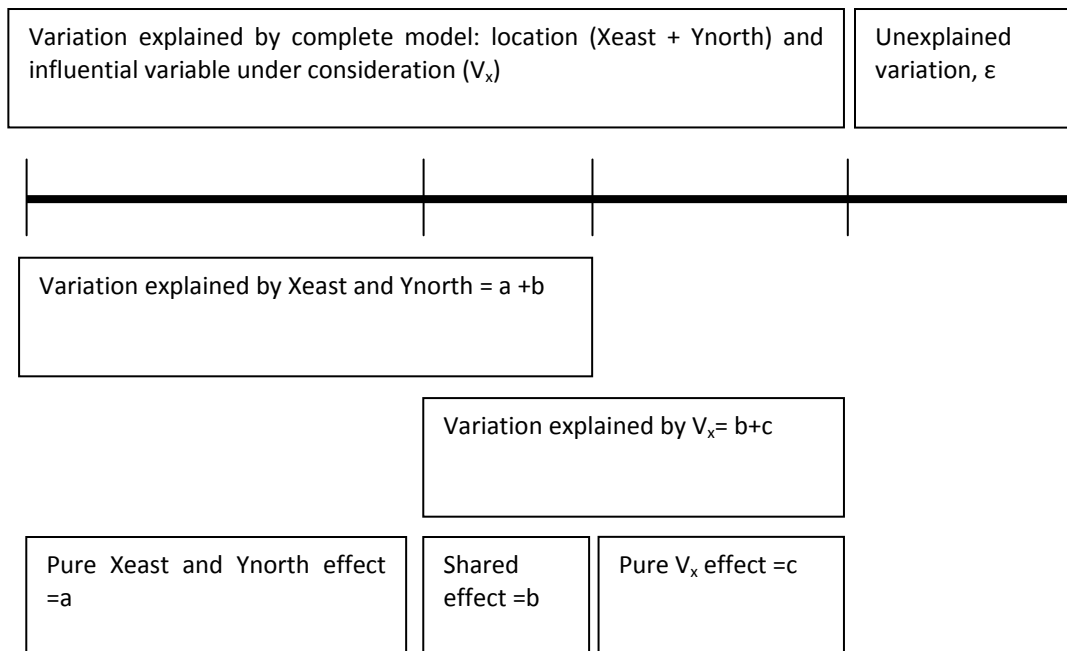


Figure 10.2. Partitioning of the variance of the response variable between location and V_x , another influential variable under consideration, in partial linear regression. The length of the horizontal line corresponds to 100% of the variance in the response variable. Fraction $[b]$ is the shared effect or intersection of linear effects of location and V_x on the response variable. Fractions $[a]$ and $[c]$ are the pure effects of location and V_x respectively. Adapted from (Legendre 1993; Legendre & Legendre 1998).

10. 3. RESULTS

10.3.1. CORRELATIONS BETWEEN RESPONSE AND EXPLANATORY VARIABLES

Preliminary explorations showed weak to moderate correlations between environmental variables and bee response variables, with Spearman's correlation coefficients mainly in the 0.20-0.40 range for the more strongly associated variables (Appendix 19). Solitary bees and bumblebees responded to different influences. Abundance and species richness, although correlated with each other, were associated with slightly different factors (Appendix 21).

Bumblebee species richness showed an association with an East-West gradient ($\rho = -0.36$, $p = 0.02$) whereas solitary bee abundance was associated with a North-South gradient ($\rho = -0.27$, $p = 0.07$). This was not mirrored by solitary bee species richness. The number of bee genera showed both latitudinal (North-South) ($\rho = -0.34$, $p = 0.02$) and longitudinal (East-West) ($\rho = 0.28$, $p = 0.06$) gradients.

Landscape composition had some of the strongest associations with bumblebee species diversity of all tested variables. A greater area of woodland, which included scrub and very young conifer plantation in its categorisation, was associated with increases in bumblebee diversity ($\rho = 0.42$, $p = 0.004$). Increases in the proportion of improved grassland were associated with declines in bumblebee diversity ($\rho = -0.48$, $p < 0.001$) and abundance ($\rho = -0.30$, $p = 0.04$).

Grasslands with vegetation typical of more calcareous conditions were associated with higher bumblebee ($\rho = 0.32$, $p = 0.03$) and solitary bee ($\rho = 0.29$, $p = 0.05$) species richness. Species rich grassland vegetation typical of low levels of fertiliser application was associated with higher numbers of bumblebees species ($\rho = 0.37$, $p = 0.01$) and bee genera ($\rho = 0.32$, $p = 0.03$).

Species poor hedgerow vegetation dominated by *Prunus spinosa* was associated with higher bumblebee abundances ($\rho = 0.35$, $p = 0.02$) and species

richness ($\rho=0.48$, $p<0.001$). The variable describing hedgerow vegetation (Hedge1) was strongly correlated with Xeast (Appendix 19) so bumblebee associations with hedgerow vegetation may, at least partially, reflect geographical distribution rather than a relationship with hedgerow vegetation. The structural complexity of hedgerows was positively associated with the number of bee genera only.

Farm and field management at the study site were not correlated with bumblebee abundances or species richness. Less intense field management was associated with higher abundance ($\rho=0.33$, $p=0.03$) and diversity ($\rho=0.32$, $p=0.03$) of solitary bees and number of bee genera ($\rho=0.36$, $p=0.02$).

10.3.2. MODELLING USING THREE DIFFERENT STATISTICAL PARADIGMS TO IDENTIFY THE MOST IMPORTANT ENVIRONMENTAL INFLUENCES ON BEES

There was general agreement between the three different statistical paradigms used in the analyses in the environmental influences each determined to be most important to bee abundances and diversity.

Stepwise regression gave some confusing results as it identified different 'best' models with completely different explanatory terms, when different starting models were used or if interactions were included. Bayesian methods showed the posterior probabilities of even the five best models for each response variable to be low (Table 10.2) meaning that no one model was outstandingly good at explaining the data and than a model averaging approach was particularly suitable with these datasets.

10.3.3. USING STEPWISE MODEL SELECTION TO IDENTIFY THE MOST IMPORTANT INFLUENCES

Bumblebee abundances

Stepwise regression, starting with all possible combinations of variables 'Xeast', 'hedgel' and 'impgrass', which described longitude, hedgerow vegetation and landscape composition respectively, and their one-way interactions, led to the selection of a model (Eq. 10.1) with only 'impgrass' as an explanatory term.

Examination of the distribution of the residuals after application of this model suggested that it was an acceptable model (Appendix 23 Model 1). In this analysis, stepwise linear regression identified landscape composition, defined in terms of area of improved grassland, as the single most influential environmental factor on bumblebee abundance.

$$\text{Ln(bumblebee abundance +4)} = 2.78 - (0.19 \cdot \text{impgrass}) + \epsilon \quad (10.1)$$

(F-statistic = 6.74 on 1 and 43 df, $p = 0.013$, adjusted $R^2 = 0.12$.)

An interaction between dairying activity and hedgerow structure upon bumblebee abundance had been noted in preliminary data exploration (Figure 10.3). An alternative starting model, with the terms 'Xeast', 'index', 'hedgel', 'dairy' and 'impgrass' describing longitude, hedgerow structure and vegetation, dairying activity and landscape composition respectively, was used in a second stepwise model selection process. In the resulting model (Eq. 10.2), the positive benefits of a more complex hedgerow structure for bumblebee abundance occurred only on dairy farms (this interaction was significant at $p = 0.02$) but dairying activity alone did not have a significant effect on bumblebee numbers on its own ($p = 0.89$). Examination of the residuals of this model (Appendix 23 Model 2) showed them to be normally distributed with homogeneity of variance. The model was therefore also a reasonable one for the data. This re-analysis of the data, identified hedgerow vegetation and structure and dairying activity as the most important influences on bumblebee abundance but omitted landscape composition.

$$\text{Ln(bumblebee abundance +4)} = 2.75 + (0.19 \cdot \text{hedgel}) + (0.32 \cdot \text{index}) + (0.02 \cdot \text{dairy}) + (-0.34 \cdot \text{index} \cdot \text{dairy}) + \epsilon \quad (10.2)$$

(F-statistic: 4.67 on 4 and 40 DF, p -value: 0.003, adjusted $R^2 = 0.25$).

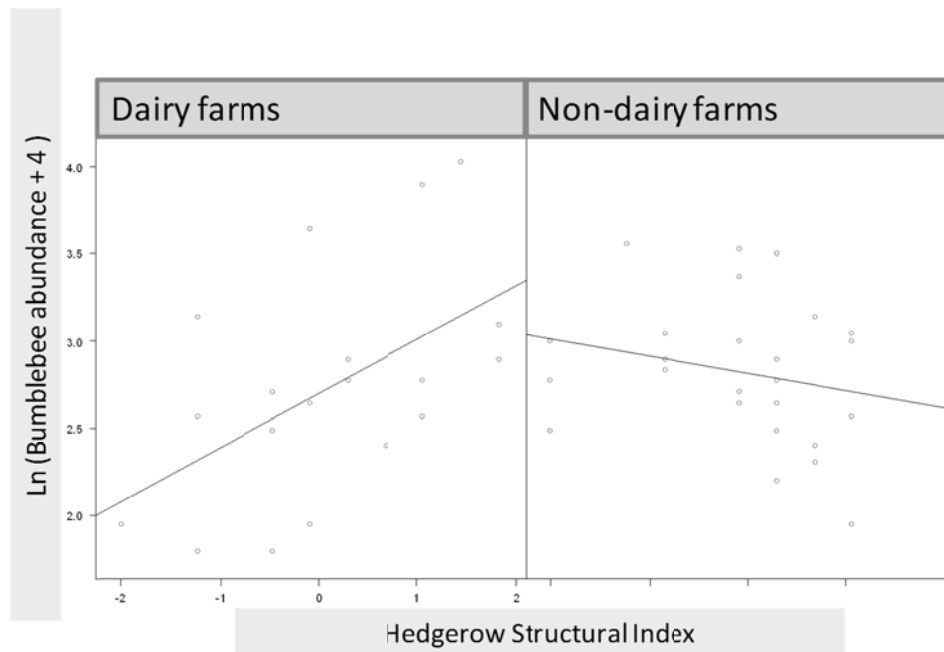


Figure 10.3. Conditional plot showing that more complex hedgerows may be associated with higher abundances of bumblebees on dairy farms but not on non-dairy farms.

Bumblebee species number

The starting model contained variables: Xeast, sward1, sward2, hedge1, dairy, manage, impgrass and wood which described longitude, sward vegetation along a species diversity and soil fertility gradient, sward vegetation along a soil pH and calcium gradient, hedgerow vegetation, the intensity of field management, landscape composition in terms of area of improved grassland and area of woodland, scrub and young forestry respectively. Stepwise regression identified three influences as important to bumblebee species richness: the extent of calcareous character of grassland vegetation, hedgerow vegetation and area of woodland, scrub and young forestry in the landscape.

The final model (Eq. 10.3) contained a number of interactions which were examined with coplots (Appendix 22). Bumblebee species diversity responded

more positively to (i) increasing area of woodland-scrub-young forestry in the landscape and (ii) along a gradient of hedgerow composition from dominated by *Crategeous monogyna* to dominated by *Prunus spinosa*, at sites where the grassland vegetation reflected calcareous conditions. Such conditions dominated one study area, in West Limerick.

$$\text{Sqrt}(\text{Number of bumblebee species}) = 1.94 + (0.03 * \text{sward2}) + (0.21 * \text{hedge1}) + (-0.05 * \text{wood}) + (0.28 * \text{sward2} * \text{wood}) + (-0.12 * \text{sward2} * \text{hedge1}) + \epsilon \quad (10.3)$$

(F-statistic = 7.21 on 5 and 39 df, p value = 0.00007, Adjusted R² = 0.41)
For the distribution of residuals, see Appendix 23.

Solitary bee abundances

The starting model contained variables: Ynorth, sward1, sward2, reseed and manage which described latitude, sward vegetation along a species diversity and soil fertility gradient, sward vegetation along a pH and calcium gradient, field management in terms of reseed and the intensity of management respectively. Stepwise regression identified three influences as important to solitary bee abundances: a north-south gradient, the extent of calcareous character of grassland vegetation and the intensity of field management (Eq. 10.4). The post-hoc check of the residuals of this model suggested the model was adequate though there was a slight divergence from normality and homogeneity of variance in the distribution of the residuals (Appendix 23).

$$\text{Ln}(\text{solitary bee abundance} + 1) = 2.20 + (-0.48 * \text{Ynorth}) + (0.47 * \text{sward2}) + (0.32 * \text{manage}) + \epsilon \quad (10.4)$$

F-statistic = 7.79 on 3 and 41DF, p=0.0003, adjusted R² = 0.32)

Solitary bee species number

The starting model contained variables: sward2, reseed and manage, which described sward vegetation along a pH and calcium gradient and field management in terms of reseed and the intensity of management respectively. Stepwise regression identified two influences (Eq. 10.5) on solitary bee species richness: negative effects of reseed and positive effects of calcareous grasslands.

$$\text{Ln}(\text{Number of solitary bee species} + 1) = 1.72 + (-0.45 * \text{reseed}) + (0.19 * \text{sward2}) + \epsilon \quad (10.5)$$

(F-statistic = 4.39 on 2 and 42DF, model p = 0.02, adjusted R² = 0.13.
For the distribution of residuals, see Appendix 23.

Number of wild bee genera

The initial terms used in the stepwise regression were Xeast, Ynorth, sward1, index, reseed, manage. These described longitude and latitude, sward vegetation along a species diversity and soil fertility gradient, complexity of hedgerow structure and field management in terms of reseed and the intensity of management respectively. Stepwise regression identified latitude and longitude and the complexity of hedgerow structure as the main influences on number of bee genera (Eq. 10.6).

$$\text{Ln}(\text{number of genera} + 1) = 1.55 + (0.13 * \text{Xeast}) + (0.02 * \text{Ynorth}) + (0.03 * \text{index}) + (-0.23 * \text{Xeast} * \text{Ynorth}) + (0.09 * \text{Ynorth} * \text{Index}) \quad (10.6)$$

(F-statistic = 4.70 on 5 and 39 df, p value = 0.002, Adjusted R-squared = 0.30.)

Examination of conditional plots suggested that the interactions in this model were driven by a small number of sites. Stepwise model selection was repeated with interactions excluded from the model search. This time the analysis identified only grassland reseed and a north-south gradient as important environmental influences upon number of wild bee genera (Eq. 10.7).

$$\text{Ln}(\text{number of genera} + 1) = 1.69 + (-0.09 * \text{Ynorth}) + (-0.17 * \text{reseed}) \quad (10.7)$$

(F-statistic = 6.60 on 2 and 42 df, p value = 0.003, Adjusted R² = 0.20)
For the distribution of residuals, see Appendix 23.

10.3.4. RANKING THE RELATIVE IMPORTANCE OF PREDICTOR VARIABLES USING BAYESIAN METHODS

Figure 10.4 shows that the most important influences on solitary bees and bumblebees differed between guilds.

Bumblebee abundance

The best model to explain bumblebee abundance, in terms of lowest BIC, included only terms describing hedgerow vegetation and structure (Figure 10.4). However the posterior probability of this model (shown by the width of its bar in Figure 10.4) was low, showing that it was not a very good fit and that other models were almost as good.

After model averaging, landscape composition (impgrass) and hedgerow vegetation (hedge1) variables had posterior probabilities greater than 50% (probability that their coefficients did not equal zero) (Table 10.4 and Figure 10.5). Bayesian methods therefore identified landscape composition (impgrass) and hedgerow vegetation (hedge1) as the most influential variables on bumblebee abundances.

Solitary bee abundance

A North-South gradient (Ynorth) , grassland vegetation reflecting calcareous nature (sward2) and the intensity of grassland management (manage) were identified as the most important influences upon solitary bee abundances by Bayesian methods (Figures 5.4 and 5.5, Table 10.4).

Bumblebee species number

Bayesian methods identified landscape composition (impgrass) and hedgerow vegetation (hedge1) as the most influential variables on bumblebee species richness (Figures 5.4 and 5.5, Table 10.4).

Solitary bee species number

A North-South gradient (Ynorth) and grassland vegetation reflecting calcareous nature (sward2) were identified as the most important influences upon solitary bee species richness by Bayesian methods (Figures 5.4 and 5.5, Table 10.4). The posterior probability of intensity of grassland management (manage) $p!=48.2\%$.

Number of wild bee genera

A North-South gradient (Ynorth) , grassland vegetation reflecting calcareous nature (sward2) and reseedling of grassland (reseed) were identified as important influences upon diversity of genera (Figures 5.4 and 5.5, Table 10.4).

10.3.5. RANKING THE RELATIVE IMPORTANCE OF PREDICTOR VARIABLES USING INFORMATION CRITERION METHODS AND EVIDENCE RATIOS

Bumblebee abundance

The sum of Akaike weights (Table 10.5) identified hedgerow vegetation (hedge1) and landscape composition (impgrass) as the most important influences upon bumblebee abundance, with reseedling and hedgerow structure as secondary influences.

Hedgerow vegetation (hedge1) was approximately three to four times as important as latitude or longitude, grassland vegetation, hedgerow structure and farm or field management.

Landscape composition, in terms of area of improved grassland, was approximately twice as important as the other explanatory variables considered.

Solitary bee abundance

The sum of Akaike weights (Table 10.5) identified geographical influences as particularly important in explaining solitary bee abundances. The strongest influences were a North-South gradient and a gradient in grassland vegetation composition driven by degree of calcareous soil conditions. These were 1.6x (evidence ratio of 0.95:0.61) more important than the next strongest influence, the intensity of field management. Intensity of field management and reseedling were the most important anthropogenic factors. Landscape composition in terms of area of woodland, scrub and young conifer plantations

was of some importance in explaining the abundance of solitary bees. It was of approximately equal importance as reseeded.

Bumblebee species richness

The sum of Akaike weights (Table 10.5) identified landscape composition (impgrass) and hedgerow vegetation (hedge1) as the most important influences upon bumblebee species richness. These were also both influential on bumblebee abundance. However, whereas hedgerow vegetation was the more important with regards to the abundance of bumblebees, landscape composition was more influential with regards to bumblebee species richness.

Other variables had more influence upon species richness than they did on bumblebee abundance. This second tier of influences were north-south and east-west gradients, the composition of grassland vegetation as it reflected soil fertility (sward1) and calcareous conditions (sward2) and the area of woodland habitat (and scrub and young forestry = wood) in the landscape. The importance of this second tier of influences was approximately half to two thirds that of landscape composition (impgrass).

Solitary bee species richness

The sum of Akaike weights (Table 10.5) identified regional geographical influences as particularly important, with a North-South gradient and gradient in grassland vegetation composition driven by the degree of calcareous soil conditions being the strongest influences on solitary bee diversity.

Reseeded and the intensity of field management (manage) were also relatively important, being, for example, at least twice as important as hedgerow structure and vegetation for solitary bee richness.

Landscape composition in terms of area of woodland, but not of improved grassland, was of some importance in explaining species richness of solitary bees.

Number of wild bee genera

The sum of Akaike weights (Table 10.5) identified a North-South gradient and a gradient in grassland vegetation composition driven by acidic to calcareous soil conditions as approximately twice as important as the next most important influences on number of wild bee genera. The factors of secondary importance were grassland management and reseeding.

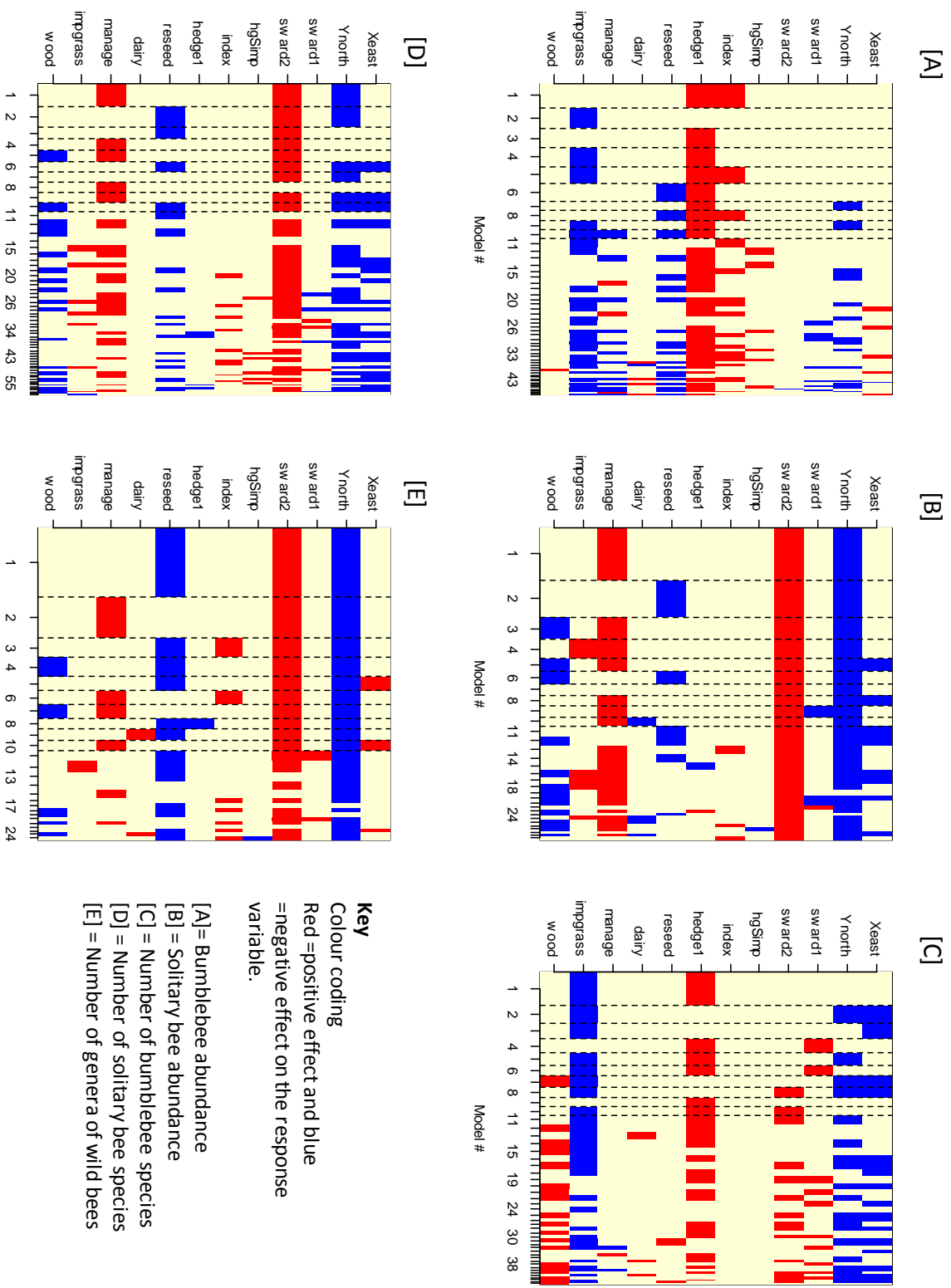


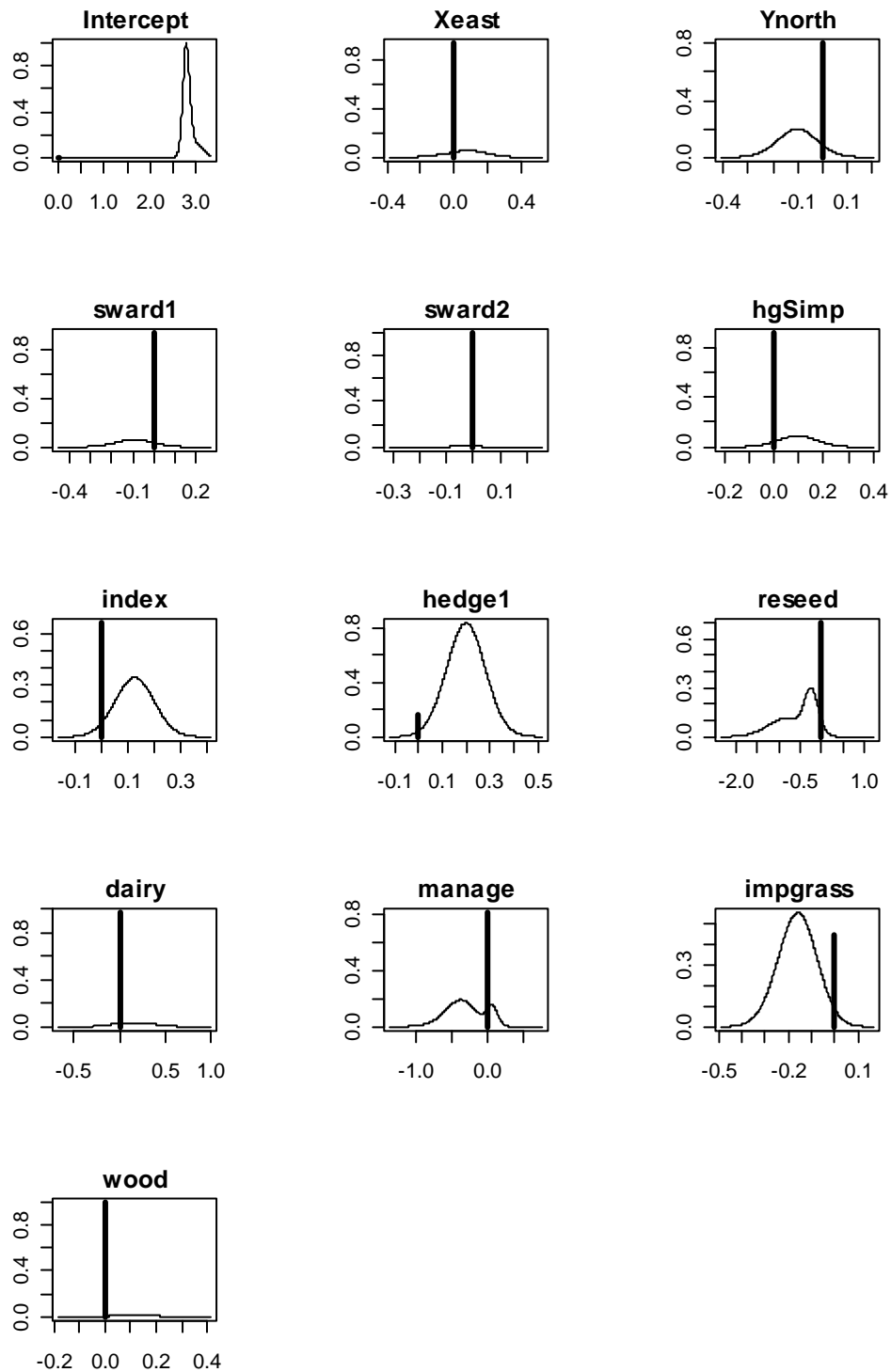
Figure 10.4. Relative importance of environmental influences on bee abundances and diversity, shown by the frequency of their inclusion in the best explanatory models, ranked using BIC.

Table 10.4 Relative importance of environmental influences on bee abundances and diversity, shown by their averaged model coefficients and their posterior probability models. p!=0 = posterior probability that the variable's $\beta \neq 0$; EV= posterior distribution mean calculated over all models; SD = standard deviation of EV.

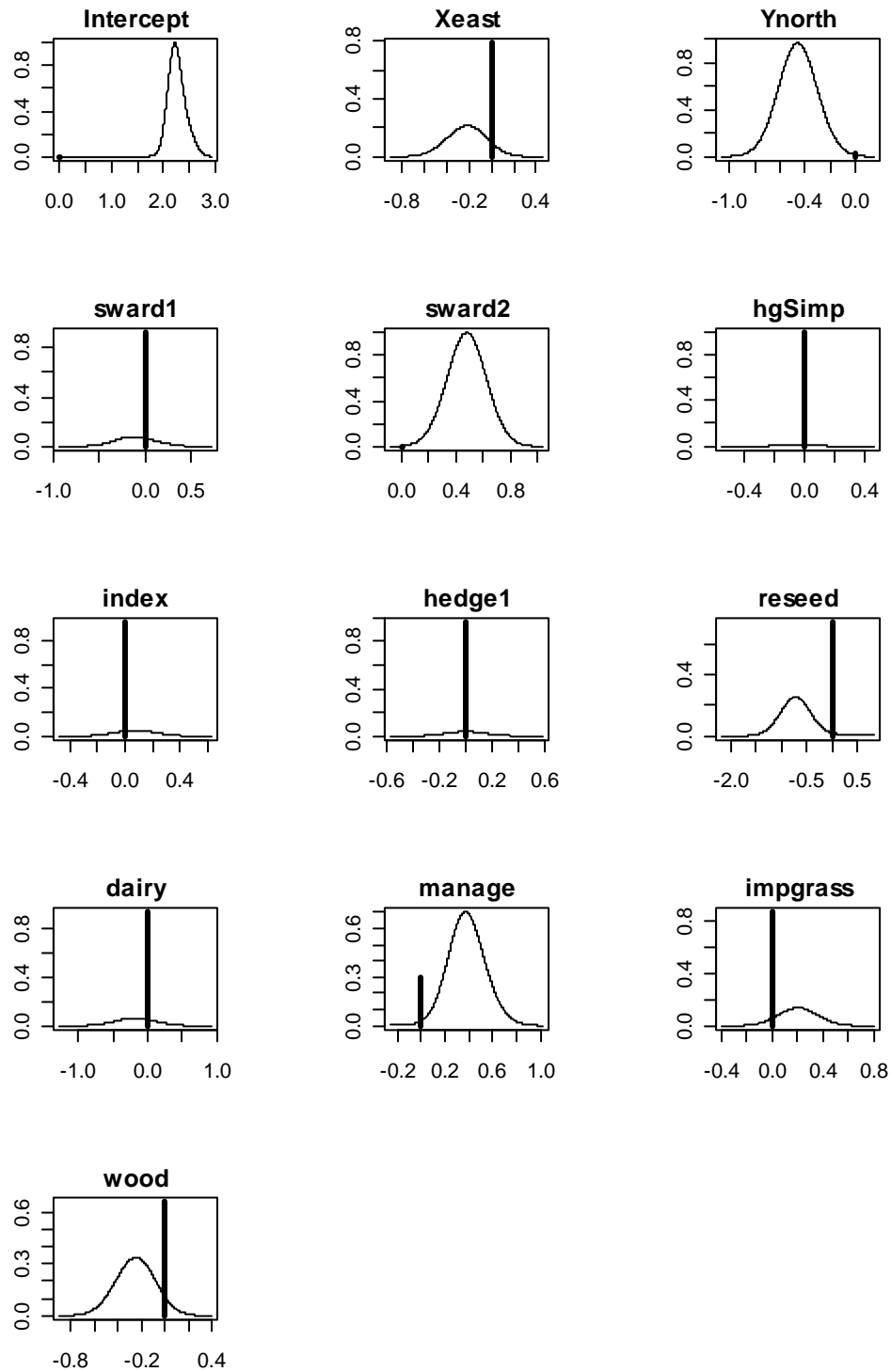
Model terms	Bumblebee abundance			Solitary bee abundance			Bumblebee species number			Solitary bee species number			Number of genera		
	p!=0	EV	SD	p!=0	EV	SD	p!=0	EV	SD	p!=0	EV	SD	p!=0	EV	SD
Intercept	100.0	2.83	0.13	100.0	2.26	0.17	100.0	1.98	0.05	100.0	0.70	0.05	100.0	0.73	0.02
Xeast	5.6	0.00	0.03	21.5	-0.05	0.12	40.6	-0.06	0.09	36.1	-0.03	0.05	9.2	0.00	0.01
Ynorth	19.8	-0.02	0.05	96.9	-0.45	0.17	45.8	-0.06	0.08	61.8	-0.06	0.06	97.1	-0.05	0.02
sward1	6.2	-0.01	0.03	7.6	-0.01	0.07	19.1	0.02	0.05	6.7	0.00	0.02	4.8	0.00	0.00
sward2	0.5	0.00	0.01	100.0	0.48	0.14	25.3	0.02	0.05	82.6	0.09	0.06	91.7	0.04	0.02
hgSimp	9.0	0.01	0.04	1.1	0.00	0.02	0.0	0.00	0.00	5.0	0.00	0.01	1.1	0.00	0.00
index	34.2	0.04	0.07	4.9	0.00	0.04	0.0	0.00	0.00	8.7	0.00	0.02	17.4	0.00	0.01
hedge1	83.4	0.16	0.10	3.8	0.00	0.03	60.1	0.09	0.09	3.0	0.00	0.01	3.6	0.00	0.00
reseed	30.2	-0.17	0.36	25.6	-0.17	0.35	2.9	0.00	0.03	33.9	-0.06	0.10	63.6	-0.05	0.05
dairy	3.3	0.01	0.05	6.4	-0.01	0.08	4.3	0.00	0.03	0.0	0.00	0.00	4.6	0.00	0.01
manage	19.1	-0.06	0.17	70.1	0.27	0.22	3.1	0.00	0.02	48.2	0.05	0.06	29.3	0.01	0.02
imprgrass	55.3	-0.09	0.10	13.7	0.03	0.09	72.0	-0.09	0.08	8.9	0.00	0.02	3.4	0.00	0.00
wood	0.8	0.00	0.01	33.8	-0.08	0.15	31.9	0.03	0.06	27.7	-0.02	0.04	15.5	0.00	0.01

Figure 10.5. Graphs showing distributions of posterior probabilities of coefficients of environmental variables for each set of models: [A] bumblebee abundance, [B] solitary bee abundance, [C] bumblebee species richness, [D] solitary bee species richness, [E] number of genera of wild bees. The maximum height of the distribution is scaled to be equal to the probability that the coefficient is not zero. The height of the solid line gives the posterior probability that the coefficient is zero.

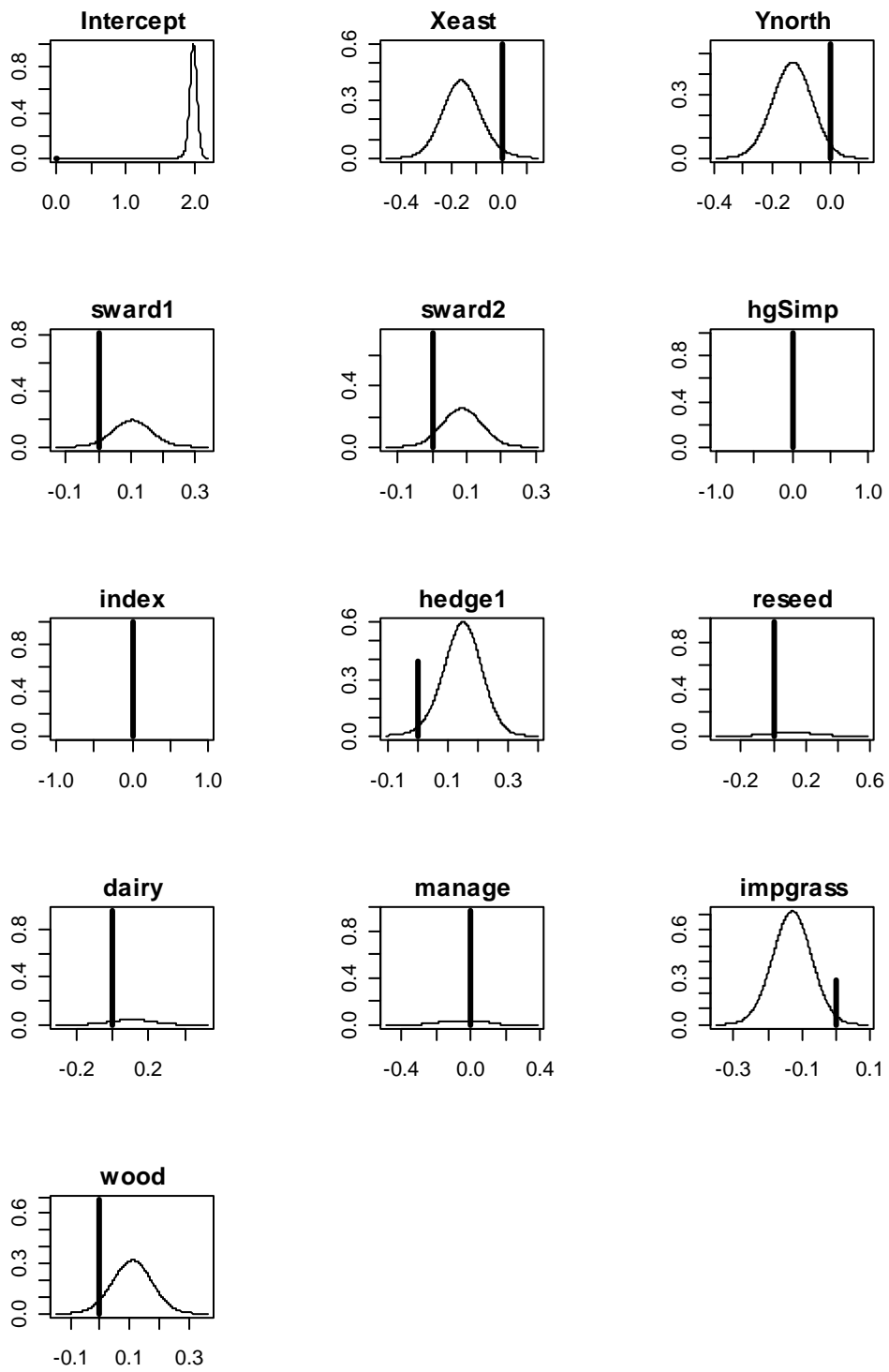
[A] Bumblebee abundance



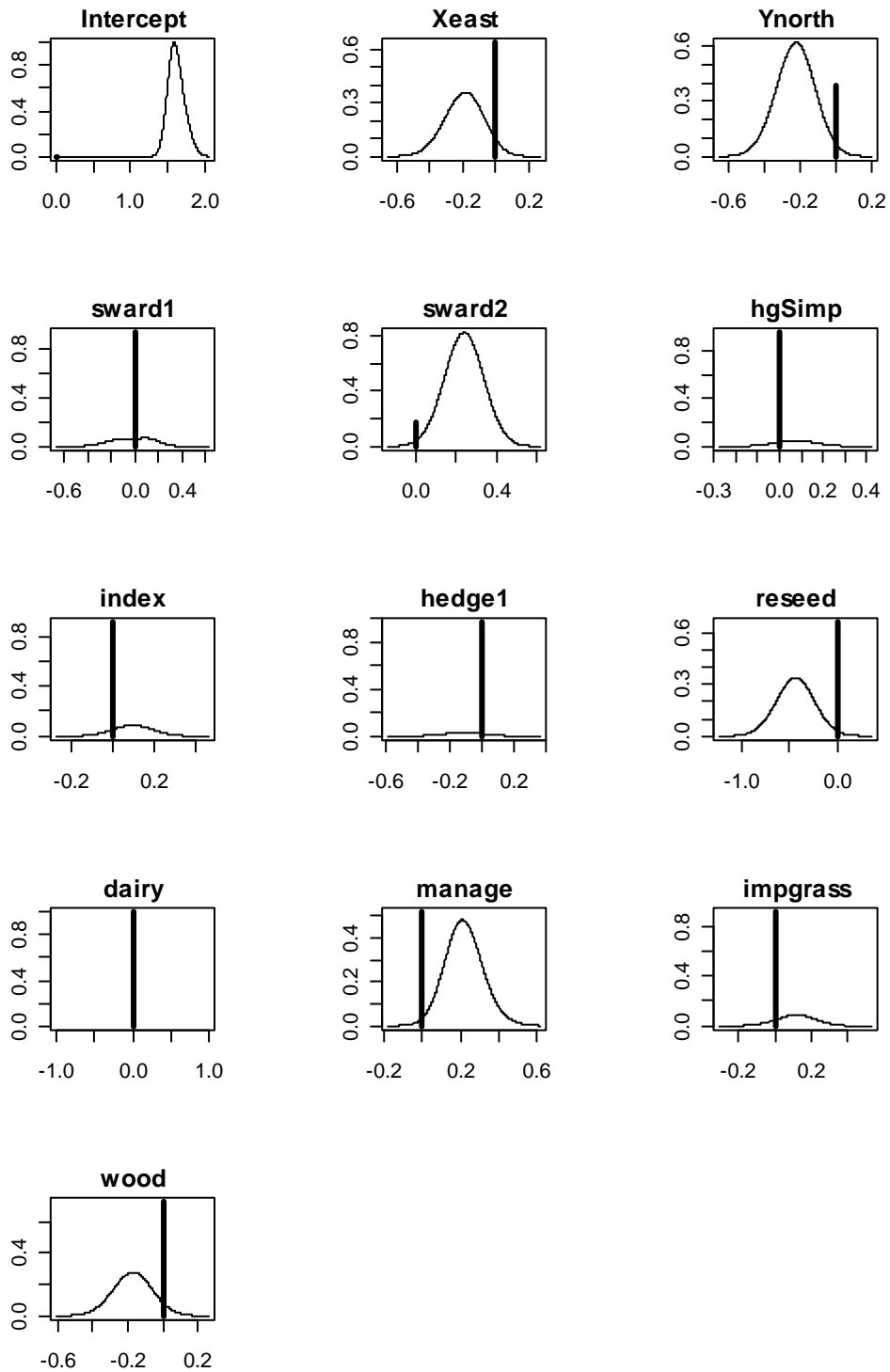
[B] Solitary bee abundance.



[C] Bumblebee species richness.



[D] Solitary bee species richness.



[E] Number of genera of wild bees.

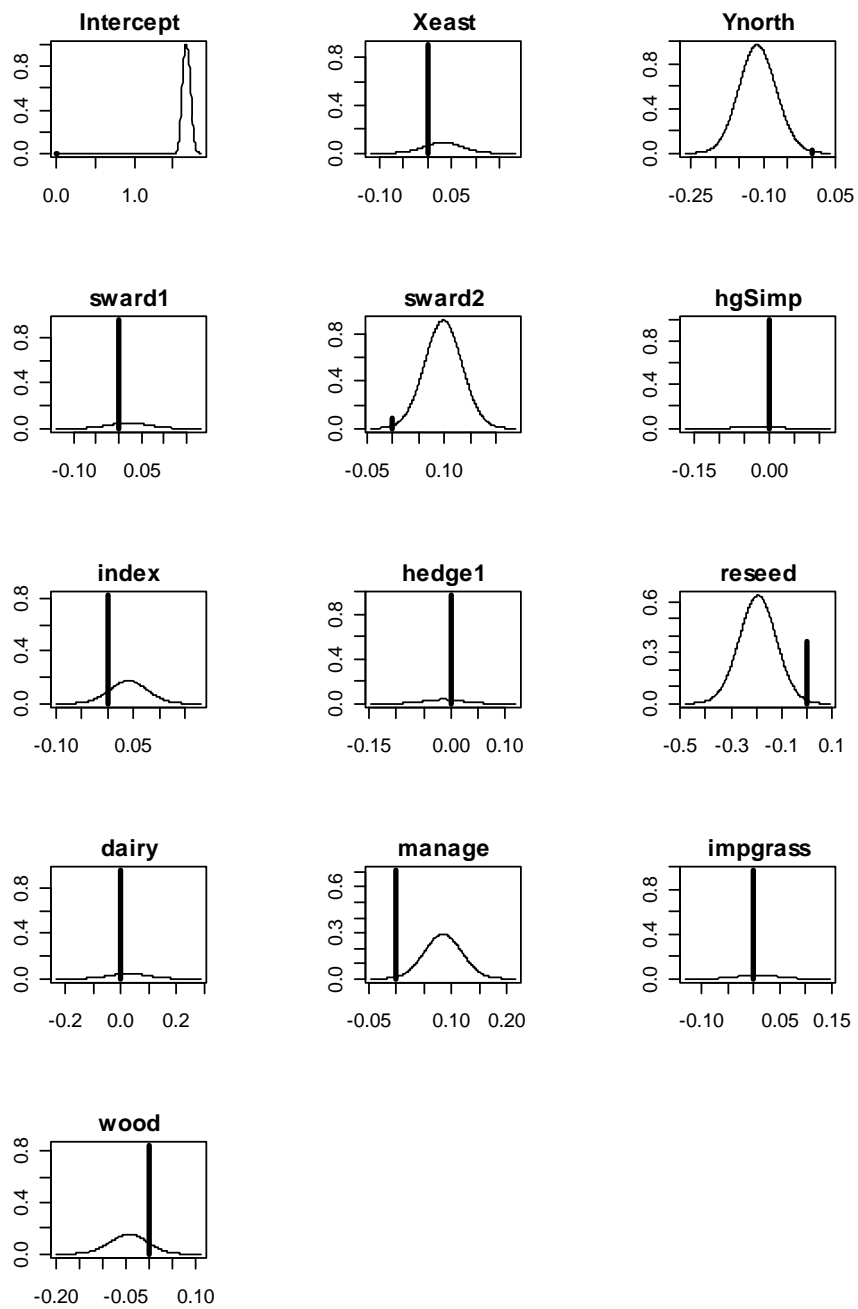


Table 10.5 Relative importance of environmental influences on bee abundances and diversity, shown by the sum of their Akaike weights for each response variable, [A] Bumblebee abundance, [B] Solitary bee abundance, [C] Number of bumblebee species, [D] Number of solitary bee species, [E] Number of bee genera. The three most influential environmental variables are highlighted for each bee response variable.

	[A] Bumblebee abundance	[B] Solitary bee abundance	[C] Number of bumblebee species	[D] Number of solitary bee species	[E] Number of bee genera
Xeast	0.17	0.29	0.43	0.39	0.20
Ynorth	0.26	0.90 (1)	0.47 (3)	0.55 (2)	0.82 (1)
sward1	0.19	0.17	0.34	0.17	0.19
sward2	0.13	0.95 (2)	0.33	0.75 (1)	0.80 (2)
hgSimp	0.20	0.14	0.14	0.17	0.14
index	0.35	0.15	0.14	0.20	0.26
hedge1	0.75 (1)	0.15	0.55 (2)	0.16	0.14
reseed	0.36 (3)	0.38	0.17	0.39	0.54 (3)
dairy	0.16	0.16	0.18	0.14	0.14
manage	0.26	0.61 (3)	0.18	0.46 (3)	0.40
imprgrass	0.54 (2)	0.24	0.64 (1)	0.19	0.14
wood	0.16	0.36	0.39	0.33	0.23

10.3.6. POST-HOC CHECKS ON RESIDUALS OF AVERAGED MODELS

The residuals had reasonably normal distributions (Appendix 24) , showed no strong violations of the assumption of homogeneity or relationships with tested variables and thus did not indicate that an important variable or interaction had been omitted. Spline correlograms showed the residuals of sites that were located near to each other to be no more similar than the residuals of more distant sites showing there was no unexplained spatial dependence remaining.

PREDICTIONS OF BEE ABUNDANCES AND DIVERSITY, BASED ON AVERAGED MODELS, IN THREE SCENARIOS

Scenario 1: North-South (latitudinal) gradient with all other factors constant

Solitary bees were predicted to be more sensitive than bumblebees to a North-South gradient. Their abundance was predicted to decline by 81% (CV = 36.1 - 77.3%) over the 42km studied whereas bumblebee abundance was predicted to decline by 8.6 % (CV = 19.1 - 19.6%). The predicted relationship between solitary bee abundance and latitudinal gradient was nonlinear, with numbers of bees expected to change more rapidly at more southerly extremes.

However, the coefficients of variance for solitary bee abundance predictions were so high that confidence in these predicted values is low.

The changes in abundance along the north-south gradient are likely to have been amplified by a corresponding gradient in altitude. The most northerly sites were 100-150m higher than the most southerly sites which were close to sea level. Part of the influence of the north-south gradient is also likely to be shared with other environmental influences, such as differences in vegetation, landscape composition and farm management that may have also varied along the latitudinal and altitudinal gradients. These pure and shared effects are distinguished in Section 10.3.7.

Species richness was predicted to vary in a similar way to abundance, with solitary bees again more sensitive than bumblebees to the latitudinal gradient. Moving 42km northwards from Northing 158890, an 18% decrease (CV =19.2-21.6%) in bumblebee species richness was predicted and a 44% decrease (CV = 38.7-51.7%) in solitary bee species (38.7-51.7%) (Figure 10.6). Variance in the estimates of solitary bee species richness was very high.

With the number of genera being strongly correlated with the number of solitary bee species (Spearman's $\rho = 0.70$) it was not surprising that the number of genera was also predicted to decrease quite dramatically, by 36% 9 (CV =14.5-25.4) over the studied 42km of North-South gradient.

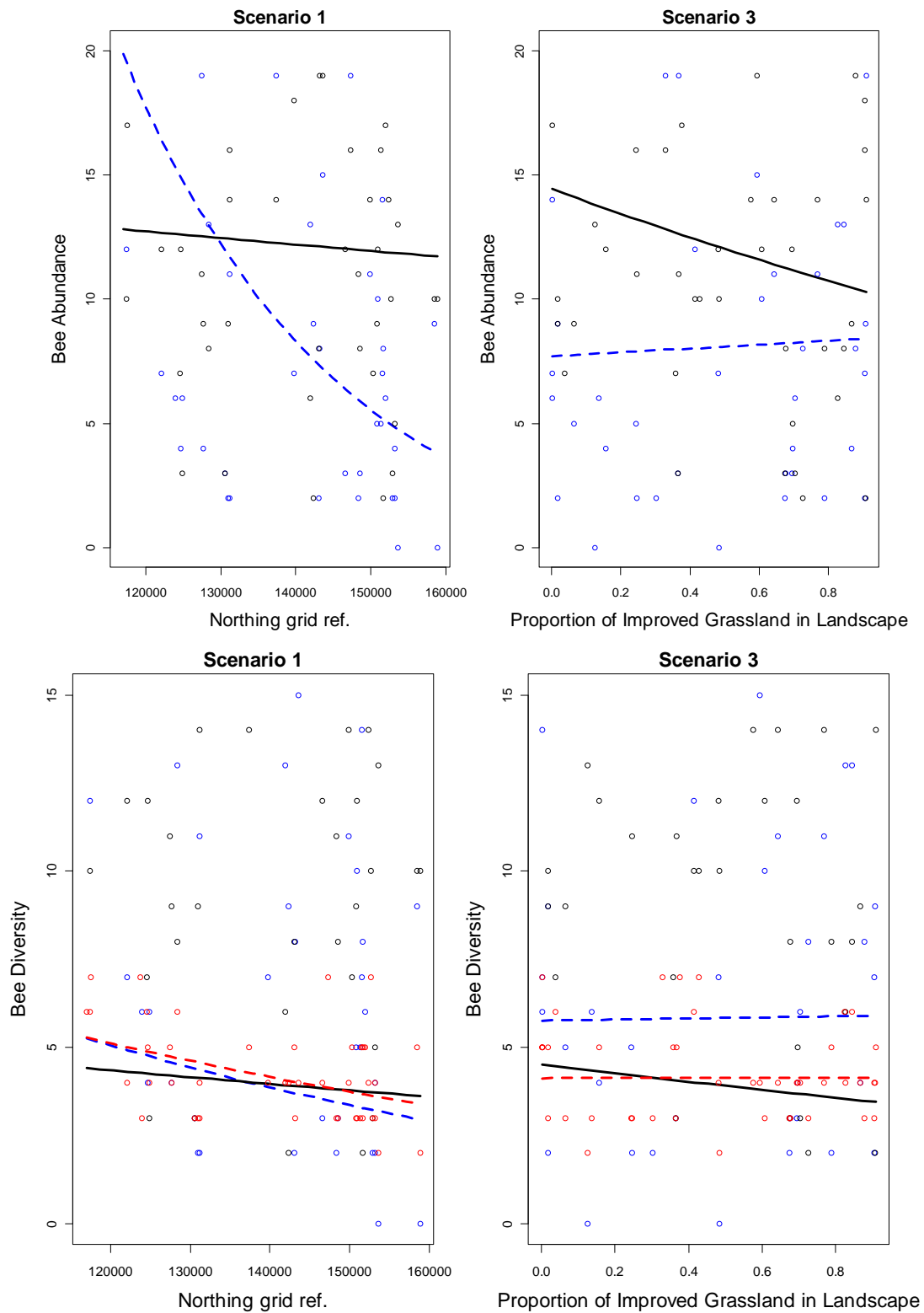


Figure 10.6. Observed and predicted bee abundances and diversities using averaged models, in Scenario 1: along North-South gradient with all other factors constant and Scenario 3: along a landscape composition gradient with all other factors constant. Key: black = bumblebees, blue = solitary bees, red = wild bee genera. Observed values are shown as open circles and predicted numbers as lines.

Scenario 2: Extremes of observed farm management with all other factors constant

Table 10.6 Predicted bee abundances and diversity at high and low extremes of farm management intensity (Scenario 2) when all other factors are constant.

Predicted (geometric mean)	High management intensity	CV	Low management intensity	CV
Bumblebee abundance	12.2	19.5	12.1	19.3
Solitary bee abundance	2.5	61.5	11.2	37.6
Bumblebee species number	3.8	19.9	3.9	19.2
Solitary bee species number	2.5	52.4	4.6	37.5
Number of genera	3.5	16.3	4.5	14.2

Farms with intensive management were predicted to have the same bumblebee abundance and diversity as farms with very low-intensity management, if located within the same landscape. For farms located in a landscape with 47% improved grassland (the sample mean) the predicted number of bumblebees per sample was 12 bees of nearly 4 species regardless of farming intensity (Table 10.6). The coefficients of variation were <20% for both estimates.

Solitary bee abundance and diversity were predicted to respond dramatically to farm and field management, with a loss of 78% in abundance of bees and 46% of species on the most intensively farmed fields compared to the least intensively managed sites (see Table 10.6). However there was a lot of variance in the data and values of CV were very high (Table 10.6). Coefficients of variation were higher for predicted values on the high intensity management farms compared to low intensity farms.

A 22% reduction in the number of bee genera was predicted for a farm managed intensively compared to one practising the least intensive management observed in this study.

Scenario 3: Traditional versus fragmented landscapes with all other factors kept constant

Bumblebee abundance and diversity were predicted to decline with an intensification of grassland management at the landscape scale. Solitary bee abundance and diversity and the number of wild bee genera were predicted to remain constant (solitary bees CV = 40.5-41.2% and Genera CV =14.7-14.7%) (Figure 10.6).

For bumblebees, abundances were predicted to reduce by 30% (CV = 19.1 - 21.4%) in the most modernised landscapes studied (90% of land cover = improved grassland) compared to traditional pastoral landscapes dominated by semi-natural grasslands and other habitats (0% land cover = improved grassland) (Figure 10.6). The number of species of bumblebee was predicted to reduce by 24% (19.1-22.9 %) with this degree of landscape change. The coefficients of variation increased with landscape homogenisation.

10.3.7. EFFECTS OF INFLUENTIAL ENVIRONMENTAL VARIABLES SHARED WITH LOCATION

Sampling location (XY) explained a large proportion of the variance (27%) in bumblebee species number but was much less important for the other bee responses studied, explaining only 10-15% of their variance. More than 50% of the effects of each of the three major environmental influences associated with bumblebee diversity were due to shared effects with location (Figure 10.7).

For solitary bee abundance, solitary bee species richness and number of bee genera, the variance explained by location and most influential environmental variables had a relatively small shared component (Figure 10.7).

Negative values for shared effects with location were obtained for hedgerow structural complexity (in bumblebee abundance model) and grassland vegetation composition driven by degree of calcareous soil conditions (in

models for solitary bee abundance, solitary bee diversity and number of genera) (Figure 10.7). This suggests collinearity between these variables and location (Legendre & Legendre 1998).

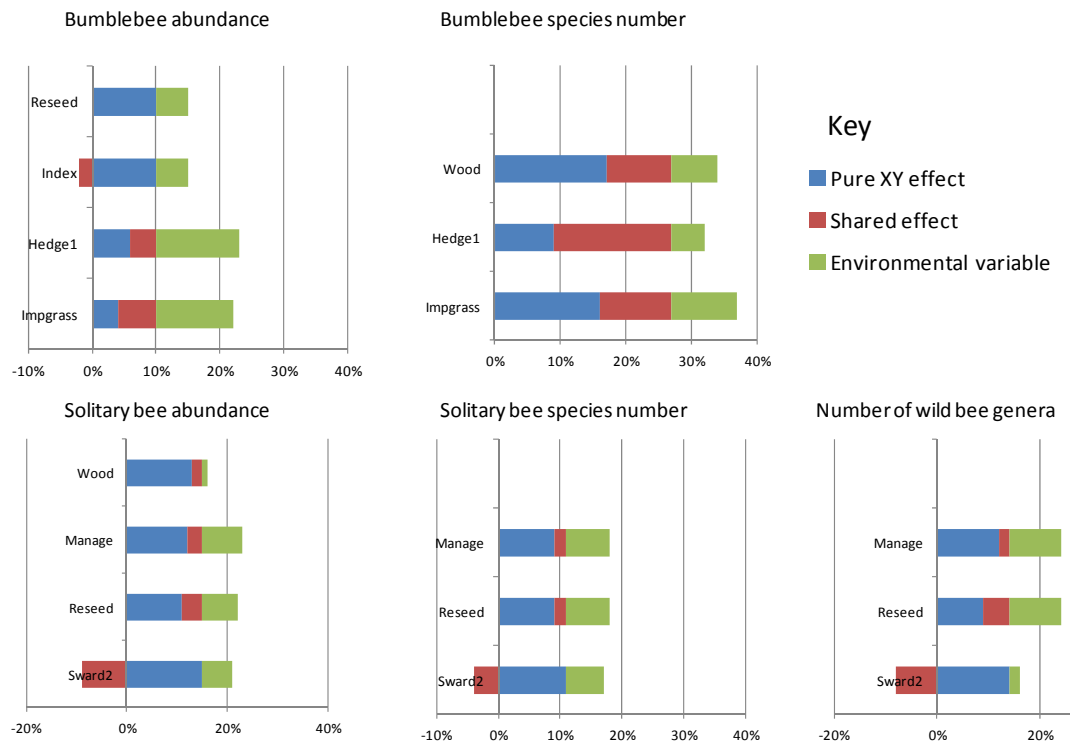


Figure 10.7. Decomposition of variance in bumblebee abundance, bumblebee species number, solitary bee abundance, solitary bee species number and number of wild bee genera between location and the most important predictors for each, showing pure and shared effects.

10.3.8. BRINGING TOGETHER THE MAIN FINDINGS FROM THE THREE STATISTICAL APPROACHES

Bumblebees and solitary bees did respond to different environmental influences, as hypothesised.

Bee abundances

All statistical methods recognised that bumblebee abundance was sensitive to landscape composition in terms of the proportion of improved grassland

within 100m. Bayesian and Information theoretic methods identified hedgerow composition, in terms of *Prunus spinosa* dominance, as the most important influence on bumblebee numbers.

Solitary bee abundance, in contrast, responded strongly to a north-south gradient and the calcareous character of grassland vegetation, followed by field management intensity. All three statistical approaches confirmed these factors to be very influential on solitary bee abundance. Information theoretic methods suggested that reseeded and landscape composition in terms of woody elements were additional minor influences on the abundance of solitary bees.

Bee diversity

Bayesian and information theoretic approaches identified landscape composition ('impgrass') and hedgerow vegetation ('hedge1') as the most influential variables on bumblebee species richness.

Information theoretic methods identified a second tier of influences as north-south and east-west gradients, the composition of grassland vegetation as it reflected soil fertility ('sward1') and calcareous conditions ('sward2') and landscape composition in terms of the wood-hedgerow ('wood') gradient.

Stepwise regression, with its focus on only one model, exaggerated the relative importance of some of the secondary influences, for example by identifying area of woodland, scrub and young forestry in the landscape but not area of improved grassland which the two other methods showed to be more influential when multiple good models are considered.

The strongest influences on solitary bee richness, like on their abundance, was the calcareous nature of grasslands (identified by stepwise regression, Bayesian and Information-theoretic approaches) and a north-south gradient (Bayesian and Information-theoretic).

Information-theoretic methods showed reseeded and intensity of field management to be of secondary importance, though at least twice as important as hedgerow structure and vegetation, for solitary bee richness. Stepwise regression also identified the negative effects of grassland

reseeding. Landscape composition, in terms of area of woodland but not of improved grassland, was a minor influence in explaining species richness of solitary bees (Information-theoretic).

The main influences on the number of wild bee genera were very similar to those identified for solitary bee species richness.

The most important influences on the number of wild bee genera were a North-South gradient (all three statistical methods agreed) and grassland vegetation composition in response to acidic to calcareous soil conditions (Bayesian and information theoretic methods).

Bayesian and information theoretic methods highlighted reseeded grasslands as a relatively important negative influence. The results of the Information theoretic analysis also identified grassland management as of equivalent importance to reseeded.

Stepwise regression identified the complexity of hedgerow structure as important to number of bee genera. This factor was not ranked very highly by Information theoretic methods, but could be considered as weak tertiary influences together with area of woodland and scrub in the landscape.

Bayesian methods showed that though these potential weak influences (grassland management, hedgerow structure and area of woodland /scrub) did feature in the best ten models as ranked using BIC, their posterior probabilities after model averaging were <0.50 , meaning that there was a high probability that their coefficients were equal to zero.

All three statistical approaches led to the same conclusions. I would recommend the use of Bayesian and information theoretic methods to evaluate the relative importance of variables.

10. 4. DISCUSSION

By studying abundance and diversity, patterns of bee response to anthropogenic and environmental factors were revealed that were not

apparent when the species abundance composition of the entire assemblage was studied in Chapter 9.

In Chapter 9, the assemblage structure of bees was shown to be shaped mainly by natural or bio-geographic factors, with a subtle shift in the relative proportions of bees in the assemblage detected in association with agricultural intensification at the field level.

This chapter shows that the effects of intensification of agricultural management in pastoral landscapes in recent decades are clearly apparent when bee abundances and diversity are studied. These characteristics of wild bee assemblages are also defined by bio-geographical factors and other naturally arising spatial pattern. However human impacts upon the diversity and abundances of wild bees in pastoral farmland in Ireland are readily discerned.

Geographical influences

Longitudinal and latitudinal gradients

The number of genera, solitary bee abundances and species diversity were sensitive to a North-South gradient. Bee abundance and diversity of species and genera declined moving northwards. A North-South transect study of Ireland also showed a decline in bee abundance in this direction (Purvis *et al.* 2010).

Climatic differences along this gradient are likely to have been accentuated by a corresponding altitudinal gradient. Climate has long been recognized as a major determinant of bee diversity and abundances (Michener 1979).

Bumblebee diversity was slightly sensitive to North-South and East-West gradients but these factors were of minor importance compared to other identified influences.

Bumblebee sensitivity to gradients in temperature is regarded as an important determinant of their distribution and of their species richness (Pekkarinen & Teras 1993; Kivinen *et al.* 2006) along latitudinal gradients

(Banaszak 1996). The short North-South distance (~40km) covered in this study had only a weak effect on bumblebee abundances and diversity.

An East-West gradient had a weak effect on bumblebee species diversity. An East-West gradient in distribution of rare species of bumblebees has been identified in Ireland recently and is considered to be driven by intensification of grassland management (Fitzpatrick *et al.* 2007) .

For solitary bees, a stronger effect of latitude and altitude could be expected due to the additional challenges that smaller bees face concerning thermoregulation (Stone 1994; Bishop & Armbruster 1999). Nevertheless the response in solitary bee numbers and diversity observed over a change in altitude of approximately 150m and in latitude of 40km was remarkably large. It suggests that solitary bees are highly sensitive to biogeographical gradients and it would seem appropriate to study their response to climate change.

(Dormann *et al.* 2008) reported that change in climate is likely to have strong effects on bee diversity in Europe. This study's findings indicate that such effects will be strongest for solitary bee species.

Bumblebee diversity hotspots

Despite the relative unimportance of latitudinal and longitudinal gradients, sampling location was shown to be very important in determining bumblebee species diversity though not their abundance. These local areas of higher bumblebee diversity may be regarded as diversity hotspots. In the UK similar 'hotspots' for bumblebee diversity have been recognized e.g. Dungeness (Williams 1989), Salisbury Plain (Carvell 2002) and a number of coastal areas (Goulson *et al.* 2006). These areas have avoided agricultural intensification (Goulson *et al.* 2006) and support high densities of flowers (Williams 1989; Carvell 2002).

The environmental conditions characteristic of 'bumblebee diversity hotspots' in Ireland were (i) hedgerow composition (species-poor Blackthorn (*Prunus spinosa*) hedgerows being associated with high abundance and species richness of bumblebee) , (ii) area of woodland and scrub and young forestry

plantations and (iii) area of improved grassland within the landscape. These associations will be described in more detail in the following sections.

Whether these factors simply describe the locations where bumblebees were particularly diverse in this study region or over a wider area and whether they are influential in maintaining diversity are questions for future study.

Hotspots of solitary bee diversity were not evident.

Calcareous soil conditions

In this study calcareous grasslands were found to be associated with higher diversity and abundances of solitary bees and higher diversity but not greater numbers of bumblebees. The value of calcareous grasslands for bees has been recognised by other workers and is attributed to their floral diversity (Steffan-Dewenter & Tschardtke 1999; Goulson *et al.* 2006; Krauss *et al.* 2009; Krewenka *et al.* 2011).

Given the flower richness of some other grasslands surveyed in this study but their inferiority for bees in comparison to flower rich calcareous grasslands, I consider that the benefits to bees of calcareous grasslands went beyond foraging resources, and that nesting resources were also important. Edaphic factors such as warmer and more freely draining soils, availability of well-protected nesting sites under piles of stone (Krauss *et al.* 2009) are regarded as likely to enhance the habitat potential of calcareous grasslands for bees. Murray *et al.* (2009) found nesting resources to be an important determinant of bee species richness in calcareous grasslands.

Agricultural management

It has previously been suggested that intensifying grassland management is responsible for bee declines in Ireland (Santorum & Breen 2005a; Fitzpatrick *et al.* 2007; Le Feon *et al.* 2010). This study provides evidence supporting this assertion.

The effects of intensifying grassland management on bees were detected at the field level in terms of reseeding and field management and at the landscape level as proportion of improved grassland.

Intensifying grassland management had a strong negative influence on solitary bees. Le Feon *et al.* (2010) found solitary bees to be more vulnerable than bumblebees to increasing nitrogen input to grasslands. If landscape composition is constant, then the results from this study support her finding that solitary bees are more vulnerable than bumblebees.

However when intensity of grassland management is considered at a landscape scale, bumblebees also show decreases in diversity and abundance. This study therefore showed both guilds of bees being impacted upon by an intensification of grassland management.

This difference in the effects of agricultural intensification at field and landscape scale on solitary bees and bumblebees can be attributed to differences between their body size, sociability and behaviour (Tscharntke *et al.* 2005). If local habitat is lost, in this study a field of semi-natural grassland, then solitary bees have limited dispersal capacity (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007) to fly to and use other habitat and are likely to be severely impacted (Zurbuchen *et al.* 2010b).

Bumblebees are more likely to be able to compensate for the loss of habitat in an individual field due to their greater flight capacity and ability to use alternative habitats (Bommarco *et al.* 2010). However this study shows that when agricultural intensification has occurred over many fields, the landscape's capacity to support abundant and species rich bumblebees reduces.

Other studies have shown that declines in bee diversity and abundance occur when organic versus conventional farms are compared (Kremen *et al.* 2002; Holzschuh *et al.* 2008; Power & Stout 2011). This study has shown that bee responses can be detected along a gradient of grassland management intensity. This offers the possibility of identifying conventional field management practices that can provide optimum conditions for bees without requiring full organic conversion.

Preliminary analyses in this chapter suggested that on dairy farms increasing hedgerow structural complexity may be associated with higher bumblebee numbers though not on non-dairying farms (Figure 10.3). This

observation requires testing. It appears to support the hypothesis of Tscharniske *et al.* (2005) that the impacts of management intensity on biodiversity are dependant on landscape composition.

Various studies have confirmed such an interaction for bees, though there have also been exceptions in some papers. For example, an interaction between landscape heterogeneity and farming intensity was confirmed for bumblebees in a study of organic and conventional cereal farms (Rundlof *et al.* 2008) and between flower abundance and landscape habitat composition for bee species richness (Kleijn & van Langevelde 2006). Batary *et al.* (2010) attributed the differing responses of bees to grazing and agri-environmental schemes in Hungary, Netherlands and Switzerland to landscape scale differences in management intensity, with an absence of detectable effect in either very intensively or very extensively managed areas and a strong bee response in intermediate landscapes. Landscape composition was initially not shown to interact and influence the effects of farm management on bee species richness in Spain (Concepcion *et al.* 2008) but a wider study across six European countries did detect an interaction (Concepcion *et al.* 2012).

Interactions between agricultural management and other factors in their effects on bees were not a primary focus of this study but should be considered in follow-up studies.

Grassland vegetation

Botanically diverse grassland vegetation associated with a low level of fertiliser input was *not* more associated with higher bee diversities and abundances (unless they were calcareous grasslands). This finding is counterintuitive.

A diversity of floral resources has been shown to be associated with bee diversity on numerous occasions (Steffan-Dewenter & Tscharniske 2001; Carvell 2002; Potts *et al.* 2003; Potts *et al.* 2004). (The effects of floral resources were not distinguished in this study but examination of model residuals did not suggest that a major influence had been omitted.)

Until recently the effects of most environmental factors on bees were thought to be either directly or indirectly associated with the availability of food resources (H. & Goodell 2011). Figure 10.8 shows this a priori hypothesis of the pathway by which the intensification of management was expected to impact on bees.

This study's findings, that field vegetation composition as it reflected soil nitrogen and management intensity was not associated with bee abundances and diversity, suggests an alternative as yet unknown pathway. A number of alternative explanations are put forward.

1. Insects (Burel *et al.* 1998) and specifically bees are more sensitive or quicker to respond to management change than plant assemblages. (Steffan-Dewenter 2003; Taki & Kevan 2007)
2. Reseeding and field management impact on bee abundance and diversity by mechanisms not captured by field vegetation composition
 - a. Direct impact on bees e.g. nests being ploughed for reseeded
 - b. Reduction of nesting resources which is not captured by species abundances of entire plant community.
 - c. Reduction in food resources which is not captured by species abundances of entire plant community.

Researchers are increasingly questioning the role of nesting resources in limiting bee populations (Murray *et al.* 2009; Murray *et al.* 2012). My findings may reflect the importance of nesting resources.

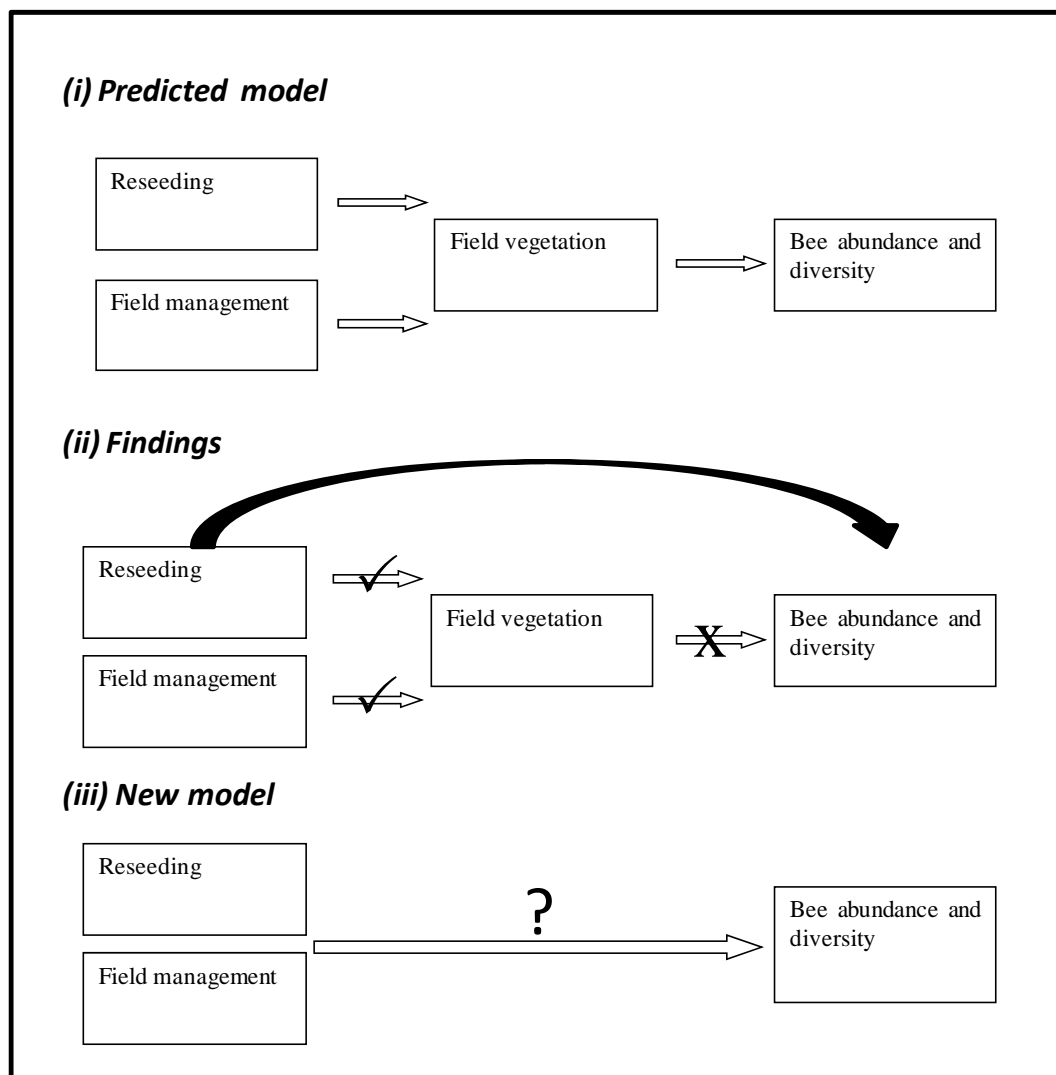


Figure 10.8. Schematic diagram summarising (i) A priori model that reseeding and an intensification of field management would be associated with altered field vegetation and reductions in bee abundance and diversity. (ii) Study findings that field vegetation responded to reseeding and field management and bee abundance and diversity responded to reseeding and field management but no association between field vegetation and bee abundance and diversity was observed. (iii) New model: mechanisms by which reseeding and field management impact on bee abundance and diversity are other than field vegetation composition and remain to be identified.

Hedgerow structure and vegetation

Hedgerows are the dominant unmanaged habitat element in the study landscape. Hedgerow botanical composition but not physical structure had a strong influence on bumblebee abundance and diversity. It was not species-rich but species-poor Blackthorn (*Prunus spinosa*) hedgerows that were

associated with a high abundance and species richness of bumblebees. Blackthorn hedgerows in their mass-flowering may provide forage at a critical time. Alternatively, Blackthorn expansion is characteristic of land abandonment and secondary succession on limestone (Dostalek & Frantik 2012; Maccherini & Santi 2012) and such boundaries may have indicated less intensive management combined with neutral to calcareous soil conditions, both favourable to bumblebees. During fieldwork it was noted that such species-poor hedgerows had grown spontaneously along wire fences and walls rather than been planted.

Hedgerows provide nesting habitat to bumblebees in agricultural areas (Osborne *et al.* 2008b) and forage (Fussell & Corbet 1991; Walther-Hellwig & Frankl 2000b; Croxton *et al.* 2002; Jacobs *et al.* 2009; Power & Stout 2011) and may help orientate bee movement in the landscape (Cranmer *et al.* 2012). Hedgerows are also known to provide resources to solitary bees (Hannon & Sisk 2009). Large earthen banks were expected to provide additional nesting habitat, particularly for ground-nesting bees and their parasitoids, which dominate the Irish fauna. Greater hedgerow widths and height and their associated increases in flowering and habitat area were also expected to benefit solitary bees. Taller or less frequently cut hedgerows have been noted to have much heavier crops of berries (Santorum & O'Sullivan 2006; Croxton & Sparks 2002), indirectly showing their value to pollinators. Simply as a function of increased habitat area, it was expected that wider hedgerows would support greater numbers of bees.

It had therefore been anticipated that structurally complex (wide, tall, earthen bank, complex vegetation structure) and species rich hedgerows would be associated with greater diversity and abundances of bees. However, this was found not to be the case. In this study, there were no effects of hedgerow composition or structure discernible on solitary bees. Structural complexity was identified as a secondary or minor influence associated with bumblebee abundance.

The absence of effects of hedgerow structure and composition on bees (bar the Blackthorn association with bumblebees) does not imply that hedgerows are unimportant to bees. Other studies have shown that habitat loss has to be

advanced before its effects on bees are detected (Winfree *et al.* 2007; Winfree *et al.* 2008; Winfree *et al.* 2009). Habitat availability in the study region may be of sufficient quality and extent that a critical point beyond which hedgerow effects on bees would be detected has not been reached. Dairy farms may have already reached that critical point. The potential interaction between dairying activity and the effects of hedgerow structure on bee abundance, suggested by this study, requires further investigation.

Landscape composition

The proportion of improved grassland within the landscape was a major influence on bumblebee diversity and abundances but had no effect on solitary bees.

The second landscape gradient, describing at its extremes, enclosed landscapes with a high density of hedgerow and open landscapes with patches of woodland and scrub or newly planted coniferous plantations and low densities of hedgerows, was of minor importance to solitary bee and bumblebee species richness and number of genera.

More open landscape areas with patches of woodland, scrub and young forestry were associated with higher bee richness than landscapes with dense hedgerow networks.

The positive association of diversity with open landscapes, though weak, was consistent across guilds and taxonomic levels. Hirsch & Wolters (2003) report 'abandoned land covered with shrubs' to be a very valuable habitat for bees.

Two alternative, but not competing, hypotheses are put forward to explain the association of greater diversity of bees with open landscapes with wooded patches rather than hedgerow-enclosed ones:

(1) open landscapes with scrub-woodland-young forestry patches provide additional habitat types in the form of core woodland and larger core grassland areas, whereas linear hedgerow features provide only woodland edge habitat and smaller core grassland areas. Greater habitat diversity supports greater species and functional diversity.

(2) enclosure of the landscape with hedgerows reflects a longer history of more productive agriculture and indicates a greater level of disturbance in the landscape, possibly since the eighteenth century (Hall 1994).

Species preferences for open versus forested landscapes have been noted amongst bees (Svensson *et al.* 2000; Diekötter *et al.* 2006; Ishii *et al.* 2008; Ushimaru *et al.* 2008; Grundel *et al.* 2010). Perhaps a landscape composed of open grasslands with patches of woodland patches satisfies the needs of more species.

The methodological approach taken to classify landscapes, using samples of only 100m radius and principal coordinates analysis to identify the main gradients for use in the bee analysis, was shown to be an efficient way to measure landscape composition in a way that was meaningful to bees.

Other studies have not found bumblebees to respond to landscape composition at such a small scale, for examples in studies of responses to mass-flowering crops bumblebee abundances have tended to be most highly correlated at distances of hundreds of meters or even kilometres (Westphal *et al.* 2006).

It is likely that the difference in scale at which a bumblebee response was detected in this study compared to other studies (Steffan-Dewenter *et al.* 2002; Kleijn & van Langevelde 2006; Westphal *et al.* 2006; Tscheulin *et al.* 2011) was due to how landscape was measured and classified rather than differences in bees' flight distances and use of the landscape. Recent studies have shown bumblebees adjust their foraging range in different resource conditions (Carvell *et al.* 2012) but this is not thought to be the cause.

It had been hypothesised that solitary bees would respond at a smaller scale than bumblebees due to correlations between the scale at which bees respond to landscape, their body size, social behaviour and foraging range (van Nieuwstadt & Ruano Iraheta 1996; Gathmann & Tschardt 2002; Greenleaf *et al.* 2007; Tscheulin *et al.* 2011). Nevertheless that no response was detected for solitary bees to landscape composition in terms of grassland management at a grain size of 100m was surprising. Associations between solitary bees and habitat availability at this scale (Taki *et al.* 2010) and

scales of 250m to 750m have been shown (Steffan-Dewenter *et al.* 2002; Kleijn & van Langevelde 2006; Tscheulin *et al.* 2011). Indeed in this study solitary bee diversity showed a weak association with the second landscape gradient describing organisation of woody vegetation at this scale.

Impacts on functional diversity / number of genera

Using the number of genera as a response variable added a few additional insights. It bolstered confidence in the suggested association between bee diversity and the secondary landscape gradient describing enclosed to open landscapes with woodland patches.

The number of genera was more sensitive to reseeded than any other of the bee response variables, signalling a loss in diversity that was not apparent from consideration of species diversity. Whether genera are a useful surrogate for the functional diversity of bees and there was also a loss in functional diversity requires further study.

Even disregarding functional diversity, as the number of genera was highly correlated with the number of solitary bee species (Spearman's $\rho = 0.70$) it might be a useful surrogate for solitary bee species richness.

Conclusions

Using different statistical approaches in this study improved confidence in the results as the methods generally agreed upon which factors are important influences upon bee diversity and abundance. Using stepwise regression alone would have given misleading results. All methods agreed that solitary bees and bumblebees respond to different factors. Solitary bees responded most to north-south gradients, to calcareous grassland vegetation and to intensity of grassland management considered at the field scale. Bumblebees were most sensitive to the intensity of grassland management considered at the landscape level and to the composition of hedgerow vegetation (Figure 10.4).

Some secondary influences and potential interactions were suggested by the various analytical approaches, for example an interaction between dairying activity and the effects of hedgerow structure. Studies with more statistical power are required, using greater sample sizes and an experimental design focused on the precise hypotheses, to examine interactions and these weaker effects.

The main findings of the study also raised further questions, such as

- (1) What are the mechanisms by which more intensive field management impacts on bees, if not vegetation composition? Flowering and nest site availability are the most likely contenders.
- (2) Are species-poor *Prunus spinosa* hedges strongly associated with higher bumblebee diversity over a wider geographical region and if so why?
- (3) Is the association of unenclosed landscapes with scrub, woodland and young forestry with higher bee diversity compared to landscapes with a dense hedgerow network a general pattern?

In future studies it would be useful to consider the intensity of landuse historically at the site (over the previous 50 years) and to include floral resources as an explanatory variable.

For bumblebee diversity to be conserved, areas where rarer species occur must be identified and conservation focused on these (Williams 2000). However to maintain pollination services across the region, a general 'all areas' approach to conservation would conserve wild bee abundances of common bumblebee species and solitary bees.

Calcareous grasslands at low altitudes and southerly locations present a special case. These are likely to support the highest diversities and abundances of bees and their conservation should be a priority.

Much of the focus on agri-environmental schemes has been on the conservation of hedgerows (Staley *et al.* 2012), particularly in Ireland (European Commission 2005). Perhaps without these initiatives bees would have fared worse. However this study has shown that the main anthropogenic factor to impact on wild bees in pastoral landscapes in Ireland

is intensifying grassland management. It reduces abundances and diversity of solitary bees on a field by field basis and impacts upon bumblebees when it occurs at a landscape scale. The conservation of bees in pastoral landscapes therefore requires initiatives focused on grassland management at the field and landscape scale, while continuing to maintain the hedgerow network that is serving bees well.

Other studies have prioritised the provision of floral resources in field margins (Pywell *et al.* 2006; Carvell *et al.* 2007; Haaland *et al.* 2011) and methods of increasing resources in intensive grasslands have been trialed (Potts *et al.* 2009).

Before a recommendation for similar nectar plantings is made for Ireland it would be preferable to have a clear understanding of how grassland management impacts on bees. A reduction of floral resources is a likely mechanism and, if confirmed, then supplying nectar and pollen resources could be a compensatory measure. However it is also possible that disturbance or the physical structure of the grassland are equally or more important. If this were the case, alternative management recommendations or conservation initiatives would be required.

CHAPTER 11: OVERALL DISCUSSION AND CONCLUSIONS

11. 1. A REVIEW OF STUDY GOALS

In this study I aimed to identify factors that influence wild bee diversity, abundance and assemblage composition in lowland, grassland-dominated landscapes. Anticipating that the effects of factors would be entangled, a goal was to distinguish between their pure and shared effects.

The intensity of agricultural management was predicted to be the main influence and was the primary focus of study. Since solitary bees and bumblebees have been shown to differ in the scales of environmental factors to which they respond, agricultural intensification was considered at three scales, the field, farm and landscape levels. This also allows recommendations for bee conservation to be directed at the appropriate management level.

I set out to study the wild bee fauna in its entirety, that is, solitary bees as well as bumblebees, with a view to adding to our knowledge of the status and ecology of a neglected part of the Irish fauna as well examining the potential of the overall bee assemblage to serve as biotic indicator.

The study aimed to inform our understanding of wild bee ecology, inform conservation of wild bees within pastoral landscapes and explore the potential of wild bees to act as indicators of ecological disturbance within pastoral landscapes.

The study was restricted to a relatively small and uniform geographical area, with sites separated by a maximum of 60km and an altitude difference of less than 170m to reduce biogeographical effects and facilitate the identification of other factors. However the effects of biogeographical gradients as well as other spatial patterning on bee abundances, diversity and assemblage composition were strong. This caused me to give more consideration to the natural environmental gradients shaping bee assemblages as well to the effects of agricultural intensification.

11. 2. THE MAIN FINDINGS

NATURAL ENVIRONMENTAL GRADIENTS SHAPE BEE ASSEMBLAGES IN LOWLAND PASTORAL LANDSCAPES OF SOUTHERN IRELAND

NORTH-SOUTH AND EAST-WEST GRADIENTS

A North-east to South-west gradient was identified as the primary environmental gradient shaping wild bee assemblages. This gradient was associated with a gradient in altitude.

The effect of this biogeographical gradient was primarily on solitary bees rather than bumblebees. This may be due to the additional challenges that smaller bees face concerning thermoregulation (Stone 1994; Bishop & Armbruster 1999).

The effects of the biogeographical gradient were particularly strong for a small number of species, such as *Andrena scotica*, which was associated with the wetter North-eastern edge of the study region, and its parasite *Nomada marshamella*.

Climate change is anticipated to have greater effects than changing land-use intensity on species richness of bees in Europe (Dormann *et al.* 2008). This study's findings highlight species that are particularly sensitive to biogeographical gradients and which may be useful subjects for studies of bee responses to climatic change in Ireland.

Bumblebee diversity, though not abundance, was sensitive to both North-South and East-West gradients but these factors were of minor importance compared to other identified influences.

Bumblebee sensitivity to gradients in temperature is regarded as an important determinant of their distribution and of their species richness (Pekkarinen & Teras 1993; Kivinen *et al.* 2006) along latitudinal gradients (Banaszak 1996) but the distances considered in this study were short enough for the effect on bumblebees not to be large.

This study's detection of an East-West gradient in bumblebee diversity, of equivalent importance to the North-South gradient may indicate an anthropogenic gradient related to farming intensity. Fitzpatrick *et al.* (2007) *also* identified an East-West contrast in the distribution of rarer species of bumblebees which they considered to be driven by agricultural intensity

VEGETATION LINKAGES

Associations between bee and plant assemblages were detected. Intuitively one might expect associations between bee assemblages and vegetation due to their interactions in pollination (Potts *et al.* 2003).

Surprisingly few studies have detected correlations between plant and bee assemblages. This study's findings suggest that the detection of a correlation between plant and bee assemblages depends in part on the method used to summarise vegetation composition and the component of vegetation that is emphasized.

A number of different approaches were used in this study and each emphasised different characteristics of the vegetation. Not all measures of vegetation composition were found to be associated with bee assemblage composition. Those that were, were not necessarily associated with floral resources. Some reflected other environmental conditions such as soil conditions that may have been more associated with bees' nesting requirements.

The strongest vegetation linkage with bee abundances and diversity was that of grassland vegetation along a calcifuge to calcicolous gradient. More calcicolous vegetation was associated with higher abundances and diversity of solitary bees at the species and genera levels. Though this influence was not important when the whole bumblebee assemblage was considered, a number of rare bumblebee species were associated with such grasslands.

The value of calcareous semi-natural grasslands for bees has been recognised by other workers (Steffan-Dewenter & Tscharntke 1999; Goulson *et al.* 2006; Krauss *et al.* 2009; Krewenka *et al.* 2011). Since many of the acidic grasslands surveyed in this study were botanically diverse and flower-rich it

is possible that the superiority of calcareous grasslands as habitat for solitary bees is due to other factors beyond nectar and pollen resources. Edaphic factors such as warmer and more freely draining soils and availability of well-protected nesting sites under piles of stone (Krauss *et al.* 2009) may be important.

Hedgerow vegetation had a strong correlation with bumblebee abundance and diversity. Surprisingly, it was not species-rich but species-poor blackthorn (*Prunus spinosa*) hedgerows that were associated with a high abundance and species richness of bumblebees. Blackthorn hedgerows in their mass-flowering may provide forage at a critical time.

Alternatively, blackthorn encroachment is characteristic of land abandonment and secondary succession on limestone (Dostalek & Frantik 2012; Maccherini & Santi 2012). Such boundaries may indicate less intensive management combined with neutral to calcareous soil conditions, both favourable to bumblebees.

In contrast to bumblebees, solitary bees were found to be more diverse where the botanical diversity of hedgerow shrubs was high.

There were also significant correlations between individual species of bumblebee and grassland vegetation but only for species with restricted distributions: *B. lapidarius*, *B. muscorum*, *B. jonellus* and *B. sylvarum*. This is consistent with the finding of Goulson *et al.* (2006) that rare species are associated with a more restricted range of biotopes.

The composition of solitary bee assemblages was correlated with hedgerow and grassland vegetation. Several qualities of vegetation were identified as important to solitary bees using indirect analyses, for example a gradient reflecting soil moisture in grassland vegetation composition and a gradient in *Agrostis* species abundance. Greater botanical diversity was associated with higher species richness of solitary bees. However constrained gradient analyses showed these vegetation characters to be correlated with each other and the strongest predictor of bee assemblage structure to be the calcicolous–calcifugous gradient in grassland vegetation.

SPATIAL EFFECTS

Underlying ecological processes were revealed by the study of spatial patterns (Legendre 1993). Spatial effects upon bees were significant for distances up to approximately 10km.

There is high natural variability of bee assemblage composition across the region. The heterogeneity is due to the solitary bee component of wild bee assemblages. Solitary bee assemblages are highly dissimilar at inter-site distances of only 1km. This finding is in accord with other studies (Minckley *et al.* 1999; Wilson *et al.* 2009; Grundel *et al.* 2010).

Dissimilarity between solitary bee and bumblebee assemblages increases for distances up to approximately 10km. This distance corresponds to the upper limit of flight distances reported for some bumblebee species. This study suggests this distance as the upper limits of dispersal distance of solitary bees.

The difference in spatial structuring of solitary bees and bumblebees at this scale was attributed to autogenic processes arising from differences in their flight capacities and dispersal. Spatial dependence, driven by associations with vegetation, mainly hedgerows, was also shown to contribute to this spatial patterning in wild bee assemblages.

ANTHROPOGENIC IMPACTS

GRASSLAND MANAGEMENT IMPACTS

Negative effects of agricultural intensification on wild bees were clearly discerned. Intensifying pastoral management has a strong depressing influence on the abundances and diversity of both solitary bee and bumblebee guilds.

Agricultural intensification at the field level was shown to impact on solitary bees. This study's models predict solitary bee abundance and diversity to respond dramatically to intensification. On average, an intensively managed dairy farm can be expected to have 78% fewer solitary bees and 46% fewer

solitary bee species than a farm which is not dairying and in which the grassland has not been reseeded and is managed at the lightest extreme of the management gradient observed within the study region. The variances for the more intensive scenario were very high, making the predicted declines unreliable, but the increasing level of variance with intensification was itself regarded as a signal of ecological instability (Tilman 1996). The finding that solitary bees were particularly sensitive to agricultural intensification was in accord with the findings of Le Feon *et al.* (2010).

Murray *et al.* (2012) found bumblebees to dominate the wild bee assemblage in special areas of conservation and to be the most responsive element of the assemblage to site management. This was not the case on most farm sites. Instead solitary bees showed the greater sensitivity to intensification at the site level, as Le Feon *et al.* (2010) also observed. I attribute this difference to the local extinction of more sensitive bumblebee species from the majority of my farm sites and from the farmland studied by Le Feon *et al.* (2010) in Belgium, France, the Netherlands and Switzerland.

Whereas the impacts of agricultural intensification were detectable chiefly at the field level for solitary bees, for bumblebees, impacts on abundance and diversity were seen when intensification was measured at the landscape level. The models predicted a loss of 24% of species diversity and 30% abundance of bumblebees between traditional pastoral landscapes and the most modernised landscapes in the sample in which 90% of land cover was improved grassland. This study shows that even though common and widespread bumblebee species come to dominate bee assemblages impacted by land-use change, that their total abundance is also declining with agricultural intensification.

Based on this study's findings, an earlier study (Santorum & Breen 2005a) and using Murray's paper (Murray *et al.* 2012) to conceptually extend the management gradient into seminatural grasslands in heterogeneous landscapes, I propose a model of extinction order from wild bee assemblages in the face of intensifying grassland management (Figure 11.1). An overview of bee assemblage composition at this superficial level may therefore serve as a broad indicator for the status of bee assemblages.

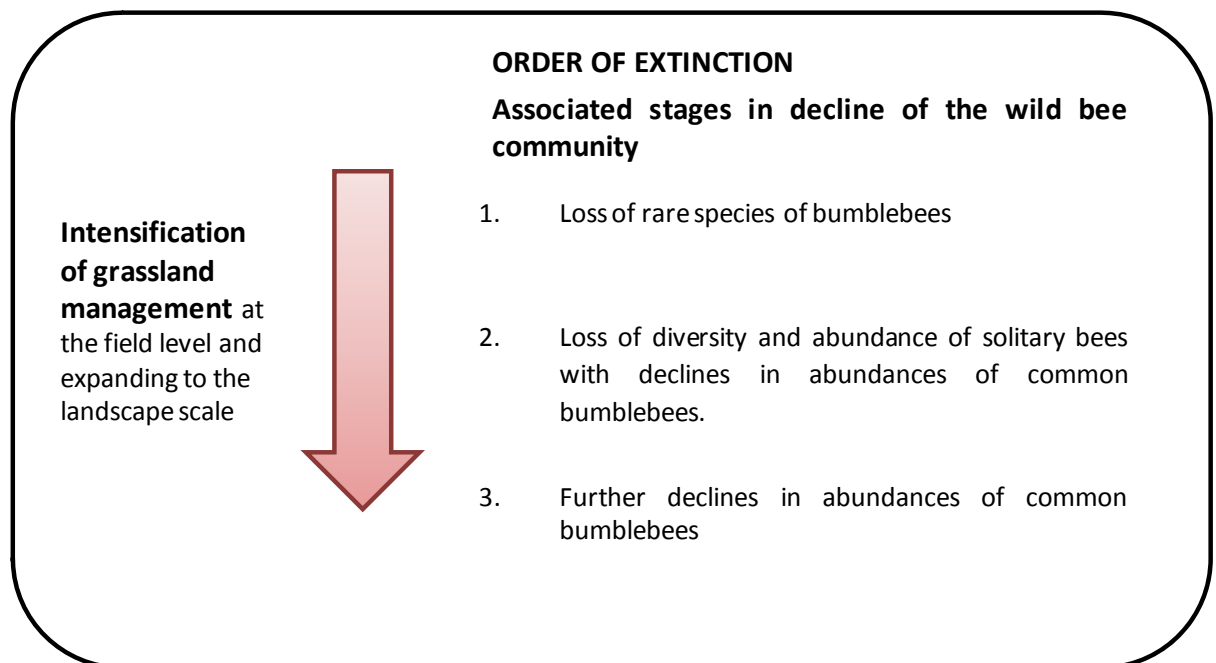


Figure 11.1. Model of extinction order within wild bee assemblages in response to intensifying grassland management in Ireland

The two scales recommended for the study of the effects of agricultural intensification on biodiversity, field and landscape scale (Tscharntke *et al.* 2005), were confirmed to be the most appropriate for the study of bee responses.

Differences in the scales of agricultural intensification at which the two guilds responded were consistent with predictions made on the basis of body size, foraging range and behaviour (van Nieuwstadt & Ruano Iraheta 1996; Gathmann & Tscharntke 2002; Tscharntke *et al.* 2005; Greenleaf *et al.* 2007; Tscheulin *et al.* 2011). The observations are in agreement with findings in other agri-environments (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2003; Albrecht *et al.* 2007; Krauss *et al.* 2009; Williams *et al.* 2010).

The number of bee genera also showed sharp declines in response to reseeded grassland. This signals a loss in genetic diversity that was not apparent from consideration of species diversity. It may also be indicative of losses of functional diversity.

Impacts on bees were detected more readily as reductions in diversity and abundance rather than shifts in species abundance composition of assemblages. Nevertheless, a shift in bee assemblage composition from assemblages dominated by diverse solitary bees to assemblages dominated by a few common bumblebees and a small number of solitary bee species was noted as field management became more intense (N.B. this gradient was also associated with a calcicole-calcifuge vegetation gradient and it was not possible to distinguish between the effects of the two factors on bee assemblage). Significant differences between bee assemblages typical of extremes of agricultural management were not detected.

Since the effects on bees of most environmental factors are thought to be indirect and via the availability of food resources (H. & Goodell 2011), the effects of agricultural intensification were expected to be via changes to the botanical composition of vegetation, especially of grasslands. The study showed clearly that grassland vegetation did respond to the intensity of field management in its composition as would be expected. What was surprising was that field vegetation composition as it reflected soil nitrogen and management intensity was not associated with bee abundances and diversity or assemblage composition. Two alternative explanations are put forward.

1. Insects (Burel *et al.* 1998) and specifically bees are more sensitive or quicker to respond to management change than plant assemblages (Steffan-Dewenter 2003; Taki & Kevan 2007);
2. Reseeding and field management impact on bee abundance and diversity by mechanisms not captured by field vegetation composition.

Other variables describing grassland vegetation that reflected management intensity such as the Simpson's Index complement and abundance of individual grasses e.g. *Agrostis* species and herbs e.g. *Leondoton autumnalis* were found to be correlated with solitary bee and bumblebee assemblage composition. It is therefore likely that the method used to describe the composition of the entire field vegetation community (axes scores from principal co-ordinates analysis) did not capture the required information

about floral resource availability and physical structure of the sward as it changed with intensification.

OTHER LANDSCAPE ASSOCIATIONS WITH BEES

In the examination of landscape composition, two gradients further to agricultural management were detected: (1) gradient in area of built land and (2) gradient describing the organisation of trees and shrubs in the landscape from hedgerows to areas of woodland, scrub and young forestry which was also associated with historic land-use intensity. Both of these landscape gradients were found to have weak associations with bees.

11.2.1. BEES AS INDICATORS?

Beyond an expectation that solitary bees would be more sensitive to small scale factors than bumblebees there were no predefined ideas of which aspect of bee assemblages might serve as a useful indicator. The study was completely exploratory, even in terms of for what bees might serve as indicators.

NUMBER OF GENERA AS INDICATORS OF SPECIES DIVERSITY AND FUNCTIONAL DIVERSITY

It emerged that number of genera of bees was more sensitive to intensification of management at the field scale, as defined by reseeded, than any other bee response variable.

The number of genera was highly correlated with the number of solitary bee species (Spearman's $\rho = 0.70$) and would therefore serve as a useful surrogate for solitary bee species richness. It may also serve as an indicator of loss in functional diversity though this requires further investigation.

BEE SPECIES AS INDICATORS OF RESPONSE TO CLIMATIC CHANGE

In analyses of species abundances of bees, a number of species emerged that were sensitive to a North-South position and to a vegetation gradient reflecting soil moisture, factors indicative of local climatic conditions. Species

Page 373 of 464

that were strongly associated with these gradients, such as *Andrena scotica* and its parasite, *Nomada marshamella*, may serve as useful subjects for studies of bee responses to climatic change in Ireland and have potential as indicators of the effects of climatic change on the bee fauna.

SPECIES AND GUILDS AS INDICATORS OF THE IMPACTS OF AGRICULTURAL INTENSIFICATION ON BEE ASSEMBLAGES

Rarer species of bumblebees may serve as indicators of good quality grassland habitat at both field and landscape scale. Though they show restricted or patchy geographical distributions in the study region these distributions appear to be unrelated to climatic gradients but determined by other environmental factors. This interpretation is supported by historic records that show these species of bumblebee (*B. muscorum*, *B. jonellus*, *B. sylvarum*) to have been more widespread in the past (Fitzpatrick *et al.* 2007). Their reduced distributions today have been attributed in the literature to an intensification of grassland management (Santorum & Breen 2005a; Fitzpatrick *et al.* 2007). This study substantiates this understanding. These species are indeed more sensitive to an environmental gradient associated with field management (that was also associated with a gradient in vegetation from calcicole to calcifuge) than other bumblebees.

The results from this study show that solitary bee diversity and abundance can be used as indicators of the degree of intensification at a field level and of the impacts on solitary bee assemblages. They also show that abundance and diversity of bumblebees are indicators of the degree of intensification at the landscape scale.

An assemblage with diverse and numerous solitary bees is indicative of a less impacted bee assemblage typical of grassland that is not managed intensely in the immediate vicinity.

An assemblage dominated by common species of bumblebees is indicative of species losses and more intensively managed farmland at the field scale. As intensification spreads at the landscape scale, even these common bumblebees are not abundant.

Given the response of solitary bees and rarer bumblebees to agricultural intensification at field and landscape scale, diverse wild bee assemblages therefore appear to have potential as indicators of High Nature Value farmland at a landscape scale.

SPATIAL VARIABILITY AS AN INDICATOR

A final attribute of bee assemblages that suggests itself as a potential biotic indicator was the natural spatial variability observed over distances greater than 5km.

Other studies have noted that anthropogenic impacts such as urbanisation (Sattler *et al.* 2010) and agricultural intensification (Clough *et al.* 2007; Dormann *et al.* 2007b; Quintero *et al.* 2010) reduce differences between assemblages over local areas, effectively homogenising assemblage composition. Such a decline in spatial variability is most likely to be detectable and test as significant in statistical analyses, when extinctions of solitary bees, the most heterogeneous part of the bee assemblage, have occurred, that is at stage 2 of the 'order of extinction' model (Figure 11.1). This quality of bee assemblages may therefore be most useful in already impacted landscapes, where one is distinguishing between regions that are moderately and severely impacted.

DIFFICULTIES ASSOCIATED WITH USING BEES AS INDICATORS

A challenge to using bees as indicators in Ireland is their low abundance, which together with spatial and temporal variability, means that considerable effort is required to observe a representative sample. A subsequent study of bees, in which I collaborated, illustrates the problem. A sampling schedule of 48 hours in 3 window pan traps per site, provided data sufficient for analysis at the level of presence-absence of bees in the sample only (Purvis *et al.* 2010).

Preliminary analyses showed that 250-500 bees would be required for accurate rankings of local areas in terms of species richness, using rarefaction or extrapolation. In the area of most intensive grassland production (Tipperary) the median number of bees per trap week was 2 bees. A sample of

250 bees would therefore be a costly effort and the removal of this number of bees is likely to impact significantly on local populations since they are already at low abundances. Using the same number of sampling units, as is the norm for most surveys, would over-sample richer areas e.g. at the most biodiverse sites over 100 bees were caught in one trap week. Such oversampling would have financial and ecological costs. Furthermore, bee identification to species level requires considerable taxonomic expertise.

Species that show a high degree of spatial variability due to natural factors cannot serve as indicators of anthropogenic impacts across wide areas. The majority of solitary bees fall into this category in Ireland. The use of guilds or functional groups may offer a solution to this issue.

11. 3. RECOMMENDATIONS

11.3.1. SUGGESTIONS FOR FURTHER RESEARCH

This exploratory research project generated a number of ideas that can be tested in future work, questions for further examination and findings that need to be checked to see if they have wider geographical application.

SPATIAL PATTERN IN BEE ASSEMBLAGES

Further exploration of the spatial patterning of bees is warranted, to determine if the pattern in bee assemblage similarity observed at inter-site distances <10km applies universally. I suggested that the more local patterning was due in part to vegetation linkages and to autogenic processes associated with flight capacity and dispersal distances. This is an area requiring further investigation. With a better understanding of natural processes structuring spatial pattern it may become worthwhile to monitor spatial patterning for change.

RARE BUMBLEBEES INDICATE HNV

The capacity of rarer bumblebees, such as *B. muscorum*, *B. jonellus* and *B. sylvarum*, to indicate High Nature Value farmland, with grasslands managed at low intensity at field and landscape scale requires further investigation. The diversity of the solitary bee component of bee assemblages where rare bumblebees occur also needs to be assessed.

ORDER OF EXTINCTION MODEL

As the proposed 'order of extinction' model has potential use in quantifying the level of impact on bee assemblages, similar to the use of ecological quality ratings (Q-Values) for water quality, it is important that it is tested. If validated it would prove very useful for monitoring the effects of environmental degradation and restoration on wild bees.

BUMBLEBEE DIVERSITY HOTSPOTS

In this study region, areas with species-poor blackthorn hedges were strongly associated with higher bumblebee diversity. This association with blackthorn needs to be checked over a wider geographical region and if found to apply, then an examination of why the correlation exists is required. Is it due to forage provided by blackthorn at a critical time in Spring or is the presence of abundant blackthorn correlated with other important environmental factors?

DISENTANGLING THE EFFECTS ASSOCIATED WITH AREA OF WOODLAND, SCRUB AND YOUNG FORESTRY

This study shows that historically unenclosed landscapes support a high diversity of wild bees. These landscapes were distinguished by their areas of seminatural woodland, scrub or young forestry. This characteristic was positively associated with the abundance and diversity of solitary bees and with bumblebee diversity. However this association is not believed to be due to the effects of area of tree cover as enclosed landscapes had similar cover. (Plate 11.1)

This landscape gradient is associated with past land-use intensity as well as today's pattern of tree cover. Enclosure of the landscape with hedgerows reflects a longer history of more productive agriculture and indicates a greater level of disturbance in the landscape, possibly since the eighteenth century (Hall 1994).

It would be useful to disentangle the effects on bees of (i) trees being organized into patches rather than hedgerows versus (ii) historical land-use. The findings will have implications for landscape planning and bee conservation.

HABITAT VALUE OF CALCAREOUS GRASSLANDS FOR BEES

Higher bee diversity was found to be associated with more calcareous grasslands. Is this association due to increased nectar and pollen resources or are there other factors related to nesting resources and microclimate?



Plate 11.1. Photograph showing density of tree cover in hedgerows associated with the bocage or enclosed landscape in part of the study region.

DIVERSITY AT THE LEVEL OF GENERA AS A MEASURE OF FUNCTIONAL DIVERSITY OF BEES

Reductions in number of genera were associated with an intensification of grassland management at the field scale. Theoretical justifications for the use of number of genera as a measure of functional diversity can be made for bees. Whether a loss of number of bee genera corresponds to a loss in functional diversity requires further study.

PROCESSES BY WHICH INTENSIVE FIELD MANAGEMENT IMPACTS ON BEES

While intensification of grassland management was unmistakably shown to impact on bees, the mechanism was not clearly demonstrated. Changes in vegetation composition, as it was measured in this study, were not the cause.

It may be fruitful to examine the effects of field management intensification on nesting resources for bees.

CLIMATE CHANGE

Given the sensitivity of solitary bees to short biogeographical gradients, their response to climate change requires investigation. This study proposes a number of species, sensitive to biogeographical gradients, for study in Ireland.

DAIRY FARMS AND HEDGEROWS

An interaction between the effects of dairying and hedgerow structure on bumblebee abundance was suggested by preliminary analyses (Chapter 10). This interaction warrants further investigation. It suggests that the presence of hedgerows with complex physical structure on dairy farms can partly compensate for management and bring the abundances of common bumblebee species up to levels similar to on non-dairying farms.

METHODOLOGICAL ISSUES

A number of suggestions also arose from the methods used.

1. The vegetation variables derived from PCO were not associated with bee response variables though other variables derived from the same vegetation dataset were e.g. Simpson's Index complement and Ellenberg scores. Alternative ways of describing floral abundances and vegetation structure for use as explanatory variables should be used in future studies.
2. The method used to describe landscape, by (i) taking a sample of 100m radius, and (ii) using a non-binary approach to habitat classification, successfully captured sufficient information about landscape composition for analyses. Both sampling and non-binary classification are recommended.
3. Inclusion of historical land use into analyses of present distributions and abundances of bees may be useful.

11.3.2. RECOMMENDATIONS FOR CONSERVATION

This study has shown that the diversity of wild bees is higher in historically open landscapes. Yet much of the focus of agri-environmental schemes has been on the conservation of hedgerows (Staley *et al.* 2012) , particularly in Ireland (European Commission 2005).

Nevertheless, bees would have fared worse without the conservation of hedgerows. This study shows hedgerow vegetation and structure to be important to bees. Higher bumblebee abundances are associated with more structurally complex hedgerows. More diverse solitary bee assemblages are associated with botanically diverse hedgerows.

However this study has shown that the main anthropogenic factor to impact on wild bees in pastoral landscapes in Ireland is intensifying grassland management. It reduces abundances and diversity of solitary bees on a field by field basis and impacts upon bumblebees when it occurs at a landscape scale.

The conservation of bees in pastoral landscapes therefore requires initiatives focused on grassland management at both the field and landscape scale, while continuing to maintain the hedgerow network that is serving bees well.

For bumblebee diversity to be conserved areas where rarer species occur must be identified and conservation focused on these (Williams 2000). Calcareous grasslands at low altitudes and southerly locations present a special case. These are likely to support the highest diversities and abundances of solitary bees and rare bumblebees. Their conservation is a priority.

At present, conservation of semi-natural grassland habitats tends to focus on maintaining plant diversity and communities but management can also incorporate the needs of bees and other taxa (Soderstrom *et al.* 2001; Vessby *et al.* 2002). For example, in this study, plant associations suggested that rarer bumblebees preferred less intensively managed areas of grassland that were in early stages of succession towards scrub, similar to the

‘abandoned land covered with shrubs’ that Hirsch and Wolters (2003) report to be a very valuable habitat for bees.

To maintain pollination services across the region, a general ‘all areas’ approach to conservation is needed. Agri-environmental schemes which can be adopted across the country offer the best means of achieving this. The aims of such a universal conservation initiative aimed at bees would be to conserve abundances of common bumblebee species and solitary bees and maintain the natural small-scale spatial heterogeneity in bee assemblages.

The restoration of native grassland vegetation, even as narrow fragments, has been shown to benefit bees (Hopwood 2008). This has potential for application even on the most intensively managed of farms. (Plate 11.2)



Plate 11.2. Potential amelioration measures to offset the negative effects of reseeded and intensive grassland management on a dairy farm. An unfertilised grassland strip composed of traditional meadow grasses and flowers is maintained alongside a reseeded, fertilised pasture. Note that the verge has grazed and ungrazed components increasing structural diversity, microclimate and flowering potential.

Other studies have prioritised the provision of floral resources in field margins (Pywell *et al.* 2006; Carvell *et al.* 2007; Haaland *et al.* 2011) and

methods of increasing these resources in intensive grasslands have been trialled (Potts *et al.* 2009).

Before a recommendation for similar nectar plantings were made for Ireland it would be preferable have a clear understanding of how grassland management impacts on bees. Removal of floral resources are a likely mechanism and if confirmed then supplying nectar and pollen resources could be a compensatory measure. However it is also possible that disturbance or the physical structure of the grassland are equally or more important. If this were the case, alternative management recommendations or conservation initiatives would be required.

Given Ireland's ambitious targets to intensify its national production of beef and dairy products (Department of Agriculture, Food and Marine Ireland, 2010); wild bees will be under increasing pressure in Ireland in the coming years.

Losses to bee diversity and abundances will continue unless efforts are made to conserve bees. Such conservation should be considered both in terms of maintaining a pollination service provided by common species across the country and in conserving and expanding hotspots of bee diversity.

In conclusion, the species composition of bee assemblages in Ireland continues to be structured predominantly by biogeographical and natural influences. Evidence for shifts in assemblage shifts in response to pastoral intensification are evident, with common bumblebee species coming to dominate the assemblage. The effects of pastoral intensification are most evident when the total abundance and species diversity of bees is considered. Both are reduced. These effects are apparent for bumblebees when agricultural intensification is considered at a landscape scale. However intensification at the scale of an individual field causes reductions in the abundance and species richness of solitary bees.

REFERENCES

- Aalen F.H.A., Whelan K. & Stout M. (1997). *Atlas of the Irish rural landscape*. Cork University Press Cork, Ireland.
- Abe T., Makino S.i. & Okochi I. (2008). Why have endemic pollinators declined on the Ogasawara Islands? *Biodiversity and Conservation*, 17, 1465-1473.
- Abrahamczyk S., Gottleuber P., Matauschek C. & Kessler M. (2011). Diversity and community composition of euglossine bee assemblages (Hymenoptera: Apidae) in western Amazonia. *Biodiversity and Conservation*, 20, 2981-3001.
- Addicott J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. & Soluk D.A. (1987). Ecological Neighborhoods-scaling environmental patterns. *Oikos*, 49, 340-346.
- Ahrne K., Bengtsson J. & Elmqvist T. (2009). Bumble Bees (*Bombus* spp) along a Gradient of Increasing Urbanization. *Plos One*, 4.
- Aickin M. & Gensler H. (1996). Adjusting for multiple testing when reporting research results: The Bonferroni vs Holm methods. *American Journal of Public Health*, 86, 726-728.
- Aizen M.A. & Feinsinger P. (1994). Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine Chaco Serrano. *Ecological Applications*, 4, 378-392.
- Akaike H. (1974). New Look at statistical-model identification. *Ieee Transactions on Automatic Control*, AC19, 716-723.
- Alarcón R., Waser N.M. & Ollerton J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, 117, 1796-1807.
- Albrecht M., Duelli P., Muller C., Kleijn D. & Schmid B. (2007). The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, 44, 813-822.
- Albrecht M., Schmid B., Obrist M.K., Schuepbach B., Kleijn D. & Duelli P. (2010). Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grassland. *Biological Conservation*, 143, 642-649.
- Alvarez A., del Corral J., Solis D. & Perez J.A. (2008). Does intensification improve the economic efficiency of dairy farms? *Journal of Dairy Science*, 91, 3693-3698.
- Andersen E., Elbersen B., Godeschalk F. & Verhoog D. (2007). Farm management indicators and farm typologies as a basis for assessments in a changing policy environment. *Journal of Environmental Management*, 82, 353-362.
- Anderson D.R. (2008). *Model Based Inference in the Life Sciences. A primer on evidence*. 2nd Edition edn. Springer Science + Business Media, New York.
- Anderson D.R., Link W.A., Johnson D.H. & Burnham K.P. (2001). Suggestions for presenting the results of data analyses. *Journal of Wildlife Management*, 65, 373-378.

- Anderson M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32-46.
- Anderson M.J. & Willis T.J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology*, 84, 511-525.
- Artz D.R. & Waddington K.D. (2006). The effects of neighbouring tree islands on pollinator density and diversity, and on pollination of a wet prairie species, *Asclepias lanceolata* (Apocynaceae). *Journal of Ecology*, 94, 597-608.
- Atmar W. & Patterson B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat *Oecologia*, 96, 373-382.
- Backman J.P.C. & Tiainen J. (2002). Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera : Bombus and Psithyrus). *Agriculture Ecosystems & Environment*, 89, 53-68.
- Banaszak-Cibicka W. & Żmihorski M. (2012). Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation*, 16, 331-343.
- Banaszak J. (1983). Ecology of bees (Apoidea) of agricultural landscape. *Polish Ecological Studies*, 421-505.
- Banaszak J. (1992). Strategy for conservation of wild bees in an agricultural landscape. *Agriculture Ecosystems & Environment*, 40, 179-192.
- Banaszak J. (1996). Variability in density of bumblebees in Europe (Hymenoptera: Apoidea: Bombus LATR.). *Polskie Pismo Entomologiczne*, 65, 21-31.
- Banaszak J., Cierznia T., Kriger R. & Wendzonka J. (2006). Bees of xerothermic swards in the lower Vistula valley: diversity and zoogeographic analyses (Hymenoptera: Apoidea: Apiformes. *Polish Journal of Entomology*, 75, 105-154.
- Banaszak J. & Rasmont P. (1994). Occurrence and distribution of the subgenus *Bombus* Latreille sensu stricto in Poland (Hymenoptera: Apoidea). *Polskie Pismo Entomologiczne*, 63, 337-356.
- Barthel S., Folke C. & Colding J. (2010). Social-ecological memory in urban gardens-Retaining the capacity for management of ecosystem services. *Global Environmental Change-Human and Policy Dimensions*, 20, 255-265.
- Bartholomew C.S. & Prowell D. (2006). Comparison of bee diversity in upland and wet flatwood longleaf pine savannas in Louisiana (Hymenoptera : Apoidea). *Journal of the Kansas Entomological Society*, 79, 199-206.
- Batary P., Baldi A., Saropataki M., Kohler F., Verhulst J., Knop E., Herzog F. & Kleijn D. (2010). Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture Ecosystems & Environment*, 136, 35-39.
- Bates A.J., Sadler J.P., Fairbrass A.J., Falk S.J., Hale J.D. & Matthews T.J. (2011). Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. *Plos One*, 6.
- Batley M. & Hogendoorn K. (2009). Diversity and conservation status of native Australian bees. *Apidologie*, 40, 347-354.
- Beals M.L. (2006). Understanding community structure: a data-driven multivariate approach. *Oecologia*, 150, 484-495.

- Beil M., Horn H. & Schwabe A. (2008). Analysis of pollen loads in a wild bee community (Hymenoptera : Apidae) - a method for elucidating habitat use and foraging distances. *Apidologie*, 39, 456-467.
- Bell J. & Watson M. (2008). *A history of Irish farming 1750-1950*. Four Courts, Dublin.
- Benton T. (2006). *Bumblebees*. Harper Collins, London.
- Benton T.G., Vickery J.A. & Wilson J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18, 182-188.
- Bestelmeyer B.T., Miller J.R. & Wiens J.A. (2003). Applying species diversity theory to land management. *Ecological Applications*, 13, 1750-1761.
- Bevilacqua S., Terlizzi A., Claudet J., Frascchetti S. & Boero F. (2012). Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *Journal of Applied Ecology*, 49, 357-366.
- Biaggini M., Consorti R., Dapporto L., Dellacasa M., Paggetti E. & Corti C. (2007). The taxonomic level order as a possible tool for rapid assessment of Arthropod diversity in agricultural landscapes. *Agriculture Ecosystems & Environment*, 122, 183-191.
- Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemueller R., Edwards M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J. & Kunin W.E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313, 351-354.
- Biesmeijer J.C. & Slaa E.J. (2006). The structure of eusocial bee assemblages in Brazil. *Apidologie*, 37, 240-258.
- Bishop J.A. & Armbruster W.S. (1999). Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Functional Ecology*, 13, 711-724.
- Bjornstad O.N. (2009). ncf: spatial nonparametric covariance functions. In. R package version 1.1-3. <http://CRAN.R-project.org/package=ncf>.
- Blacquiere T., Smagghe G., van Gestel C.A.M. & Mommaerts V. (2012). Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment. *Ecotoxicology*, 21, 973-992.
- Blitzer E.J., Dormann C.F., Holzschuh A., Klein A.-M., Rand T.A. & Tscharntke T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture Ecosystems & Environment*, 146, 34-43.
- Blondel J. (1987). From biogeography to life-history theory - A multithematic approach illustrated by the biogeography of vertebrates. *Journal of Biogeography*, 14, 405-422.
- Bluethgen N., Dormann C.F., Prati D., Klaus V.H., Kleinebecker T., Hoelzel N., Alt F., Boch S., Gockel S., Hemp A., Mueller J., Nieschulze J., Renner S.C., Schoening I., Schumacher U., Socher S.A., Wells K., Birkhofer K., Buscot F., Oelmann Y., Rothenwoehrer C., Scherber C., Tscharntke T., Weiner C.N., Fischer M., Kalko E.K.V., Linsenmair K.E., Schulze E.-D. & Weisser W.W. (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, 13, 207-220.

- Bolotov I. & Kolosova Y. (2006). Trends in the formation of biotopic complexes of bumblebees (Hymenoptera, Apidae:Bombini) in northern taiga karst landscapes of the Western Russian Plain. *Russian Journal of Ecology*, 37, 156-166.
- Bommarco R., Biesmeijer J.C., Meyer B., Potts S.G., Poyry J., Roberts S.P.M., Steffan-Dewenter I. & Ockinger E. (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B-Biological Sciences*, 277, 2075-2082.
- Bommarco R., Lundin O., Smith H.G. & Rundlof M. (2012). Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B-Biological Sciences*, 279, 309-315.
- Borcard D. & Legendre P. (2012). Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology*, 93, 1473-1481.
- Borcard D., Legendre P. & Drapeau P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045-1055.
- Bossenbroek J.M., Wagner H.H. & Wiens J.A. (2005). Taxon-dependent scaling: beetles, birds, and vegetation at four North American grassland sites. *Landsc. Ecol.*, 20, 675-688.
- Boutin C., Baril A. & Martin P.A. (2008). Plant diversity in crop fields and woody hedgerows of organic and conventional farms in contrasting landscapes. *Agriculture Ecosystems & Environment*, 123, 185-193.
- Bowers M.A. (1985). Bumble bee colonization, extinction, and reproduction in subalpine meadows in Northeastern Utah. *Ecology*, 66, 914-927.
- Bowers M.A. (1986). Density dynamics of bumblebees in sub-alpine meadows - competition and resource limitation. *Holarctic Ecology*, 9, 175-184.
- Brittain C., Bommarco R., Vighi M., Settele J. & Potts S.G. (2010a). Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation*, 143, 1860-1867.
- Brittain C.A., Vighi M., Bommarco R., Settele J. & Potts S.G. (2010b). Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, 11, 106-115.
- Brosi B.J., Armsworth P.R. & Daily G.C. (2008). Optimal design of agricultural landscapes for pollination services. *Conservation Letters*, 1, 27-36.
- Brosi B.J., Daily G.C., Shih T.M., Oviedo F. & Durán G. (2008). The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology*, 45, 773-783.
- Brown M.J.F. & Paxton R.J. (2009). The conservation of bees: a global perspective. *Apidologie*, 40, 410-416.
- Burel F. (1996). Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences*, 15, 169-190.
- Burel F., Baudry J., Butet A., Clergeau P., Delettre Y., Le Coeur D., Dubs F., Morvan N., Paillat G., Petit S., Thenail C., Brunel E. & Lefeuvre J.C. (1998). Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica-International Journal of Ecology*, 19, 47-60.
- Burnham K.P. & Anderson D.R. (2002a). *Model selection and multimodel inference*. Springer, Berlin.

- Burnham K.P. & Anderson D.R. (2002b). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edn. Springer-Verlag.
- Calabuig I. (2000). Solitary bees and Bumblebees in a Danish Agricultural Landscape. In: *Department of Population Ecology*. University of Copenhagen.
- Cameron S.A., Lozier J.D., Strange J.P., Koch J.B., Cordes N., Solter L.F. & Griswold T.L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 662-667.
- Campbell J.W. & Hanula J.L. (2007). Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation*, 11, 399-408.
- Cane J.H. (1991). Soils of ground-nesting bees (Hymenoptera, Apodidea) - texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society*, 64, 406-413.
- Cane J.H., Minckley R.L. & Kervin L.J. (2000). Sampling bees (Hymenoptera : Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, 73, 225-231.
- Cane J.H., Minckley R.L., Kervin L.J., Roulston T.H. & Williams N.M. (2006). Complex responses within a desert bee guild (Hymenoptera : Apiformes) to urban habitat fragmentation. *Ecological Applications*, 16, 632-644.
- Cardoso P., Silva I., de Oliveira N.G. & Serrano A.R.M. (2004). Higher taxa surrogates of spider (Araneae) diversity and their efficiency in conservation. *Biological Conservation*, 117, 453-459.
- Carolan J.C., Murray T.E., Fitzpatrick U., Crossley J., Schmidt H., Cederberg B., McNally L., Paxton R.J., Williams P.H. & Brown M.J.F. (2012). Colour Patterns Do Not Diagnose Species: Quantitative Evaluation of a DNA Barcoded Cryptic Bumblebee Complex. *Plos One*, 7.
- Carré G., Roche P., Chifflet R., Morison N., Bommarco R., Harrison-Cripps J., Krewenka K., Potts S.G., Roberts S.P.M., Rodet G., Settele J., Steffan-Dewenter I., Szentgyorgyi H., Tscheulin T., Westphal C., Woyciechowski M. & Vaissiere B.E. (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems & Environment*, 133, 40-47.
- Carvell C. (2002). Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation*, 103, 33-49.
- Carvell C., Jordan W.C., Bourke A.F.G., Pickles R., Redhead J.W. & Heard M.S. (2012). Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumblebee species. *Oikos*, 121, 734-742.
- Carvell C., Meek W.R., Pywell R.F., Goulson D. & Nowakowski M. (2007). Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44, 29-40.

- Carvell C., Roy D.B., Smart S., Pywell R., Preston C.D. & Goulson D. (2006). Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, 132, 481-489.
- CBD (2005). COP 5 Decisions. Fifth Ordinary Meeting of the Conference of the Parties to the Convention on Biological Diversity, 15 - 26 May 2000 - Nairobi, Kenya. URL <http://www.cbd.int/decision/cop/?id=7147>
- Chao A. (1984). Nonparametric-estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11, 265-270.
- Chao A., Chazdon R.L., Colwell R.K. & Shen T.J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, 62, 361-371.
- Chessel D., Dufour A.B. & Dray S. (2012). Package 'ade4': Analysis of Ecological Data: Exploratory and Euclidean methods in Environmental sciences, R package version 1.5-1. In: <http://cran.r-project.org/web/packages/ade4/>.
- Chiarucci A., Enright N.J., Perry G.L.W., Miller B.P. & Lamont B.B. (2003). Performance of nonparametric species richness estimators in a high diversity plant community. *Diversity and Distributions*, 9, 283-295.
- Cliff A.D. & Ord J.K. (1973). *Spatial autocorrelation*. Pion, London.
- Clough Y., Holzschuh A., Gabriel D., Purtauf T., Kleijn D., Kruess A., Steffan-Dewenter I. & Tscharntke T. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology*, 44, 804-812.
- Cobb D., Dolman P. & O'Riordan T. (1999). Interpretations of sustainable agriculture in the UK. *Progress in Human Geography*, 23, 209-235.
- Colla S.R. & Packer L. (2008). Evidence for decline in eastern North American bumblebees (Hymenoptera : Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation*, 17, 1379-1391.
- Colwell R.K. (2006). EstimateS 8.0 User's Guide. In. Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, USA.
- Colwell R.K. & Coddington J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 345, 101-118.
- Colwell R.K., Mao C.X. & Chang J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85, 2717-2727.
- Commins P., Lafferty S. & Walsh J.A. (1999). A Census Atlas of Irish Agriculture Final Report. In. Teagasc.
- Concepcion E.D., Diaz M. & Baquero R.A. (2008). Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landsc. Ecol.*, 23, 135-148.
- Concepcion E.D., Diaz M., Kleijn D., Baldi A., Batary P., Clough Y., Gabriel D., Herzog F., Holzschuh A., Knop E., Marshall E.J.P., Tscharntke T. & Verhulst J. (2012). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, 49, 695-705.

- Connop S., Hill T., Steer J. & Shaw P. (2010). The role of dietary breadth in national bumblebee (*Bombus*) declines: Simple correlation? *Biological Conservation*, 143, 2739-2746.
- Connop S., Hill T., Steer J. & Shaw P. (2011). Microsatellite analysis reveals the spatial dynamics of *Bombus humilis* and *Bombus sylvarum*. *Insect Conservation and Diversity*, 4, 212-221.
- Cranmer L., McCollin D. & Ollerton J. (2012). Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos*, 121, 562-568.
- Crawley M.J., Johnston A.E., Silvertown J., Dodd M., Mazancourt C.d., Heard M.S., Henman D.F. & Edwards G.R. (2005). Determinants of Species Richness in the Park Grass Experiment. *The American Naturalist*, 165, 179-192.
- Creighton P., Kennedy E., Shalloo L., Boland T.M. & O' Donovan M. (2011). A survey analysis of grassland dairy farming in Ireland, investigating grassland management, technology adoption and sward renewal. *Grass and Forage Science*, 66, 251-264.
- Croxton P.J., Carvell C., Mountford J.O. & Sparks T.H. (2002). A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. *Biological Conservation*, 107, 365-374.
- Croxton P.J. & Sparks T.H. (2002). A farm-scale evaluation of the influence of hedgerow cutting frequency on hawthorn (*Crataegus monogyna*) berry yields. *Agriculture Ecosystems & Environment*, 93, 437-439.
- Cushman S.A. & McGarigal K. (2002). Hierarchical, multi-scale decomposition of species-environment relationships. *Landsc. Ecol.*, 17, 637-646.
- Dauber J., Hirsch M., Simmering D., Waldhardt R., Otte A. & Wolters V. (2003). Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture Ecosystems & Environment*, 98, 321-329.
- Dennis R.L.H., Shreeve T.G. & Van Dyck H. (2003). Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos*, 102, 417-426.
- Department of Agriculture and Food (Ireland). (2006). AgriVision 2015 Action Plan. www.agriculture.gov.ie
- Department of Agriculture, Food and the Marine (2010). Food Harvest 2020. www.agriculture.gov.ie
- Department of Agriculture, Food and the Marine (Ireland). (2011). Annual Review and Outlook for Agriculture, Fisheries and Food 2010/2011. www.agriculture.gov.ie
- Department of Agriculture Food and the Marine (Ireland). (2012). Fact Sheet on Irish Agriculture – April 2012. www.agriculture.gov.ie
- Diekötter T., Walther-Hellwig K., Conradi M., Suter M. & Frankl R. (2006). Effects of landscape elements on the distribution of the rare bumblebee species *Bombus muscorum* in an agricultural landscape. *Biodiversity and Conservation*, 15, 57-68.
- Dormann C.F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16, 129-138.

- Dormann C.F., McPherson J.M., Araujo M.B., Bivand R., Bolliger J., Carl G., Davies R.G., Hirzel A., Jetz W., Kissling W.D., Kuehn I., Ohlemueller R., Peres-Neto P.R., Reineking B., Schroeder B., Schurr F.M. & Wilson R. (2007a). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609-628.
- Dormann C.F., Schweiger O., Arens P., Augenstein I., Aviron S., Bailey D., Baudry J., Billeter R., Bugter R., Bukacek R., Burel F., Cerny M., De Cock R., De Blust G., DeFilippi R., Diekoetter T., Dirksen J., Durka W., Edwards P.J., Frenzel M., Hamersky R., Hendrickx F., Herzog F., Klotz S., Koolstra B., Lausch A., Le Coeur D., Liira J., Maelfait J.P., Opdam P., Roubalova M., Schermann-Legionnet A., Schermann N., Schmidt T., Smulders M.J.M., Speelmans M., Simova P., Verboom J., van Wingerden W. & Zobel M. (2008). Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecology Letters*, 11, 235-244.
- Dormann C.F., Schweiger O., Augenstein I., Bailey D., Billeter R., de Blust G., DeFilippi R., Frenzel M., Hendrickx F., Herzog F., Klotz S., Liira J., Maelfait J.P., Schmidt T., Speelmans M., van Wingerden W. & Zobel M. (2007b). Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography*, 16, 774-787.
- Dostalek J. & Frantik T. (2012). The Impact of Different Grazing Periods in Dry Grasslands on the Expansive Grass *Arrhenatherum elatius* L. and on Woody Species. *Environmental Management*, 49, 855-861.
- Dramstad W. & Fry G. (1995). Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land *Agriculture Ecosystems & Environment*, 53, 123-135.
- Dramstad W.E. (1996). Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behavior*, 9, 163-182.
- Duelli P. & Obrist M.K. (1998). In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity and Conservation*, 7, 297-309.
- Duelli P. & Obrist M.K. (2003). Biodiversity indicators: the choice of values and measures. *Agriculture Ecosystems & Environment*, 98, 87-98.
- Duelli P., Obrist M.K. & Schmatz D.R. (1999). Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture Ecosystems & Environment*, 74, 33-64.
- Dufrene M. & Legendre P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345-366.
- Dunn A.G. & Majer J.D. (2007). In response to the continuum model for fauna research: a hierarchical, patch-based model of spatial landscape patterns. *Oikos*, 116, 1413-1418.
- Dupont Y.L., Damgaard C. & Simonsen V. (2011). Quantitative Historical Change in Bumblebee (*Bombus* spp.) Assemblages of Red Clover Fields. *Plos One*, 6, 1-7.
- Eardley C.D., Gikungu M. & Schwarz M.P. (2009). Bee conservation in Sub-Saharan Africa and Madagascar: diversity, status and threats. *Apidologie*, 40, 355-366.

- EC (1985). Commission Decision 85/377/EEC of 7 June 1985. In: (ed. European Commission).
- Éireann M. (2013). www.met.ie
- Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W. & Paulissen D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 1-248.
- Ellis E.C. & Ramankutty (2008). Putting people on the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6, 439-447
- Ellison A.M. (1996). An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecological Applications*, 6, 1036-1046.
- Environmental Protection Agency., European Environment Agency. & ERA Maptec. (2009). CORINE Land Cover - IRELAND Land Cover Update for 2006
- ESRI (2009). ArcMap 9.2. In. ESRI (Environmental Systems Resource Institute) Redlands, California.
- European Commission (2005). Agri-environment Measures Overview on General Principles, Types of Measures, and Application. ed. Directorate General for Agriculture and Rural Development.
- Ewers R.M. & Didham R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, 81, 117-142.
- Exeler N., Kratochwil A. & Hochkirch A. (2009). Restoration of riverine inland sand dune complexes: implications for the conservation of wild bees. *Journal of Applied Ecology*, 46, 1097-1105.
- Fahrig L. (2003). Effects of habitat fragmentation on biodiversity. In: *Annual Review of Ecology, Evolution and Systematics*, pp. 487-515.
- Faith D.P. & Norris R.H. (1989). Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biological Conservation*, 50, 77-98.
- FAO (2006). Food and Agriculture Statistics Global Outlook. <http://faostat.fao.org/Portals/Faostat/documents/pdf/world.pdf>
- FAO (2008). Rapid Assessment of Pollinators' Status. In: *Pollination Services for Sustainable Agriculture*. Food and Agriculture Organization of the United Nations Rome, Italy.
- Firbank L.G., Petit S., Smart S., Blain A. & Fuller R.J. (2008). Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363, 777-787.
- Fischer J. & Lindenmayer D.B. (2006). Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, 112, 473-480.
- Fitzpatrick U., Murray T.E., Byrne A., Paxton R.J. & Brown M.J.F. (2006a). Regional Red List of Irish Bees. In.

- Fitzpatrick U., Murray T.E., Byrne A., Paxton R.J. & Brown M.J.F. (2006b). Regional red list of Irish Bees. In: Report to National Parks and Wildlife Service (Ireland) and Environment and Heritage Service (N. Ireland).
- Fitzpatrick U., Murray T.E., Paxton R.J., Breen J., Cotton D., Santorum V. & Brown M.J.F. (2007). Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna. *Biological Conservation*, 136, 185-194.
- Forest Service (1998). FIPS98.
<http://www.agriculture.gov.ie/forests-service/forests-service-general-information/about-the-forests-service/forest-cover-datasets/>.
- Forman R.T.T. & Baudry J. (1984). Hedgerows and hedgerow networks in landscape ecology. *Environmental Management*, 8, 495-510.
- Forman R.T.T. & Godron M. (1981). Patches and structural components for a landscape ecology. *Bioscience*, 31, 733-740.
- Fossitt J.A. (2000). *A Guide to Habitats in Ireland*. The Heritage Council, Dublin.
- Frame J. (1992). *Improved grassland management*. Farming Press, Ipswich
- Franzen M. & Nilsson S.G. (2008). How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography*, 31, 698-708.
- Franzen M. & Ockinger E. (2012). Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *Journal of Insect Conservation*, 16, 227-238.
- Freitas B.M., Imperatriz-Fonseca V.L., Medina L.M., Peixoto Kleinert A.d.M., Galetto L., Nates-Parra G. & Quezada-Euan J.J.G. (2009). Diversity, threats and conservation of native bees in the Neotropics. *Apidologie*, 40, 332-346.
- French D.D. & Cummins R.P. (2001). Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science*, 4, 213-228.
- Friendly M. (1994). Mosaic displays for multiway contingency-tables *Journal of the American Statistical Association*, 89, 190-200.
- Friendly M. (1999). Extending mosaic displays: Marginal, conditional, and partial views of categorical data. *Journal of Computational and Graphical Statistics*, 8, 373-395.
- Fründ J., Linsenmair K.E. & Blüthgen N. (2010). Pollinator diversity and specialization in relation to flower diversity. *Oikos*, 119, 1581-1590.
- Fuller S., Schwarz M. & Simon T. (2005). Phylogenetics of the Allodapine Bee Genus *Braunsapis*: Historical Biogeography and Long-Range Dispersal over Water. *Journal of Biogeography*, 32, 2135-2144.
- Furnival G.M. & Wilson R.W. (1974). Regressions by leaps and bounds. *Technometrics*, 16, 499-511.
- Fussell M. & Corbet S.A. (1991). Forage for bumble bees and honey-bees in farmland - a case-study. *Journal of Apicultural Research*, 30, 87-97.
- Garibaldi L.A., Steffan-Dewenter I., Kremen C., Morales J.M., Bommarco R., Cunningham S.A., Carvalheiro L.G., Chacoff N.P., Dudenhofer J.H., Greenleaf S.S., Holzschuh A., Isaacs R., Krewenka K., Mandelik Y., Mayfield M.M., Morandin L.A., Potts S.G., Ricketts T.H., Szentgyorgyi H., Viana B.F., Westphal C., Winfree R. & Klein A.M. (2011). Stability of

- pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14, 1062-1072.
- Gathmann A., Greiler H.J. & Tschardt T. (1994). Trap-nesting bees and wasps colonizing set-aside fields - succession and body-size, management by cutting and sowing. *Oecologia*, 98, 8-14.
- Gathmann A. & Tschardt T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71, 757-764.
- Gelman A. (2011). Induction and Deduction in Bayesian Data Analysis. *Rationality, Markets and Morals*, <http://www.rmm-journal.de/>, 2, 67-78.
- Gelman A. & Shalizi C.R. (2012). Philosophy and the practice of Bayesian statistics. *British Journal of Mathematical and Statistical Psychology*, 0, 1-31.
- Gollan J.R., Ashcroft M.B. & Batley M. (2011). Comparison of yellow and white pan traps in surveys of bee fauna in New South Wales, Australia (Hymenoptera: Apoidea: Anthophila). *Australian Journal of Entomology*, 50, 174-178.
- Goslee S.C. & Urban D.L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1-19.
- Goulson D. (2003). Bumblebees: Their behaviour and ecology. *Bumblebees: Their behaviour and ecology*, i-ix, 1-235.
- Goulson D. & Darvill B. (2004). Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie*, 35, 55-63.
- Goulson D., Hanley M.E., Darvill B. & Ellis J.S. (2006). Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation*, 10, 95-103.
- Goulson D., Hanley M.E., Darvill B., Ellis J.S. & Knight M.E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, 122, 1-8.
- Goulson D., Lepais O., O'Connor S., Osborne J.L., Sanderson R.A., Cussans J., Goffe L. & Darvill B. (2010). Effects of land use at a landscape scale on bumblebee nest density and survival D. Goulson et al. Landscape effects on bumblebee nest survival. *Journal of Applied Ecology*, 47, 1207-1215.
- Goulson D., Lye G.C. & Darvill B. (2008). Diet breadth, coexistence and rarity in bumblebees. *Biodiversity and Conservation*, 17, 3269-3288.
- Goulson D., Stout J.C. & Kells A.R. (2002). Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania? *Journal of Insect Conservation*, 6, 179-189.
- Gower J.C. (1971). General coefficient of similarity and some of its properties. *Biometrics*, 27, 857-874.
- Greenleaf S.S., Williams N.M., Winfree R. & Kremen C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589-596.
- Grimbacher P.S., Catterall C.P. & Kitching R.L. (2008). Detecting the effects of environmental change above the species level with beetles in a fragmented tropical rainforest landscape. *Ecological Entomology*, 33, 66-79.

- Grixti J.C. & Packer L. (2006). Changes in the bee fauna (Hymenoptera : Apoidea) of an old field site in southern Ontario, revisited after 34 years. *Canadian Entomologist*, 138, 147-164.
- Grixti J.C., Wong L.T., Cameron S.A. & Favret C. (2009). Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation*, 142, 75-84.
- Grundel R., Jean R.P., Frohnapple K.J., Glowacki G.A., Scott P.E. & Pavlovic N.B. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, 20, 1678-1692.
- H. R.T. & Goodell K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. In: *Annual Review of Entomology, Vol 56* (eds. Berenbaum MR, Carde RT & Robinson GE), pp. 293-312.
- Haaland C., Naisbit R.E. & Bersier L.-F. (2011). Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4, 60-80.
- Hagen M., Wikelski M. & Kissling W.D. (2011). Space Use of Bumblebees (*Bombus* spp.) Revealed by Radio-Tracking. *Plos One*, 6.
- Haila Y. (2002). A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications*, 12, 321-334.
- Hall V.A. (1994). Landscape development in Northeast Ireland over the last half millenium *Review of Palaeobotany and Palynology*, 82, 75-82.
- Hannon L.E. & Sisk T.D. (2009). Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation*, 142, 2140-2154.
- Harrell Jr F.E. (2012). Hmisc: Harrell Miscellaneous: Version 3.10-1. In: (ed. Dupont C) <http://cran.r-project.org/web/packages/Hmisc/>.
- Harrison S. & Bruna E. (1999). Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, 22, 225-232.
- Hartigan J.A. & Kleiner B. (1981). Mosaics for Contingency Tables. In: *Proceedings of the 13th Symposium on the Interface between Computer Science and Statistics* (ed. Eddy WF). Springer-Verlag New York.
- Hartigan J.A. & Kleiner B. (1984). A mosaic of television ratings. *American Statistician*, 38, 32-35.
- Haskell M.J., Brotherstone S., Lawrence A.B. & White I.M.S. (2007). Characterization of the dairy farm environment in great Britain and the effect of the farm environment on cow life span. *Journal of Dairy Science*, 90, 5316-5323.
- Hatfield R.G. & LeBuhn G. (2007). Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera : Apidae), in montane meadows. *Biological Conservation*, 139, 150-158.
- Hegarty C.A. & Cooper A. (1994). Regional variation of hedge structure and composition in Northern-Ireland in relation to management and land-use *Biology and Environment-Proceedings of the Royal Irish Academy*, 94B, 223-236.
- Heinrich B. & Esch H. (1994). Thermoregulation in Bees. *American Scientist*, 82, 164-170.

- Hendrix S.D., Kwaizer K.S. & Heard S.B. (2010). Bee communities (Hymenoptera: Apoidea) of small Iowa hill prairies are as diverse and rich as those of large prairie preserves. *Biodiversity and Conservation*, 19, 1699-1709.
- Hennekens S.M. & Schaminee J.H.J. (2001). TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science*, 12, 589-591.
- Herrera C.M. (1995). Microclimate and individual variation in pollinators - flowering plants are more than their flowers *Ecology*, 76, 1516-1524.
- Herzog F., Steiner B., Bailey D., Baudry J., Billeter R., Bukacek R., De Blust G., De Cock R., Dirksen J., Dormann C.F., De Filippi R., Frossard E., Liira J., Schmidt T., Stockli R., Thenail C., van Wingerden W. & Bugter R. (2006). Assessing the intensity of temperate European agriculture at the landscape scale. *European Journal of Agronomy*, 24, 165-181.
- Hilbe J.M. (2011). *Negative Binomial Regression*. 2nd edn. Cambridge University Press, Cambridge, UK and New York, USA.
- Hill M.O., Mountford J.O., Roy D.B. & Bunce R.G.H. (1999). ECOFACT 2a Technical Annex - Ellenberg's Indicator Values for British Plants. In: *ECOFACT research report series*. Institute of Terrestrial Ecology Huntingdon, UK.
- Hines H.M. (2008). Historical Biogeography, Divergence Times, and Diversification Patterns of Bumble Bees (Hymenoptera: Apidae: Bombus). *Systematic Biology*, 57, 58-75.
- Hines H.M. & Hendrix S.D. (2005). Bumble bee (Hymenoptera : Apidae) diversity and abundance in tallgrass prairie patches: Effects of local and landscape floral resources. *Environmental Entomology*, 34, 1477-1484.
- Hirsch M. & Wolters V. (2003). Response of aculeate Hymenoptera to spatial features of an agricultural landscape. *Journal for Nature Conservation*, 11, 179-185.
- Hisamatsu M. & Yamane S. (2006). Faunal makeup of wild bees and their flower utilization in a semi-urbanized area in central Japan. *Entomological Science*, 9, 137-145.
- Hobbs N.T. & Hilborn R. (2006). Alternatives to statistical hypothesis testing in ecology: A guide to self teaching. *Ecological Applications*, 16, 5-19.
- Hoehn P., Tschardt T., Tylianakis J.M. & Steffan-Dewenter I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B-Biological Sciences*, 275, 2283-2291.
- Holm S. (1979). A simple sequentially rejective multiple test procedure *Scandinavian Journal of Statistics*, 6, 65-70.
- Holzschuh A., Steffan-Dewenter I., Kleijn D. & Tschardt T. (2007). Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, 44, 41-49.
- Holzschuh A., Steffan-Dewenter I. & Tschardt T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, 117, 354-361.
- Hopwood J.L. (2008). The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, 141, 2632-2640.
- Huggett A.J. (2005). The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation*, 124, 301-310.

- Hurlbert S.H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54, 187-211.
- Hymettus Ltd (2006). Aculeate Information Sheets, How the habitat requirements of BAP aculeates relate to their HAP In: *Bumblebees, Bombus species, associated with open grasslands*. Hymettus Ltd- The UK Aculeate Conservation Group, Conservation Action for Ants, Bees and Wasps
- Ishii H.S., Kadoya T., Kikuchi R., Suda S. & Washitani I. (2008). Habitat and flower resource partitioning by an exotic and three native bumble bees in central Hokkaido, Japan. *Biological Conservation*, 141, 2597-2607.
- Jacobs J.H., Clark S.J., Denholm I., Goulson D., Stoate C. & Osborne J.L. (2009). Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set. *Annals of Botany*, 104, 1397-1404.
- Johnson J.B. & Omland K.S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19, 101-108.
- Kearns C.A., Inouye D.W. & Waser N.M. (1998). Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 29, 83-112.
- Keegan E. (2007). Final Year Project: Grasslands. In: *Department of Life Sciences*. University of Limerick.
- Keitt T.H. (2009). Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecological Applications*, 19, 1561-1573.
- Kells A.R. & Goulson D. (2003). Preferred nesting sites of bumblebee queens (Hymenoptera : Apidae) in agroecosystems in the UK. *Biological Conservation*, 109, 165-174.
- Kim J., Williams N. & Kremen C. (2006). Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*, 79, 309-320.
- Kivinen S., Luoto M., Kuussaari M. & Helenius J. (2006). Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. *Journal of Biogeography*, 33, 862-875.
- Kleijn D., Baquero R.A., Clough Y., Diaz M., De Esteban J., Fernandez F., Gabriel D., Herzog F., Holzschuh A., Johl R., Knop E., Kruess A., Marshall E.J.P., Steffan-Dewenter I., Tscharntke T., Verhulst J., West T.M. & Yela J.L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, 9, 243-254.
- Kleijn D. & van Langevelde F. (2006). Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, 7, 201-214.
- Klein A.M., Steffan-Dewenter I. & Tscharntke T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 955-961.
- Knight M.E., Martin A.P., Bishop S., Osborne J.L., Hale R.J., Sanderson A. & Goulson D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, 14, 1811-1820.

- Knight M.E., Osborne J.L., Sanderson R.A., Hale R.J., Martin A.P. & Goulson D. (2009). Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conservation and Diversity*, 2, 116-124.
- Köbrich C., Rehman T. & Khan M. (2003). Typification of farming systems for constructing representative farm models: two illustrations of the application of multi-variate analyses in Chile and Pakistan. *Agricultural Systems*, 76, 141-157.
- Koenig W.D. (1999). Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, 14, 22-26.
- Kohler F., Verhulst J., Knop E., Herzog F. & Kleijn D. (2007). Indirect effects of grassland extensification schemes on pollinators in two contrasting European countries. *Biological Conservation*, 135, 302-307.
- Kohler F., Verhulst J., van Klink R. & Kleijn D. (2008). At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *Journal of Applied Ecology*, 45, 753-762.
- Kovacs-Hostyanszki A., Batary P. & Baldi A. (2011). Local and landscape effects on bee communities of Hungarian winter cereal fields. *Agricultural and Forest Entomology*, 13, 59-66.
- Krauss J., Alfert T. & Steffan-Dewenter I. (2009). Habitat area but not habitat age determines wild bee richness in limestone quarries. *Journal of Applied Ecology*, 46, 194-202.
- Kremen C., Williams N.M., Bugg R.L., Fay J.P. & Thorp R.W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7, 1109-1119.
- Kremen C., Williams N.M. & Thorp R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 16812-16816.
- Krewenka K.M., Holzschuh A., Tscharrntke T. & Dormann C.F. (2011). Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation*, 144, 1816-1825.
- Kruess A. & Tscharrntke T. (2002). Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation*, 106, 293-302.
- Kuhlmann M., Guo D., Veldtman R. & Donaldson J. (2012). Consequences of warming up a hotspot: species range shifts within a centre of bee diversity. *Diversity and Distributions*, 1-13.
- Laliberté E. & Legendre P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299-305.
- Laliberté E. & Shipley B. (2011). FD: measuring functional diversity from multiple traits, and other tools for functional ecology: R package version 1.0-11. In: <http://cran.r-project.org/web/packages/FD/>.
- Lande R., DeVries P.J. & Walla T.R. (2000). When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos*, 89, 601-605.
- Lander T.A., Bebbier D.P., Choy C.T.L., Harris S.A. & Boshier D.H. (2011). The Circe Principle Explains How Resource-Rich Land Can Waylay Pollinators in Fragmented Landscapes. *Current Biology*, 21, 1302-1307.

- Larsen T.H., Williams N.M. & Kremen C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8, 538-547.
- Le Feon V., Schermann-Legionnet A., Delettire Y., Aviron S., Billeter R., Bugter R., Hendrickx F. & Burel F. (2010). Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agriculture Ecosystems & Environment*, 137, 143-150.
- Lechner A.M., Langford W.T., Jones S.D., Bekessy S.A. & Gordon A. (2012). Investigating species-environment relationships at multiple scales: Differentiating between intrinsic scale and the modifiable areal unit problem. *Ecological Complexity*, 11, 91-102.
- Legendre P. (1990). Quantitative methods and biogeographic analysis. In: *Evolutionary biogeography of the marine algae of the North Atlantic* (eds. Garbary DJ & South RR). Springer-Verlag Berlin, Germany.
- Legendre P. (1993). Spatial autocorrelation - trouble or new paradigm. *Ecology*, 74, 1659-1673.
- Legendre P. & Anderson M.J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69, 1-24.
- Legendre P., Dale M.R.T., Fortin M.J., Gurevitch J., Hohn M. & Myers D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, 25, 601-615.
- Legendre P. & Fortin M.J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, 80, 107-138.
- Legendre P. & Gallagher E.D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280.
- Legendre P. & Legendre L. (1998). *Numerical Ecology*. Elsevier, Amsterdam.
- Legendre P., Oksanen J. & Ter Braak C.J.F. (2011). Testing the significance of canonical axes in redundancy analysis. *Methods in Ecology and Evolution*, 2, 269-277.
- Leong J.M. & Thorp R.W. (1999). Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecological Entomology*, 24, 329-335.
- Lepš J. & Šmilauer P. (2003). *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge, UK.
- Ligges U. & Mächler M. (2003). Scatterplot3d - an R Package for Visualizing Multivariate Data. *Journal of Statistical Software*, 8, 1-20.
- Lindenmayer D., Hobbs R.J., Montague-Drake R., Alexandra J., Bennett A., Burgman M., Cale P., Calhoun A., Cramer V., Cullen P., Driscoll D., Fahrig L., Fischer J., Franklin J., Haila Y., Hunter M., Gibbons P., Lake S., Luck G., MacGregor C., McIntyre S., Mac Nally R., Manning A., Miller J., Mooney H., Noss R., Possingham H., Saunders D., Schmiegelow F., Scott M., Simberloff D., Sisk T., Tabor G., Walker B., Wiens J., Woinarski J. & Zavaleta E. (2008). A checklist for ecological management of landscapes for conservation. *Ecology Letters*, 11, 78-91.

- Lindenmayer D.B., Fischer J. & Hobbs R. (2007). The need for pluralism in landscape models: a reply to Dunn and Majer. *Oikos*, 116, 1419-1421.
- Link W.A. & Barker R.J. (2006). Model weights and the foundations of multimodel inference. *Ecology*, 87, 2626-2635.
- Løken A. (1972). Studies on Scandinavian bumblebees (Hymenoptera, Apidae). *Norsk Entomologisk Tidsskrift*, 20, 1-218.
- Longino J.T., Coddington J. & Colwell R.K. (2002). The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology*, 83, 689-702.
- Lonsdorf E., Kremen C., Ricketts T., Winfree R., Williams N. & Greenleaf S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, 103, 1589-1600.
- Louwagie G., Northey G., Finn J.A. & Purvis G. (2012). Development of indicators for assessment of the environmental impact of livestock farming in Ireland using the Agri-environmental Footprint Index. *Ecological Indicators*, 18, 149-162.
- Ludwig J.A., Wiens J.A. & Tongway D.J. (2000). A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. *Ecosystems*, 3, 84-97.
- Mac Nally R. (2000). Regression and model-building in conservation biology, biogeography and ecology: The distinction between and reconciliation of 'predictive' and 'explanatory' models. *Biodiversity and Conservation*, 9, 655-671.
- Maccherini S. & Santi E. (2012). Long-term experimental restoration in a calcareous grassland: Identifying the most effective restoration strategies. *Biological Conservation*, 146, 123-135.
- Magurran A.E. (2004). Measuring Biological Diversity In. Blackwell Publishing Oxford.
- Mardia K.V., Kent J.T. & Bibby J.M. (1979). *Multivariate analysis*. Academic Press, London ; New York.
- Marlin J.C. & LeBerge W.E. (2001). The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conservation Ecology*, 5, art. no.-9.
- Marshall E.J.P. & Moonen A.C. (2002). Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment*, 89, 5-21.
- Matesanz S., Gimeno T.E., de la Cruz M., Escudero A. & Valladares F. (2011). Competition may explain the fine-scale spatial patterns and genetic structure of two co-occurring plant congeners. *Journal of Ecology*, 99, 838-848.
- McCordle B.H. & Anderson M.J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, 82, 290-297.
- McCune B. & Grace J.B. (2002). Analysis of Ecological Communities. In. MjM Software Design Gleneden Beach, Oregon.
- McGeoch M.A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, 73, 181-201.

- McIntyre S. & Barrett G.W. (1992). Habitat variegation, an alternative to fragmentation. *Conservation Biology*, 6, 146-147.
- Melo A.S. (2004). A critique of the use of jackknife and related non-parametric techniques to estimate species richness. *Community Ecology*, 5, 149-157.
- Meyer D., Zeileis A. & Hornik K. (2006). The Strucplot Framework: Visualizing Multi-Way Contingency Tables with vcd. *Journal of Statistical Software*, 17, 1-48.
- Meyer D., Zeileis A. & Hornik K. (2012). vcd: Visualizing Categorical Data. R package version 1.2-13. In: <http://cran.r-project.org/web/packages/vcd/>.
- Michener C.D. (1979). Biogeography of the Bees. *Annals of the Missouri Botanical Garden*, 66, 277-347.
- Michener C.D. (2000). *The Bees of the World*. Johns Hopkins University Press.
- Minckley R. (2008). Faunal composition and species richness differences of bees (Hymenoptera : Apiformes) from two north American regions. *Apidologie*, 39, 176-U134.
- Minckley R.L., Cane J.H., Kervin L. & H. R.T. (1999). Spatial predictability and resource specialization of bees (Hymenoptera : Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society*, 67, 119-147.
- Moretti M., de Bello F., Roberts S.P.M. & Potts S.G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, 78, 98-108.
- Moron D., Szentgyoergyi H., Wantuch M., Celary W., Westphal C., Settele J. & Woyciechowski M. (2008). Diversity of wild bees in wet meadows: implications for conservation. *Wetlands*, 28, 975-983.
- Munyuli M., Nyeko P., Potts S., Atkinson P., Pomeroy D. & Vickery J. (2013). Patterns of bee diversity in mosaic agricultural landscapes of central Uganda: implication of pollination services conservation for food security. *Journal of Insect Conservation*, 1-15.
- Murray A. & Foulkes N. (2006). A methodology for the recording of hedgerow extent, species composition, structure, and condition in Ireland. *Tearmann*, 75-90.
- Murray T.E., Fitzpatrick U., Byrne A., Fealy R., Brown M.J.F. & Paxton R.J. (2012). Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, 49, 998-1008.
- Murray T.E., Kuhlmann M. & Potts S.G. (2009). Conservation ecology of bees: populations, species and communities. *Apidologie*, 40, 211-236.
- N. Erik Sjödin J.B.B.E. (2008). The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology*, 45, 763-772.
- National Research Council (2007). *Status of pollinators in North America*. The National Academies Press, Washington, D.C.
- Noordijk J., Delille K., Schaffers A.P. & Sykora K.V. (2009). Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, 142, 2097-2103.

- NPWS (2010). Designated Site Data. National Parks and Wildlife Service. Department of the Environment, Heritage and Local Government <http://www.npws.ie/mapsanddata/designatedsitedata/>.
- NPWS & BEC Consultants (2010). NSNW Woodland Habitats 2010 shapefiles. <http://www.npws.ie/mapsanddata/habitatspeciesdata/>.
- O'Sullivan A.M. (1968). *The lowland grasslands (Molinio-Arrhenatheretea) of County Limerick*. An Foras Talúntais, Dublin, Ireland.
- O'Toole C. & Raw A. (2004). *Bees of the World*. Facts On File.
- O'Rourke E., Kramm N. & Chisholm N. (2012). The influence of farming styles on the management of the Iveragh uplands, southwest Ireland. *Land Use Policy*, 29, 805-816.
- Öckinger E., Lindborg R., Sjödin N.E. & Bommarco R. (2012). Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, 35, 259-267.
- Ockinger E. & Smith H.G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44, 50-59.
- Oden N.L. & Sokal R.R. (1986). Directional autocorrelation - an extension of spatial correlograms to 2 dimensions. *Systematic Zoology*, 35, 608-617.
- Oertli S., Muller A. & Dorn S. (2005). Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera : Apoidea : Apiformes). *European Journal of Entomology*, 102, 53-63.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. & Wagner H. (2013). vegan: Community Ecology Package, R package version 2.0-6. In. <http://cran.r-project.org/web/packages/vegan/index.html>.
- Osborne J.L., Clark S.J., Morris R.J., Williams I.H., Riley J.R., Smith A.D., Reynolds D.R. & Edwards A.S. (1999). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*, 36, 519-533.
- Osborne J.L., Martin A.P., Carreck N.L., Swain J.L., Knight M.E., Goulson D., Hale R.J. & Sanderson R.A. (2008a). Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, 77, 406-415.
- Osborne J.L., Martin A.P., Shortall C.R., Todd A.D., Goulson D., Knight M.E., Hale R.J. & Sanderson R.A. (2008b). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, 45, 784-792.
- Patiny S., Michez D., Kuhlmann M., Pauly A. & Barbier Y. (2009a). Factors limiting the species richness of bees in Saharan Africa. *Bulletin of Entomological Research*, 99, 337-346.
- Patiny S., Rasmont P. & Michez D. (2009b). A survey and review of the status of wild bees in the West-Palaearctic region. *Apidologie*, 40, 313-331.
- Pawlikowski T. (1985). Wild bee (Hymenoptera Apoidea) communities of the xerothermic dune habitats in the Torun Basin Poland. *Studia Societatis Scientiarum Torunensis Sectio E (Zoologia)*, 10, 3-58.

- Pearson D.L. (1994). Selecting indicator taxa for the quantitative assessment of biodiversity *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 345, 75-79.
- Pekkarinen A. & Teras I. (1993). Zoogeography of *Bombus* and *Psithyrus* in northwestern Europe (Hymenoptera, Apidae). *Annales Zoologici Fennici*, 30, 187-208.
- Pekkarinen A., Teras I., Viramo J. & Paatela J. (1981). Distribution of Bumble bees *Bombus* and *Psithyrus* (Hymenoptera Apidea) in Eastern Fennoscandia. *Notulae Entomologicae*, 61, 71-89.
- Pelosi C., Goulard M. & Balent G. (2010). The spatial scale mismatch between ecological processes and agricultural management: Do difficulties come from underlying theoretical frameworks? *Agriculture, Ecosystems & Environment*, 139, 455-462.
- Peres-Neto P.R. & Jackson D.A. (2001). How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, 129, 169-178.
- Persson A.S., Olsson O., Rundlof M. & Smith H.G. (2010). Land use intensity and landscape complexity-Analysis of landscape characteristics in an agricultural region in Southern Sweden. *Agriculture Ecosystems & Environment*, 136, 169-176.
- Podani J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, 48, 331-340.
- Potts S.G., Biesmeijer J.C., Kremen C., Neumann P., Schweiger O. & Kunin W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345-353.
- Potts S.G., Vulliamy B., Dafni A., Ne'eman G. & Willmer P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, 84, 2628-2642.
- Potts S.G., Vulliamy B., Roberts S., O'Toole C., Dafni A., Ne'Eman G. & Willmer P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30, 78-85.
- Potts S.G., Vulliamy B., Roberts S., O'Toole C., Dafni A., Ne'eman G. & Willmer P.G. (2004). Nectar resource diversity organises flower-visitor community structure. *Entomologia Experimentalis Et Applicata*, 113, 103-107.
- Potts S.G. & Willmer P. (1997). Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, 22, 319-328.
- Potts S.G., Woodcock B.A., Roberts S.P.M., Tscheulin T., Pilgrim E.S., Brown V.K. & Tallowin J.R. (2009). Enhancing pollinator biodiversity in intensive grasslands. *Journal of Applied Ecology*, 46, 369-379.
- Power E.F. & Stout J.C. (2011). Organic dairy farming: impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology*, 48, 561-569.
- Purvis G., Anderson G., McMahon B., Sheridan H., Carnus T., Kelly-Quinn M., Breen J. & Santorum V. (2010). AGRI-BASELINE - Creating an Environmental Baseline for evaluation of Irish agr-environmental policy. (Synthesis report for Task 11 (Summary, Preliminary analyses and

- Illustration of the Potential of the Assembled Database) Research Stimulus Fund (RSF) - 2006). In. Prepared for the Department of Agriculture, Fisheries & Food (DAFF) by University College Dublin (UCD) (Farmland Ecology Research Group, School of Agriculture, Food Science & Veterinary Medicine) University College Dublin
- Purvis G., Bolger T., Kennedy T. & Breen J. (2008). Ag-Biota: Monitoring, Functional Significance and Management for the Maintenance and Economic Utilisation of Biodiversity in the Intensively Farmed Landscape. In. Environmental Protection Agency Ireland Secure Archive For Environmental Research Data (SAFER) <http://erc.epa.ie/safer/resource?id=f0314697-6c16-102c-9c91-0a68ec663af0>.
- Pywell R.F., Warman E.A., Hulmes L., Hulmes S., Nuttall P., Sparks T.H., Critchley C.N.R. & Sherwood A. (2006). Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, 129, 192-206.
- Quintero C., Laura Morales C. & Adrian Aizen M. (2010). Effects of anthropogenic habitat disturbance on local pollinator diversity and species turnover across a precipitation gradient. *Biodiversity and Conservation*, 19, 257-274.
- R Core Team (2012). R: A Language and Environment for Statistical Computing. In: <http://www.R-project.org>. R Foundation for Statistical Computing Vienna, Austria.
- Rackham O. (1995). Looking for ancient woodland in Ireland. In: *Wood, trees and forests in Ireland* (eds. Pilcher JR & Mac an tSaoir S). Royal Irish Academy Dublin.
- Raftery A.E. (1995). Bayesian Model Selection in Social Research. *Sociological Methodology*, 25, 111-163.
- Raftery A.E., Hoeting J., Volinsky C., Painter I. & Yeung K.Y. (2012). BMA: Bayesian Model Averaging. In. R package version 3.15. <http://CRAN.R-project.org/package=BMA>.
- Rasmont P., Jean L., Annie J.-R., Pauly A. & Gaspar C. (1993). The faunistic drift of Apoidea in Belgium. In: *Bees for Pollination. Proceedings of an EC Workshop* (ed. Bruneau E). Directorate-General for Agriculture, Commission of the European Communities Brussels (Belgium), pp. 65-87.
- Redpath N., Osgathorpe L.M., Park K. & Goulson D. (2010). Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. *Biological Conservation*, 143, 492-500.
- Ricketts T.H., Regetz J., Steffan-Dewenter I., Cunningham S.A., Kremen C., Bogdanski A., Gemmill-Herren B., Greenleaf S.S., Klein A.M., Mayfield M.M., Morandin L.A., Ochieng A. & Viana B.F. (2008). Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11, 499-515.
- Righi E., Dogliotti S., Stefanini F.M. & Pacini G.C. (2011). Capturing farm diversity at regional level to up-scale farm level impact assessment of sustainable

- development options. *Agriculture, Ecosystems & Environment*, 142, 63-74.
- Riveiro J.A., Marey M.F., Marco J.L. & Alvarez C.J. (2008). Procedure for the classification and characterization of farms for agricultural production planning: Application in the Northwest of Spain. *Computers and Electronics in Agriculture*, 61, 169-178.
- Roberts D.W. (2013). Package 'labdsv': Ordination and Multivariate Analysis for Ecology. In: <http://cran.r-project.org/web/packages/labdsv/>.
- Robinson R.A. & Sutherland W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39, 157-176.
- Rodriguez-Girones M.A. (2012). Possible top-down control of solitary bee populations by ambush predators. *Behavioral Ecology*, 23, 559-565.
- Rodwell J.S. (1991). *British Plant Communities. Volume 1. Woodlands and scrub*. Cambridge University Press, Cambridge.
- Rodwell J.S. (1992). *British Plant Communities. Volume 3. Grasslands and Montane Communities*. Cambridge University Press, Cambridge, UK.
- Roschewitz I., Thies C. & Tschardt T. (2005). Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? *Agriculture Ecosystems & Environment*, 105, 87-99.
- Rosser N. & Eggleton P. (2012). Can higher taxa be used as a surrogate for species-level data in biodiversity surveys of litter/soil insects? *Journal of Insect Conservation*, 16, 87-92.
- Roulston T.H., Smith S.A. & Brewster A.L. (2007). A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera : Apiformes) fauna. *Journal of the Kansas Entomological Society*, 80, 179-181.
- Rundlof M., Nilsson H. & Smith H.G. (2008). Interacting effects of farming practice and landscape context on bumblebees. *Biological Conservation*, 141, 417-426.
- Samnegard U., Persson A.S. & Smith H.G. (2011). Gardens benefit bees and enhance pollination in intensively managed farmland. *Biological Conservation*, 144, 2602-2606.
- Santorum V. & Breen J. (2005a). Bumblebee diversity on Irish farmland. *Tearmann*, 79-90.
- Santorum V. & Breen J. (2005b). A comparison of pan traps and transects for the sampling of bumblebees in biodiversity surveys of agricultural landscapes (poster presentation). In: *3rd European Congress on Social Insects, Meeting of European Sections of IUSSI* (ed. Kipyatkov VE). St. Petersburg University Press St. Petersburg, Russia.
- Santorum V. & O'Sullivan E. (2006). Ballyhoura Hedgerow Survey Report 2006. In: Ballyhoura Development Ltd. Kilfinane, County Limerick, Ireland.
- Sarospataki M., Baldi A., Batary P., Jozan Z., Erdoes S. & Redei T. (2009). Factors affecting the structure of bee assemblages in extensively and intensively grazed grasslands in Hungary. *Community Ecology*, 10, 182-188.
- Sattler T., Borcard D., Arlettaz R., Bontadina F., Legendre P., Obrist M.K. & Moretti M. (2010). Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology*, 91, 3343-3353.

- Saville N.M., Dramstad W.E., Fry G.L.A. & Corbet S.A. (1997). Bumblebee movement in a fragmented agricultural landscape. *Agriculture Ecosystems & Environment*, 61, 145-154.
- Schaffers A.P., Raemakers I.P., Sykora K.V. & Ter Braak C.J.F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, 89, 782-794.
- Schwarz G. (1978). Estimating dimension of a model. *Annals of Statistics*, 6, 461-464.
- Schweiger O., Maelfait J.P., Van Wingerden W., Hendrickx F., Billeter R., Speelmans M., Augenstein I., Aukema B., Aviron S., Bailey D., Bukacek R., Burel F., Diekötter T., Dirksen J., Frenzel M., Herzog F., Liira J., Roubalova M. & Bugter R. (2005). Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, 42, 1129-1139.
- Sepp K., Mikk M., Mand M. & Truu J. (2004). Bumblebee communities as an indicator for landscape monitoring in the agri-environmental programme. *Landscape and Urban Planning*, 67, 173-183.
- Shaffer J.P. (1995). Multiple hypothesis-testing. *Annual Review of Psychology*, 46, 561-584.
- Sheridan H., McMahon B.J., Carnus T., Finn J.A., Anderson A., Helden A.J., Kinsella A. & Purvis G. (2011). Pastoral farmland habitat diversity in south-east Ireland. *Agriculture, Ecosystems & Environment*, 144, 130-135.
- Simpson G. (2011). What is ordisurf doing. In: <http://ucfagls.wordpress.com/2011/06/10/what-is-ordisurf-doing/>, accessed 25 August 2011.
- Sjodin N.E. (2007). Pollinator behavioural responses to grazing intensity. *Biodiversity and Conservation*, 16, 2103-2121.
- Sjodin N.E., Bengtsson J. & Ekbom B. (2008). The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology*, 45, 763-772.
- Skandalis D.A., Richards M.H., Sformo T.S. & Tattersall G.J. (2011). Climate limitations on the distribution and phenology of a large carpenter bee, *Xylocopa virginica* (Hymenoptera: Apidae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 89, 785-795.
- Sladen F.W.L. (1912). *The humble-bee, its life-history and how to domesticate it, with descriptions of all the British species of Bombus and Psithyrus*, by F. W. L. Sladen. Macmillan and co., limited, London.
- Soderstrom B., Svensson B., Vessby K. & Glimskar A. (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, 10, 1839-1863.
- Sokal R.R. & Oden N.L. (1978a). Spatial autocorrelation in biology: 1. Methodology. *Biological Journal of the Linnean Society*, 10, 199-228.
- Sokal R.R. & Oden N.L. (1978b). Spatial autocorrelation in biology: 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society*, 10, 229-249.

- Somers R.H. (1962). A new asymmetric measure of association for ordinal variables. *American Sociological Review*, 27, 799-811.
- Southwood T.R.E. (1988). Tactics, strategies and templets. *Oikos*, 52, 3-18.
- Spengler A., Hartmann P., Buchori D. & Schulze C.H. (2011). How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. *Journal of Biogeography*, 38, 247-258.
- Staley J.T., Sparks T.H., Croxton P.J., Baldock K.C.R., Heard M.S., Hulmes S., Hulmes L., Peyton J., Amy S.R. & Pywell R.F. (2012). Long-term effects of hedgerow management policies on resource provision for wildlife. *Biological Conservation*, 145, 24-29.
- Steffan-Dewenter I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, 17, 1036-1044.
- Steffan-Dewenter I., Munzenberg U., Burger C., Thies C. & Tscharntke T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421-1432.
- Steffan-Dewenter I., Munzenberg U. & Tscharntke T. (2001). Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 1685-1690.
- Steffan-Dewenter I. & Tscharntke T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, 121, 432-440.
- Steffan-Dewenter I. & Tscharntke T. (2000). Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*, 122, 288-296.
- Steffan-Dewenter I. & Tscharntke T. (2001). Succession of bee communities on fallows. *Ecography*, 24, 83-93.
- Stephens P.A., Buskirk S.W., Hayward G.D. & Del Rio C.M. (2005). Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology*, 42, 4-12.
- Stone G.N. (1994). Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body-size. *Ecological Entomology*, 19, 177-189.
- Sullivan C.A., Skeffington M.S., Gormally M.J. & Finn J.A. (2010). The ecological status of grasslands on lowland farmlands in western Ireland and implications for grassland classification and nature value assessment. *Biological Conservation*, 143, 1529-1539.
- Svensson B., Lagerlof J. & Svensson B.G. (2000). Habitat preferences of nest-seeking bumble bees (Hymenoptera : Apidae) in an agricultural landscape. *Agriculture Ecosystems & Environment*, 77, 247-255.
- Szczepko K., Pawlikowski T. & Kowalczyk J.K. (2002). Apoidea (Hymenoptera) in habitats of former agriculture area in a renaturation stage of Kampinos National Park (Poland). *Fragmenta Faunistica (Warsaw)*, 45, 115-122.
- Taki H. & Kevan P.G. (2007). Does habitat loss affect the communities of plants and insects equally in plant-pollinator interactions? Preliminary findings. *Biodiversity and Conservation*, 16, 3147-3161.

- Taki H., Okabe K., Yamaura Y., Matsuura T., Sueyoshi M., Makino S. & Maeto K. (2010). Effects of landscape metrics on Apis and non-Apis pollinators and seed set in common buckwheat. *Basic and Applied Ecology*, 11, 594-602.
- Talley T.S. (2007). Which spatial heterogeneity framework? Consequences for conclusions about patchy population distributions. *Ecology*, 88, 1476-1489.
- Tallowin J.R.B., Smith R.E.N., Goodyear J. & Vickery J.A. (2005). Spatial and structural uniformity of lowland agricultural grassland in England: a context for low biodiversity. *Grass and Forage Science*, 60, 225-236.
- Ter Braak C.J.F. (1986). Canonical correspondence-analysis - a new eigenvector technique for multivariate direct gradient analysis *Ecology*, 67, 1167-1179.
- Ter Braak C.J.F. (1987). The analysis of vegetation-environment relationships by canonical correspondence-analysis. *Vegetatio*, 69, 69-77.
- Ter Braak C.J.F. (1994). Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience*, 1, 127-140.
- Ter Braak C.J.F. & Prentice I.C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, 18, 271-317.
- Ter Braak C.J.F. & Prentice I.C. (2004). A Theory of Gradient Analysis. In: *Advances in Ecological Research* (ed. Caswell H). Academic Press, pp. 235-282.
- Tilman D. (1987). Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. *Ecological Monographs*, 57, 189-214.
- Tilman D. (1996). Biodiversity: Population versus ecosystem stability. *Ecology*, 77, 350-363.
- Townsend P.A. & Levey D.J. (2005). An experimental test of whether habitat corridors affect pollen transfer. *Ecology*, 86, 466-475.
- Tscharntke T., Gathmann A. & Steffan-Dewenter I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, 35, 708-719.
- Tscharntke T., Klein A.M., Kruess A., Steffan-Dewenter I. & Thies C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, 8, 857-874.
- Tscharntke T., Steffan-Dewenter I., Kruess A. & Thies C. (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, 17, 229-239.
- Tscheulin T., Neokosmidis L., Petanidou T. & Settele J. (2011). Influence of landscape context on the abundance and diversity of bees in Mediterranean olive groves. *Bulletin of Entomological Research*, 101, 557-564.
- Tylianakis J.M., Klein A.M. & Tscharntke T. (2005). Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology*, 86, 3296-3302.
- Ushimaru A., Ishida C., Sakai S., Shibata M., Tanaka H., Niiyama K. & Nakashizuka T. (2008). The effects of human management on spatial distribution of

- two bumble bee species in a traditional agro-forestry Satoyama landscape. *Journal of Apicultural Research*, 47, 296-303.
- van der Ploeg J.D., Laurent C., Blondeau F. & Bonnafous P. (2009). Farm diversity, classification schemes and multifunctionality. *Journal of Environmental Management*, 90, S124-S131.
- van Nieuwstadt M.G.L. & Ruano Iraheta C.E. (1996). Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie*, 27, 219-228.
- Venables W.N. & Ripley B.D. (2002). Modern Applied Statistics with S. In. Springer New York.
- Vessby K., Soderstrom B., Glimskar A. & Svensson B. (2002). Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology*, 16, 430-439.
- Vickery J.A., Tallowin J.R., Feber R.E., Asteraki E.J., Atkinson P.W., Fuller R.J. & Brown V.K. (2001). The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, 38, 647-664.
- Vitousek P.M., Mooney H.A., Lubchenco J. & Melillo J.M. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494-499.
- Vrdoljak S.M. & Samways M.J. (2011). Optimising coloured pan traps to survey flower visiting insects. *Journal of Insect Conservation*.
- Vulliamy B., Potts S.G. & Willmer P.G. (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos*, 114, 529-543.
- Walther-Hellwig K. & Frankl R. (2000a). Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behavior*, 13, 239-246.
- Walther-Hellwig K. & Frankl R. (2000b). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., apidae), in an agricultural landscape. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 124, 299-306.
- Walther B.A. & Morand S. (1998). Comparative performance of species richness estimation methods. *Parasitology*, 116, 395-405.
- Wcislo W.T. & Cane J.H. (1996). Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology*, 41, 257-286.
- Weiner C.N., Werner M., Linsenmair K.E. & Bluethgen N. (2011). Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks. *Basic and Applied Ecology*, 12, 292-299.
- Westphal C., Bommarco R., Carre G., Lamborn E., Morison N., Petanidou T., Potts S.G., Roberts S.P.M., Szentgyorgyi H., Tscheulin T., Vaissiere B.E., Wojciechowski M., Biesmeijer J.C., Kunin W.E., Settele J. & Steffan-Dewenter I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78, 653-671.

- Westphal C., Steffan-Dewenter I. & Tscharntke T. (2006). Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia*, 149, 289-300.
- Westphal C., Steffan-Dewenter I. & Tscharntke T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46, 187-193.
- Westrich P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In: *Linnean Society Symposium Series; The conservation of bees* (eds. Matheson A, Buchmann SL, O'Toole C, Westrich P & Williams IH), pp. 1-16.
- White T.A., Snow V.O. & King W.M. (2010). Intensification of New Zealand beef farming systems. *Agricultural Systems*, 103, 21-35.
- Whittingham M.J., Krebs J.R., Swetnam R.D., Vickery J.A., Wilson J.D. & Freckleton R.P. (2007). Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecology Letters*, 10, 25-35.
- Whittingham M.J., Stephens P.A., Bradbury R.B. & Freckleton R.P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, 75, 1182-1189.
- Wiens J.A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3, 385-397.
- Williams N.M. (2011). Restoration of Nontarget Species: Bee Communities and Pollination Function in Riparian Forests. *Restoration Ecology*, 19, 450-459.
- Williams N.M., Crone E.E., Roulston T.H., Minckley R.L., Packer L. & Potts S.G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143, 2280-2291.
- Williams N.M. & Kremen C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17, 910-921.
- Williams N.M., Minckley R.L. & Silveira F.A. (2001). Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*, 5.
- Williams N.M., Regetz J. & Kremen C. (2012). Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology*, 93, 1049-1058.
- Williams P. (2000). Some properties of rarity scores used in site quality assessment. *British Journal of Entomology and Natural History*, 13, 73- 86.
- Williams P. (2005a). Does specialization explain rarity and decline British bumblebees? - A response to Goulson et al. *Biological Conservation*, 122, 33-43.
- Williams P., Colla S. & Xie Z. (2009). Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents. *Conservation Biology*, 23, 931-940.
- Williams P.H. (1982). The distribution and decline of British Bumble bees (*Bombus* Latr). *Journal of Apicultural Research*, 21, 236-245.
- Williams P.H. (1986). Environmental change and the distribution of British bumble bees (*Bombus* Latr.). *Bee World*, 67, 50-61.

- Williams P.H. (1988). Habitat use by Bumble bees (*Bombus* spp) *Ecological Entomology*, 13, 223-237.
- Williams P.H. (1989). Why are there so many species of Bumble bees at Dungeness *Botanical Journal of the Linnean Society*, 101, 31-44.
- Williams P.H. (1991). The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum (Natural History) (Entomology)*, 60, 1-204.
- Williams P.H. (1994). Phylogenetic-relationships among Bumble bees (*Bombus* Latr) - a reappraisal of morphological evidence *Systematic Entomology*, 19, 327-344.
- Williams P.H. (1996). Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society B-Biological Sciences*, 263, 579-588.
- Williams P.H. (2005b). Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biological Conservation*, 122, 33-43.
- Williams P.H., Araujo M.B. & Rasmont P. (2007). Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation*, 138, 493-505.
- Wilson J.S., Messinger O.J. & Griswold T. (2009). Variation between bee communities on a sand dune complex in the Great Basin Desert, North America: Implications for sand dune conservation. *Journal of Arid Environments*, 73, 666-671.
- Winfree R. (2010). The conservation and restoration of wild bees. In: *Year in Ecology and Conservation Biology 2010* (eds. Ostfeld RS & Schlesinger WH), pp. 169-197.
- Winfree R., Aguilar R., Vazquez D.P., LeBuhn G. & Aizen M.A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068-2076.
- Winfree R., Bartomeus I. & Cariveau D.P. (2011). Native Pollinators in Anthropogenic Habitats. In: *Annual Review of Ecology, Evolution, and Systematics, Vol 42* (eds. Futuyma DJ, Shaffer HB & Simberloff D), pp. 1-22.
- Winfree R., Griswold T. & Kremen C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, 21, 213-223.
- Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, 45, 793-802.
- With K.A. & Crist T.O. (1995). Critical thresholds in species responses to landscape structure. *Ecology*, 76, 2446-2459.
- Wolf S. & Moritz R.F.A. (2008). Foraging distance in *Bombus terrestris* L. (Hymenoptera : Apidae). *Apidologie*, 39, 419-427.
- Wu J.G. & David J.L. (2002). A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecological Modelling*, 153, 7-26.

- Wu J.G. & Loucks O.L. (1995). From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology*, 70, 439-466.
- Xie Z.H., Williams P.H. & Tang Y. (2008). The effect of grazing on bumblebees in the high rangelands of the Eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation*, 12, 695-703.
- Yaacobi G., Ziv Y. & Rosenzweig M.L. (2007). Habitat fragmentation may not matter to species diversity. *Proceedings of the Royal Society B-Biological Sciences*, 274, 2409-2412.
- Yoshihara Y., Chimeddorj B., Buuveibaatar B., Lhagvasuren B. & Takatsuki S. (2008). Effects of livestock grazing on pollination on a steppe in eastern Mongolia. *Biological Conservation*, 141, 2376-2386.
- Zobel M. (1997). The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution*, 12, 266-269.
- Zurbuchen A., Bachofen C., Mueller A., Hein S. & Dorn S. (2010a). Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species. *Apidologie*, 41, 497-508.
- Zurbuchen A., Cheesman S., Klaiber J., Mueller A., Hein S. & Dorn S. (2010b). Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, 79, 674-681.
- Zurbuchen A., Landert L., Klaiber J., Mueller A., Hein S. & Dorn S. (2010c). Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143, 669-676.
- Zuur A.F., Ieno E.N. & Elphick C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14.

APPENDICES

Poster presentation in 3rd European Congress on Social Insects, Meeting of European Sections of IUSSI (Ed. Kipyatkov V.E.) St. Petersburg University Press, Russia

Page 416 of 464

APPENDIX 2. Definition of habitat categories for landscape mapping.

BOUNDARY HABITAT

DESCRIPTION

Hedgerows, earthen banks, ditches, walls and tree lines were classed together as boundary habitat. Where boundary habitat overlapped with woody habitats, it was regarded as part of the woodland or forest.

MAPPING PROCEDURE

Boundary maps were created by manually digitising boundaries visible on orthorectified aerial photographs (from 2000, OSI). Boundary habitat was mapped as linear polygons of 2m width (an average value determined from field survey).

NON-NATIVE FOREST

DESCRIPTION

Maturing or mature coniferous forests with a closed canopy and forests composed of nonnative deciduous tree species were included in this category.

MAPPING PROCEDURE

Forest parcels (FIPS) mapped by the Forest Service were overlaid with areas categorised as native woodland in the NPWS maps. Forests that were present on both maps were regarded as semi-natural woodland and were removed from the 'nonnative forests' category. The remaining FIPS forest parcels were then examined on aerial photographs and young plantations, for which the field layer was clearly visible in the 2006 aerial photography, were removed from this category.

SEMI-NATURAL WOODLAND

DESCRIPTION

This habitat class included

1. broadleaved woodlands composed of native species of tree growing on sites that have had continuous woodland cover for at least 160 years*.

2. woodlands made up of mixtures of native and nonnative trees growing on sites that have had continuous woodland cover for at least 160 years*.
3. orchards
4. transitional woodland scrub
5. gorse or blackthorn scrub
6. recently planted coniferous forestry which did not have a closed canopy.

* Ireland's first OSI maps, which included high woodland cover, date to the 1840s.

These varied woody habitats were grouped together because they were expected to have a flowering component attractive to bees, either in the herb layer or shrubs and trees, provide undisturbed habitat for nesting and overwintering and are likely to provide a similar sheltered and moist microclimate.

MAPPING PROCEDURE

Maps of Native woodlands supplied boundaries of woodlands as polygons. FIPS maps, in combination with aerial photography, were used to identify recently planted coniferous forestry. All other types of woodland or scrub were identified using aerial photography and mapped manually in the GIS using polygons.

SEMI NATURAL / SEMI-IMPROVED GRASSLANDS AND 'INTENSIVELY MANAGED' GRASSLANDS

DESCRIPTION

The semi-natural / semi-improved grassland category grouped a diverse range of grassland types together, such as wet and dry grasslands, calcareous and acidic grasslands etc. Semi-improved grasslands (Sullivan *et al.* 2010) were also included in this category. In the final analyses, other open habitats such as fens and saltmarsh were added to the semi-natural grassland category. These habitats were very rare.

'Intensively managed' grasslands were those regarded as having a uniformly structured sward of low species diversity, dominated by a few agricultural grasses. Grasslands used for recreation and leisure, e.g. golf course or horse racing track were also regarded as intensively managed (site 101). The area

of 'intensively managed' grassland was calculated by summing all other habitat areas and subtracting this value from the total area sampled of 3.142 ha.

MAPPING PROCEDURE

A visual assessment of the colour composition of fields in aerial photographs from 2006 and 2000 was used to classify grassland fields as either 'semi-natural / semi-improved' or 'intensively managed' grasslands. Fields with heterogeneity in the colour of their sward, with colours such as yellow, red, buff or brown apparent, in images from either or both years, were classified as semi-natural. All other grasslands were left unclassified and considered 'intensively managed'.

BUILT

DESCRIPTION

This landuse category included any land that had a building upon it, or that was used for industrial purposes such as mining and waste disposal. Roads and car parks were also included.

MAPPING PROCEDURE

Aerial photographs were used to identify areas within this category and they were mapped manually using polygons.

WATER

DESCRIPTION

All bodies of water that were easily distinguishable on aerial photographs were included in this category. This included rivers, estuaries, sea, ponds, lakes and lagoons.

MAPPING PROCEDURE

Visual inspection of aerial photographs was used to locate water and areas were mapped manually as polygons. Small rivers and streams with a closed

Page 419 of 464

canopy of trees or shrubs may not have been distinguished on aerial photographs and could have been mapped as boundary habitat.

NB preliminary data exploration using PCA showed an outlier (site F114) to dominate the third PCA axis, due to the site's proximity to a large pond. Since the area of water was considered relatively unimportant and only occurred at one site, it was removed as a habitat category.

APPENDIX 3. Automatic digitisation of hedgerows

The process of hedgerow classification for one photograph, using automatic digitisation methods, is summarised below.

1. Isocluster analysis on the 3 colour bands of the aerial photograph to create a signature file.
2. +- editing of the signature file.
3. Maximum likelihood classification of the aerial photograph using the prepared signature file.
4. Squaring of the class values of the resulting maximum likelihood classification.
5. Blockstats calculating the mean value of the resulting file using a window of 8x8 cells.
6. Use the 'boundary clean' function with ascend sorting in order to emphasise the finer details of the map.
7. Reclassify the classes that found exclusively in hedge or woodland to one category.
8. Extract this hedgerow category
9. Convert the raster of the hedgerow category to polygons.

APPENDIX 4. Rescoring of FBEGS categories

In the standard FBEGS field boundary survey, there are five categories to score most observations. These categories were regrouped and scores calculated as shown below.

Variables used to describe boundary structure and how they were scored. Those marked * applied to hedgerows only.

Variable	Scale	Observed range	Category	Score
Type	Nominal / binary	Hedgerow, treeline, scrub or woodland edge.	1	NA
		Bank, wall or drainage ditch without woody component.	2	NA
Height* (average)	Ordinal	0.5m – 2m	1	1
		2-4m	2	2
		>4m	3	3
Width* (average at base)	Ordinal	0.5m – 2m	1	1
		2-4m	2	2
		>4m	3	3
Structural complexity of vegetation*	Ordinal	matched to FBEG images and rescored into fewer categories.	1	1
			2	2
			3	3
Earthen bank height	Ordinal	Absent	1	0
		<1m	2	2
		>1m	3	3
Presence of drain	Nominal / binary	Absent	1	0
		Present	2	1

APPENDIX 5. Field-proofing of Grassland classification in habitat maps

To further check the habitat maps, in particular the division of semi-natural / semi-improved and intensively managed grasslands, a field survey was undertaken in late August-early September 2008. Seven square kilometres or 252 fields around nine sites were inspected and their grassland categorised according to the species diversity and height and structure of the sward on the day of the visit. Fields that had just been cut had only bare earth and a few roots visible and were omitted from the sample. 203 fields were used in the validation process.

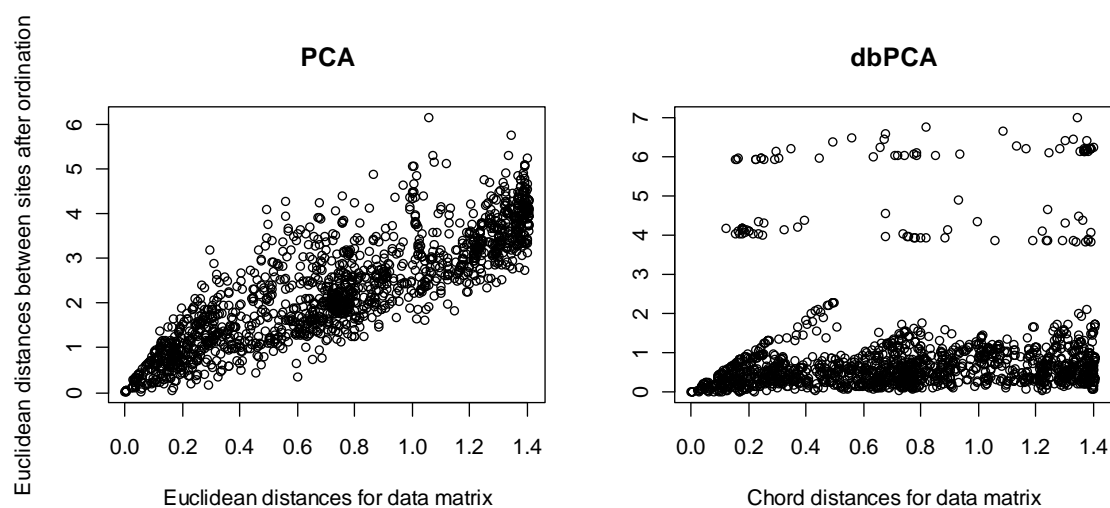
A comparison of the grassland classifications derived from visual inspection of aerial photographs and field survey was carried out. Discrepancies were identified. The proportion of false positives and false negatives were quantified and the types of grassland management that were difficult to identify from aerial photography identified. The habitat maps were corrected in favour of the field survey description of grassland type.

The table overleaf shows the proportion of grasslands that were misidentified using aerial photographs. The level of error in misidentifying grassland type from aerial photography compared to field survey was found to be 22.1%. Only 1.5% were false positives (improved grassland misidentified as semi-natural / semi-improved on aerial photography) and 20.6% were false negatives (semi-natural/ semi-improved grassland misidentified as improved on aerial photography).

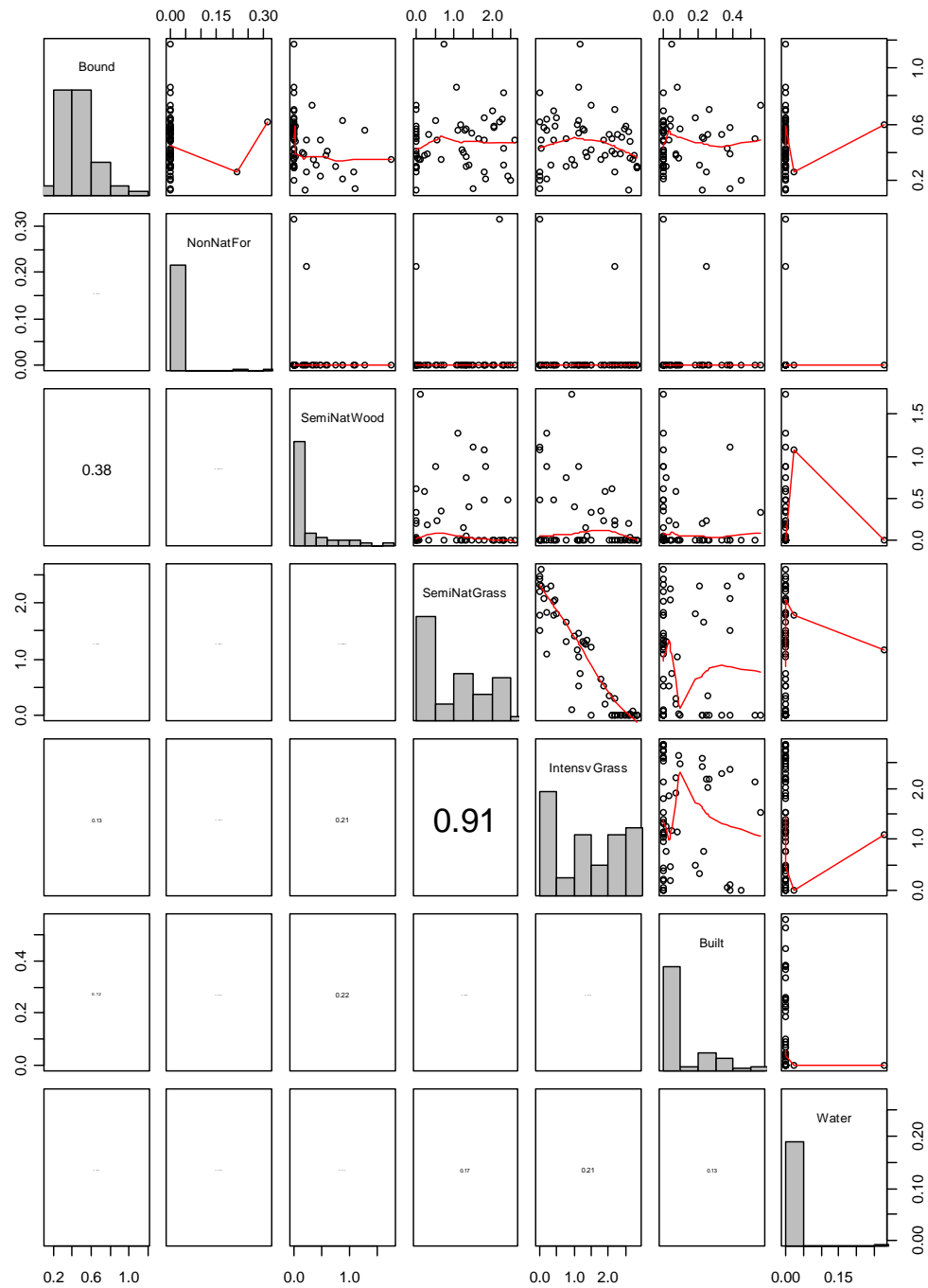
The identification of semi-natural / semi-improved grasslands was therefore conservative, with few false positives (highly modified grasslands wrongly identified semi-natural grasslands) but many false negatives (semi-natural grasslands that were missed). A consequence of the reliance on aerial photography is that semi-natural / semi-improved grassland has probably been underestimated.

Grassland classification in field survey	Number of fields	of false positives	false negatives
Highly modified (3a)	3	0	0
Semi-natural/semi-improved (3b)	9	0	4 (44.4%)
Highly modified (4a)	81	2 (2.4%)	0
Semi-natural/ semi-improved (4b)	86	0	38 (44.2%)
Highly modified (5)	21	1 (4.8%)	0
other	4	0	0

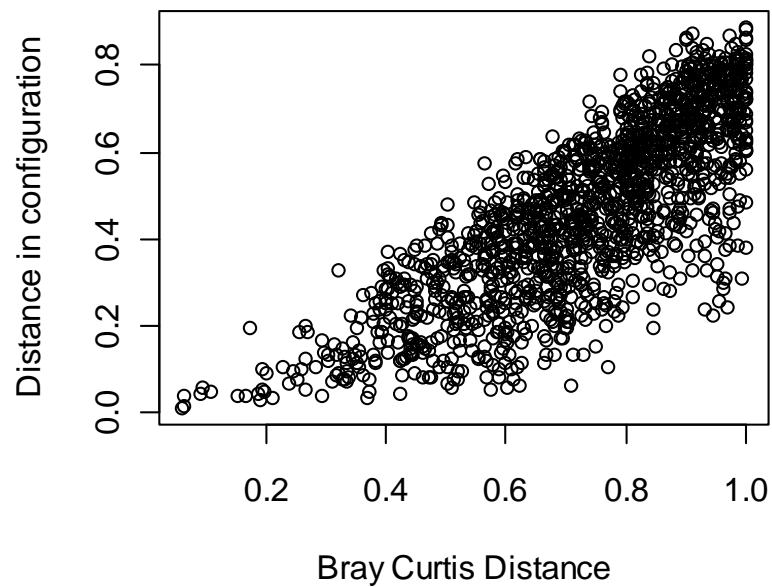
APPENDIX 6. Landscape composition – shepard diagrams for selection of appropriate ordination method



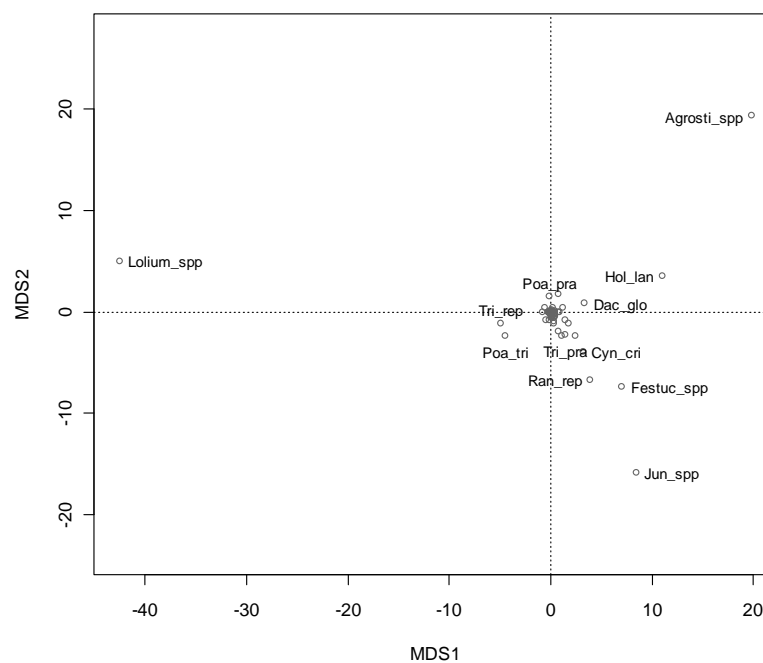
APPENDIX 7. Correlations between habitat areas within 100m radius of each sampling point.



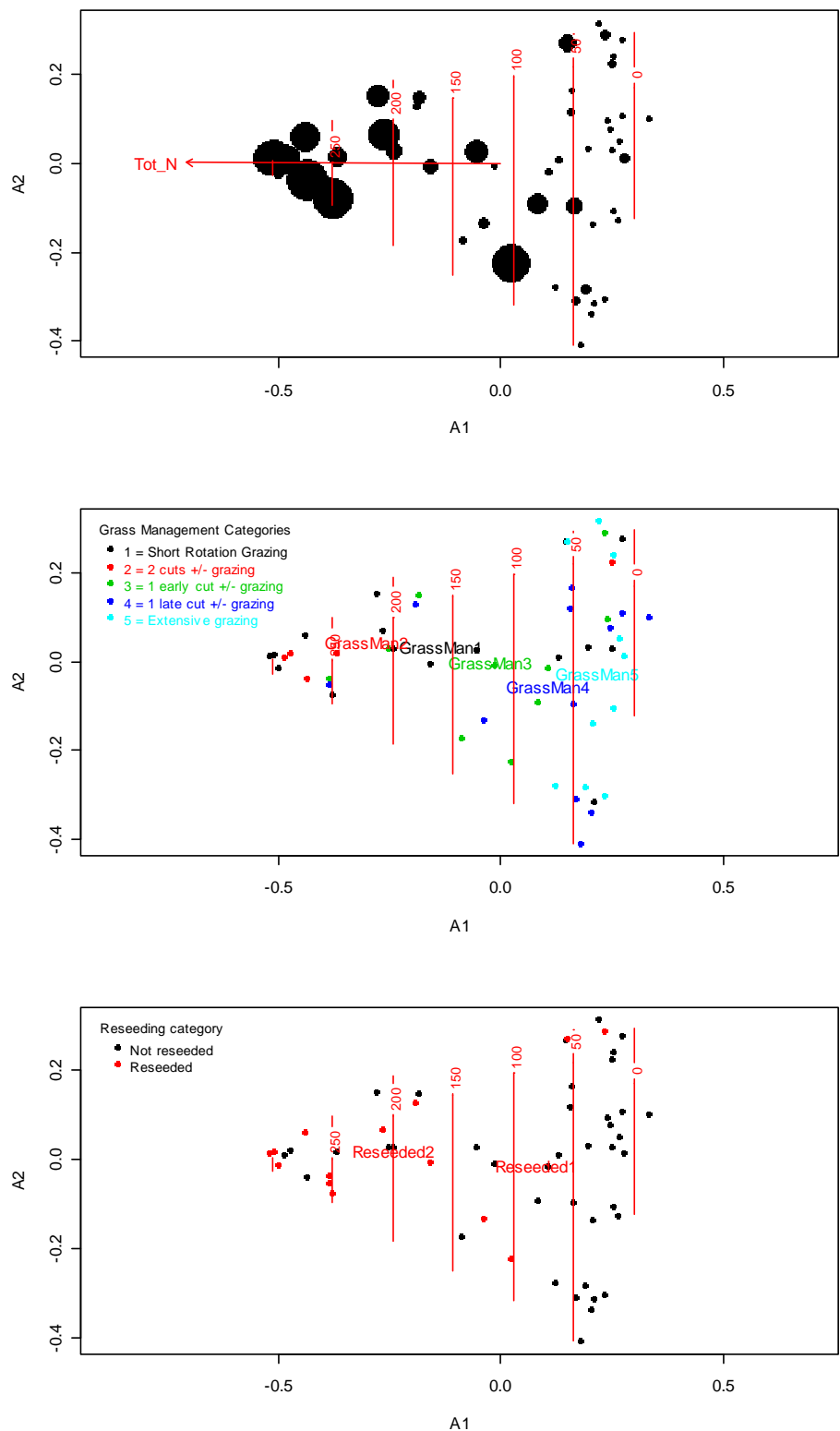
APPENDIX 8. Shepard plot for PCO of grassland vegetation



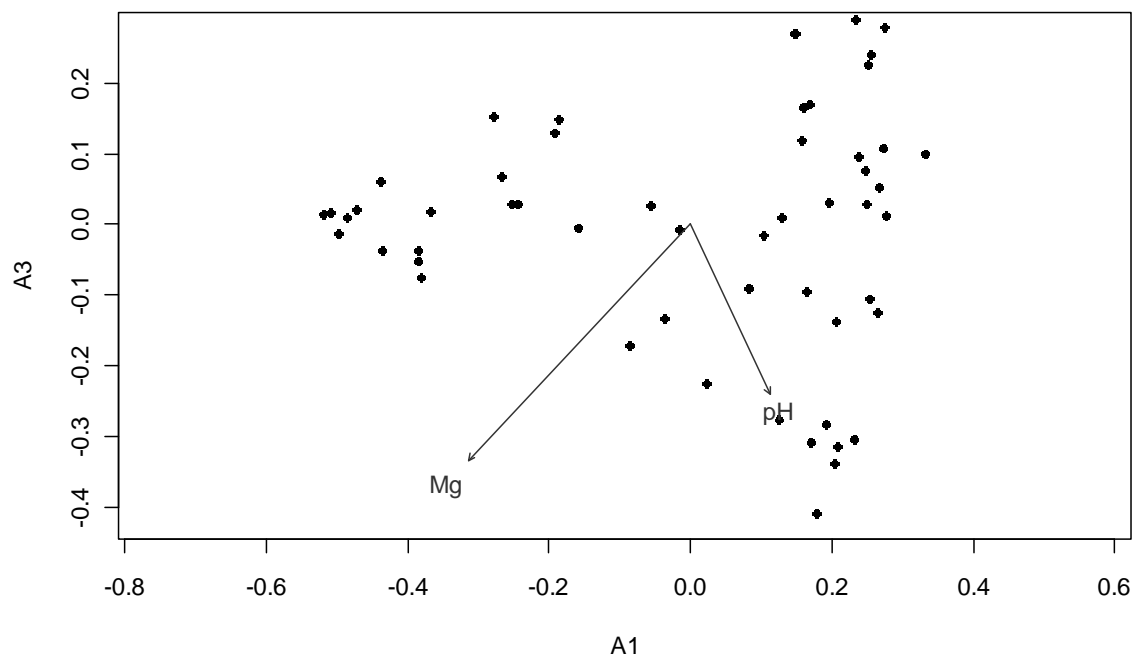
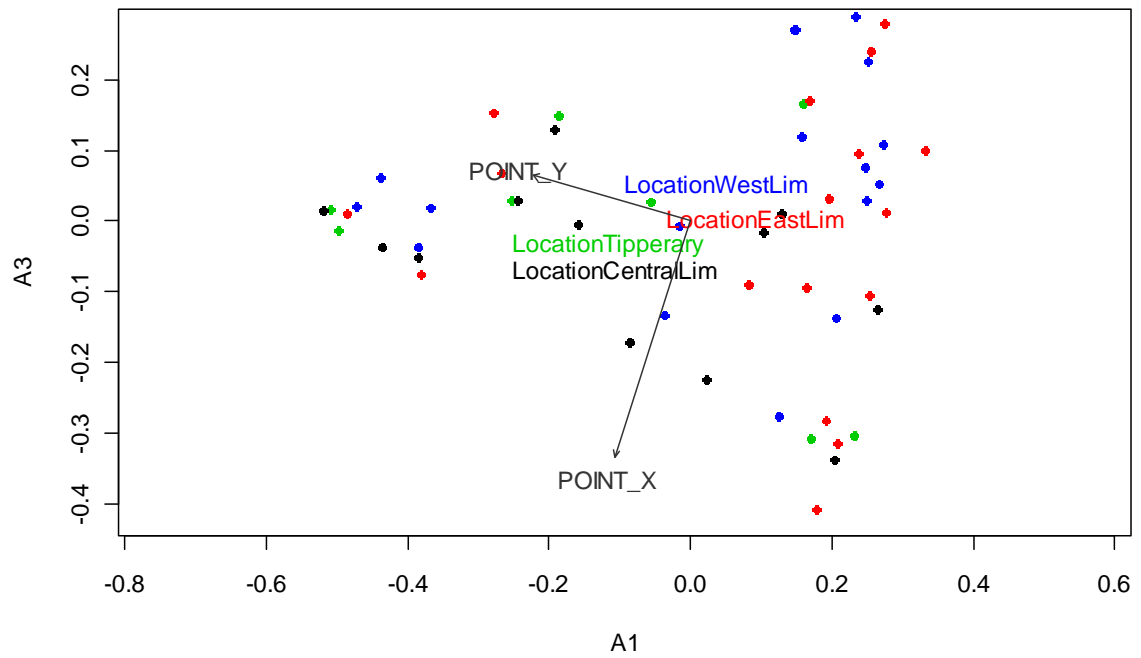
APPENDIX 9. Grassland vegetation PCO showing the position of species projected into the ordination



APPENDIX 10. Grassland vegetation PCO showing correlations with management

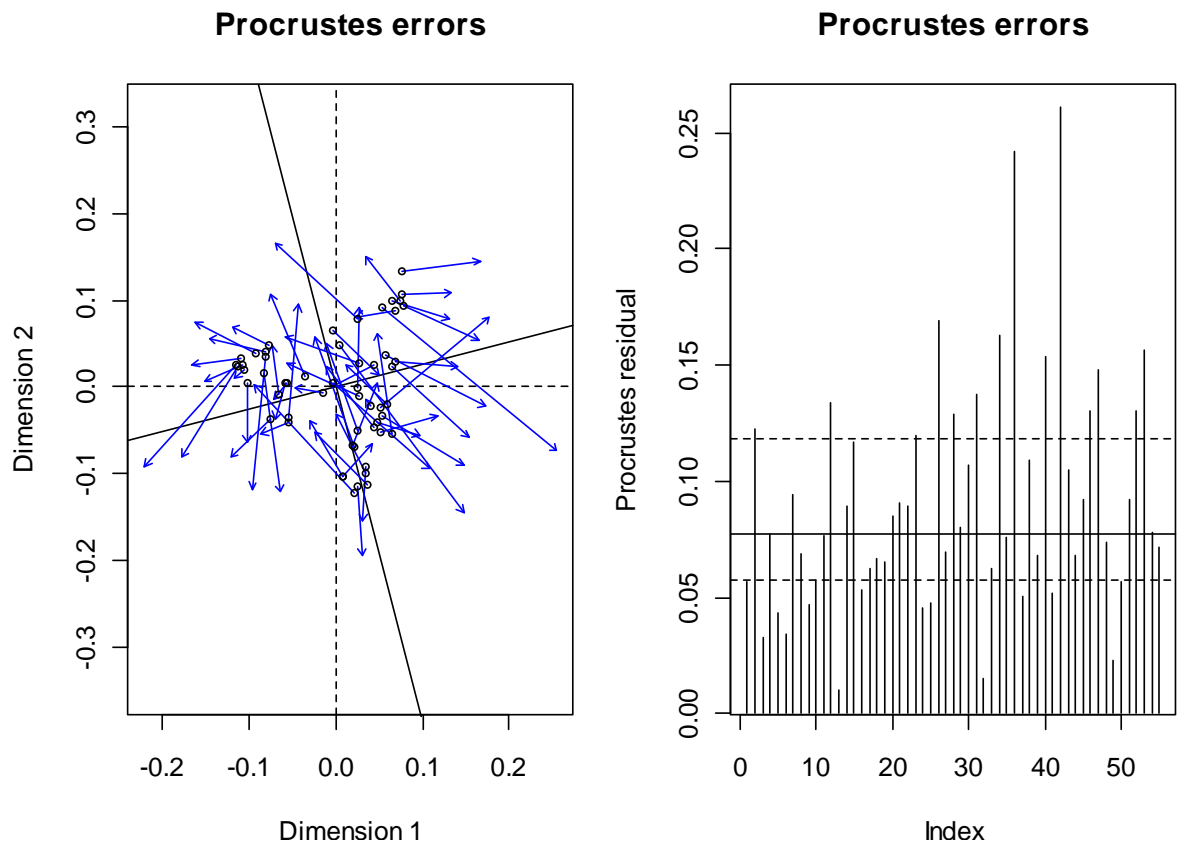


APPENDIX 11. Grassland vegetation PCO showing correlations with sampling location and soil factors



APPENDIX 12. Results of Procrustes analysis comparing NMDS and PCO of sward vegetation

Procrustes sum of squares = 0.58, Procrustes root mean squared error = 0.10



APPENDIX 13. Farm management Interview Schedule

FARM – OVERALL

How big is your farm? (ha/acres)

Is the farm in REPS? (Y/N)

3. Is the farm organic? (Y/N)

What type of farm is it? (Tick each category that applies)

Drystock	Dairy	Other cattle – specify	Sheep	Horses	Tillage

How many animals are on the farm? (Give numbers in the different age categories)

Cattle aged 0-2 (0.6LU)	Cattle aged 2+ (1LU)	Sheep (0.15LU)	Horses

FIELD in which trap was placed:

How big is the field? _____

How many times in the year does the field get **slurry or manure**?- -----

SLURRY / MANURE

Application	Time of year	Type of slurry (pig, cattle etc OR manure & type)	Consistency of slurry thick, heavy and black; medium or watery	Gallons per acre

EXAMPLE	March	Cattle slurry	watery	4600
1				
2				
3				
4				

How many times in the year does the field get **chemical fertiliser**? -----

CHEMICAL FERTILISER

Application	Time of year	Type (27 ½ % CAN, urea, compound 18:6:12 etc.)	How many bags per acre?	Note
EXAMPLE	March	18:6:12	3	
1				
2				
3				
4				

CUTTING

How many times in the year was the field cut in 2005? When?

Was it baled on the same day? (Y/N)

GRAZING

When are animals in the field?

Period	Which animals	Number of animals	For how many weeks	Note
	Cattle aged 0-2			
	Cattle aged 2+			
	Sheep			
	Horses			
March-May	EXAMPLE cattle aged 2+	30	3 wks	

RESEEDING

When was the field last reseeded? (tick the time period)

Last 5 y	5-10 y	10-15 y	15-20 y	20-30y	30y+

CHEMICALS

Has herbicide or pesticide been applied to the field? What /when?

Has there been any spot spraying of weeds? (details)

Have the ditches been sprayed? (details)

HEDGEROW MANAGEMENT

When were the hedges around the field last cut?

APPENDIX 14. Treatment of interview responses and preparation of data

FARM STOCKING LEVELS

Farm stocking levels were defined in terms of livestock units per hectare, calculated for the whole farm. Livestock units are commonly used in budgeting for feed or estimating excreted nutrients for nutrient management plans. (For example, 1 LSU (livestock unit) is estimated to excrete 85kg of N per year (REPS). There are no universally accepted standard livestock units. The values used in this study were

- Large animals e.g. a horse , a cow or bullock over 2 years of age were classed as one livestock unit.
- Cattle younger than 2 years were considered equivalent to 0.6 livestock units.
- Sheep were counted as 0.15 livestock units.

The figures are simplified from those published by Gillmore (1970) which break categories down further, e.g. cattle <1 year = 0.33 L.U.; cattle 1-2y = 0.67 L.U. and sheep are broken down into 3 categories. However these average figures were considered adequate as animals are aging through the year and their equivalent livestock unit values changing. The use of these broader average values also allowed the interview to be simpler and shorter ensuring a higher response rate.

Since the entire holding was used in the calculation of stocking densities, discrepancies may arise between a farm's overall stocking density and the stocking density in fields when the farm is composed of land varying in agricultural quality. For example, a farm with large areas of ground that cannot be heavily grazed, e.g. steep slopes or wet land, will have a reduced estimated stocking density compared to the real stocking level in fields on the farm.

CALCULATION OF NUTRIENT INPUTS

Fertiliser inputs were considered for the study field. They were therefore not necessarily representative of field management across the entire farm. The inputs of phosphates and nitrates from chemical and organic fertilisers were quantified from information regarding the types of fertiliser, frequency of applications and application rates used by each farmer.

CALCULATION OF NUTRIENT INPUTS FROM CHEMICAL FERTILISERS

The chemical nitrogen and phosphorus applied in each month was calculated from farmers' responses to question 7. Farmers used a number of ways to report fertiliser applications including units of N/acre; bags per acre; kg per acre. These values were converted to kg/ha for comparison. A variety of chemical fertilisers were used and their respective Nitrogen, Phosphorus and Potassium contents are shown below.

Fertiliser	%N	%P	%K
CAN	27.5	0	0
Fertiliser 4:8:16	4	8	16
urea 46%	46	0	0
pasture sward 27:2.5:5	27	2.5	5
Fertiliser 27%N and 6 sulphur	27	0	0
Fertiliser 24:2.5:10	24	2.5	10

Worked example

If a farmer applies 2 bags of CAN fertiliser per acre, the amount of nitrogen supplied was calculated as follows.

$$2 \text{ bags} = 2 \times 50\text{kg} = 100\text{kg fertiliser}$$

$$\text{Fertiliser CAN} = 27.5\% \text{ nitrogen}$$

$$100\text{kg of this fertiliser therefore contains } 27.5\text{kg of nitrogen.}$$

$$\text{The application rate is } 27.5\text{kg of nitrogen per acre.}$$

$$\begin{aligned} \text{There are } 2.471 \text{ acres in } 1 \text{ hectare. Therefore the application rate per hectare} \\ = 2.471 \times 27.5\text{kg} \end{aligned}$$

$$= 67.9\text{kg/ha}$$

CALCULATION OF NUTRIENT INPUTS FROM ORGANIC FERTILISERS

Applications of manure, slurry and dairy washings were considered in the calculation of organic fertiliser inputs. The contributions of grazing animals were not included.

The following were noted: animal source of the manure; if slurry its consistency was categorised as watery, medium or thick, heavy and black; the application rate, usually reported as gallons per acre or tonnes per acre and timing and number of applications.

Variations in the nutrient levels of organic manures may arise due to storage; the animals' diet, for example animals fed on concentrate will produce slurry richer in phosphorus; the time of year, warm weather enhances the volatilisation of nitrogen from slurry and the method of application: injection of slurry will reduce the volatilisation of nitrogen compared to spreading. Such variation was ignored and average values for NPK were used in calculations. Further error may have arisen due to the subjective evaluation of thickness of slurry.

Organic fertiliser	N (kg/1000L or 1m³)	P (kg/1000L or 1m³)	K (kg/1000L or 1m³)
Cattle slurry - watery (~2.5% dry matter)	0.975	0.15	1
Cattle slurry - medium (10% dry matter)	3.9	0.6	4
Cattle slurry - heavy	4.6	0.72	4.5
Pig slurry - watery	3	1	1.9
Dungstead manure (from bedding)	3.5	0.9
Farmyard manure (dried slurry)	4.5	1.2

Source: Specification for REPS Planners in the Preparation of REPS 4 Plans, Department of Agriculture and Food (2008) and pers. comm. with Solohead research farm regarding dry matter % value in watery slurry leading to NPK values of ¼ of medium slurry.

Application rates were converted to cubic metres per hectare and then average values for the Nitrogen and Phosphorus levels in different types of slurries and manure were used to calculate the nutrients provided from these sources.

Worked example

A farmer applies 1000 gallons of medium thickness cattle slurry per acre,

Converting to litres per acre, $1000/0.22 = 4545.46$ litres/acre

Converting to litres per hectare, $4545.46 \times 2.471 = 11231.82$ litres/hectare

Converting to cubic metres per hectare, $11231.82/1000$ cubic metres/hectare

1000 gallons/acre = 11.2 m³/ha

The nitrogen application = 3.9×11.2 Kg /Ha = 43.68 Kg /Ha

GRASSLAND MANAGEMENT – CUTTING AND GRAZING CATEGORIES

Landowners were asked the timing and duration of grazing periods and when the field was cut, resulting in a grazing category and a cutting category, outlined below. Following preliminary explorations of the data, these two categories were collapsed together and reduced from 16 possible combinations to five new ‘cutting and grazing’ categories.

Cutting category

- | | |
|---|--------------------------|
| 1 | cut once early=cut1 or 2 |
| 2 | cut once mid-late |
| 3 | cut twice |
| 4 | not cut at all |

Grazing category

- | | |
|---|--|
| 1 | rotational grazing, for periods of ½ to 7 days. |
| 2 | continuous grazing for period >4months. |
| 3 | 1 or 2 periods of continuous grazing for short periods, typically 3-7 weeks. |
| 4 | no grazing |

Cutting and Grazing category

- | | |
|---|---|
| 1 | Short rotation grazing (Graze =1), with or without cutting. |
| 2 | 2 harvests of grass, (Cut =3), with or without grazing. |
| 3 | One cut early in summer, (Cut =1), +- grazing |
| 4 | One cut late in summer (Cut =2) +- grazing |
| 5 | Grazed continuously with no cutting (Cut =4, Graze =2) |

Note: One field did not fit into any cutting and grazing category as it was cut for silage twice and rotationally grazed. This field was classified as ‘cutting and grazing’ category 2.

APPENDIX 15. Bee species and abbreviations

Solitary bees	Abbreviation
<i>Andrena angustior</i> (Kirby, 1802)	Aangust
<i>Andrena barbilabris</i> (Kirby, 1802)	Abarbil
<i>Andrena bicolor</i> (Fabricius, 1775)	Abicolo
<i>Andrena cineraria</i> (Linnaeus, 1758)	Acinera
<i>Andrena clarkella</i> (Kirby, 1802)	Aclarke
<i>Andrena coitana</i> (Kirby, 1802)	Acoitan
<i>Andrena denticulata</i> (Kirby, 1802)	Adentic
<i>Andrena fucata</i> (Smith, 1847)	Afucata
<i>Andrena haemorrhoa</i> (Fabricius, 1781)	Ahaemor
<i>Andrena nigroaenea</i> (Kirby, 1802)	Anigroa
<i>Andrena scotica</i> Perkins, R.C.L., 1916	Ascotic
<i>Andrena subopaca</i> Nylander, 1848	Asubopa
<i>Coelioxys</i> spp Latreille, 1809	Coeliox
<i>Halictus rubicundus</i> (Christ, 1791)	Hrubicu
<i>Halictus tumulorum</i> (Linnaeus, 1758)	Htumulo
<i>Hylaeus brevicornis</i> Nylander, 1852	Hbrevic
<i>Hylaeus confusus</i> Nylander, 1852	Hconfus
<i>Lasioglossum albipes</i> (Fabricius, 1781)	Lalbcal
<i>Lasioglossum calceatum</i> (Scopoli, 1763)	Lalbcal
<i>Lasioglossum cupromicans</i> (Perez, 1903)	Lcuprom
<i>Lasioglossum fratellum</i> (Perez, 1903)	Lfratel
<i>Lasioglossum leucopus</i> (Kirby, 1802)	Lleucop
<i>Lasioglossum nitidiusculum</i> (Kirby, 1802)	Lnitidi
<i>Lasioglossum punctatissimum</i> (Schenck, 1853)	Lpuncta
<i>Lasioglossum villosulum</i> (Kirby, 1802)	Lvillos
<i>Megachile versicolor</i> Smith, F., 1844	Mversic
<i>Nomada fabriciana</i> (Linnaeus, 1767)	Nfabric
<i>Nomada flavoguttata</i> (Kirby, 1802)	Nflavog
<i>Nomada leucophthalma</i> (Kirby, 1802)	Nleucop
<i>Nomada marshamella</i> (Kirby, 1802)	Nmarsha
<i>Nomada panzeri</i> Lepeletier, 1841	Npanzer
<i>Nomada ruficornis</i> (Linnaeus, 1758)	Nrufico
<i>Nomada rufipes</i> Fabricius, 1793	Nrufipe
<i>Nomada striata</i> Fabricius, 1793	Nstriata
<i>Sphecodes ephippius</i> (Linnaeus, 1767)	Sephipp
<i>Sphecodes ferruginatus</i> von Hagens, 1882	Sferrug
<i>Sphecodes geoffrellus</i> (Kirby, 1802)	Sgeoffr
<i>Sphecodes hyalinatus</i> von Hagens, 1882	Shyalin

Bumblebees	Abbreviation
'Free-living' bumblebees	
<i>B. cryptarum</i> (Fabricius)	BterGp
<i>B. hortorum</i> (L.)	Bhortor
<i>B. jonellus</i> (Kirby)	Bjonell
<i>B. lapidarius</i> (L.)	Blapida
<i>B. lucorum</i> (L.)	BterGp
<i>B. magnus</i> Vogt	BterGp
<i>B. muscorum</i> (L.)	Bmuscor
<i>B. pascuorum</i> (Scopoli)	Bpascuo
<i>B. pratorum</i> (L.)	Bprator
<i>B. ruderarius</i> (Müller)	Brudera
<i>B. sylvarum</i> (L.)	Bsylvar
<i>B. terrestris</i> (L.)	BterGp
Parasitic 'cuckoo' bumblebees	
<i>B. (P.) bohemicus</i> Seidl	Bbohemi
<i>B. (P.) campestris</i> (Panzer)	Bcampes
<i>B. (P.) rupestris</i> (Fabricius)	Brupest
<i>B. (P.) sylvestris</i> (Lepeletier)	Bsylves

APPENDIX 16. Grassland plant species and abbreviations

NAME	Abbreviation		
		<i>Dactylorhiza species</i>	Dactylo_spp
<i>Achillea millefolium</i>	Ach_mil	<i>Daucus carota</i>	Dau_car
<i>Agrostis canina</i>	Agr_can	<i>Deschampsia cespitosa</i>	Des_ces
<i>Agrostis capillaris</i>	Agr_cap	<i>Elytrigia repens</i>	Ely_rep
<i>Agrostis gigantea</i>	Agr_gig	<i>Epilobium parviflorum</i>	Epi_par
<i>Agrostis species</i>	Agr_sto	<i>Equisetum fluviatile</i>	Equ_flu
<i>Agrostis stolonifera</i>	Agrosti_spp	<i>Equisetum palustre</i>	Equ_pal
<i>Alopecurus pratensis</i>	Alo_pra	<i>Equisetum species</i>	Equiset_spp
<i>Anagallis tenella</i>	Ana_ten	<i>Euphrasia officinalis ag.</i>	Eup_off
<i>Angelica sylvestris</i>	Ang_syl	<i>Festuca arundinacea</i>	Fes_aru
<i>Anthoxanthum odoratum</i>	Ant_odo	<i>Festuca ovina</i>	Fes_ovi
<i>Anthriscus vulgaris</i>	Ant_vul	<i>Festuca pratensis</i>	Fes_pra
<i>Arrhenatherum elatius</i>	Arr_ela	<i>Festuca rubra</i>	Fes_rub
<i>Bellis perennis</i>	Bel_per	<i>Filipendula ulmaria</i>	Fil_ulm
<i>Blackstonia perfoliata</i>	Bla_per	<i>Galeopsis tetrahit</i>	Gal_pal
<i>Briza media</i>	Bri_med	<i>Galium palustre</i>	Gal_tet
<i>Bromus species</i>	Bromus_spp	<i>Galium verum</i>	Gal_ver
<i>Cardamine pratensis</i>	Car_pra	<i>Gentianella amarella</i>	Gen_ama
<i>Carex binervis</i>	Car_bin	<i>Glyceria declinata</i>	Gly_dec
<i>Carex disticha</i>	Car_dis	<i>Glyceria fluitans</i>	Gly_flu
<i>Carex hirta</i>	Car_hir	<i>Heracleum sphondylium</i>	Her_sph
<i>Carex nigra</i>	Car_nig	<i>Holcus lanatus</i>	Hol_lan
<i>Carex panicea</i>	Car_pan	<i>Hydrocotyle vulgaris</i>	Hyd_vul
<i>Carex species</i>	Carex_spp	<i>Hypericum perforatum</i>	Hyp_per
<i>Carex viridula</i>	Car_vir	<i>Hypochaeris radicata</i>	Hyp_rad
<i>Catapodium rigidum</i>	Cat_rig	<i>Iris pseudacorus</i>	Iri_pse
<i>Centaurea nigra</i>	Cen_nig	<i>Juncus acutiflorus</i>	Jun_acu
<i>Cerastium fontanum</i>	Cer_fon	<i>Juncus articulatus</i>	Jun_art
<i>Cerastium holosteoides</i>	Cer_hol	<i>Juncus bufonius</i>	Jun_buf
<i>Cirsium arvense</i>	Cir_arv	<i>Juncus effusus</i>	Jun_eff
<i>Cirsium palustre</i>	Cir_pal	<i>Juncus inflexus</i>	Jun_inf
<i>Cirsium vulgare</i>	Cir_vul	<i>Lathyrus pratensis</i>	Lat_pra
<i>Convolvulus arvensis</i>	Con_arv	<i>Leontodon autumnalis</i>	Leo_aut
<i>Crepis capillaris</i>	Cre_cap	<i>Leontodon hispidus</i>	Leo_his
<i>Crepis paludosa</i>	Cre_pal	<i>Leucanthemum vulgare</i>	Leu_vul
<i>Cuscuta epithymum</i>	Cus_epi	<i>Lolium multiflorum</i>	Lol_mul
<i>Cynosurus cristatus</i>	Cyn_cri	<i>Lolium perenne</i>	Lol_per
<i>Dactylis glomerata</i>	Dac_glo	<i>Lotus corniculatus</i>	Lot_cor
		<i>Lotus pedunculatus</i>	Lot_ped
		<i>Lychnis flos-cuculi</i>	Lyc_flo
		<i>Matricaria discoidea</i>	Mat_dis
		<i>Medicago lupulina</i>	Med_lup

<i>Medicago sativa</i>	Med_sat	<i>Trifolium pratense</i>	Tri_pra
<i>Mentha aquatica</i>	Men_aqu	<i>Trifolium repens</i>	Tri_rep
<i>Myosotis laxa</i>	Myo_lax	<i>Urtica dioica</i>	Urt_dio
<i>Odontites vernus</i>	Odo_ver	<i>Veronica chamaedrys</i>	Ver_cha
<i>Phleum bertolonii</i>	Phl_ber	<i>Veronica hederifolia</i>	Ver_hed
<i>Phleum pratense</i>	Phl_pra	<i>Veronica polita</i>	Ver_pol
<i>Plantago lanceolata</i>	Pla_lan	<i>Vicia cracca</i>	Vic_cra
<i>Plantago major</i>	Pla_maj	<i>Vicia sepium</i>	Vic_sep
<i>Plantago species</i>	Plantag_spp		
<i>Poa annua</i>	Poa_ann		
<i>Poa pratensis</i>	Poa_pra		
<i>Poa species</i>	Poa_tri		
<i>Poa trivialis</i>	Poaceae_spp		
<i>Potentilla anserina</i>	Pot_ans		
<i>Potentilla erecta</i>	Pot_ere		
<i>Potentilla reptans</i>	Pot_rep		
<i>Prunella vulgaris</i>	Pru_spi		
<i>Prunus spinosa</i>	Pru_vul		
<i>Pteridium aquilinum</i>	Pte_aqu		
<i>Pulicaria dysenterica</i>	Pul_dys		
<i>Ranunculus acris</i>	Ran_acr		
<i>Ranunculus bulbosus</i>	Ran_bul		
<i>Ranunculus lingua</i>	Ran_lin		
<i>Ranunculus repens</i>	Ran_rep		
<i>Rhinanthus minor</i>	Rhi_min		
<i>Rosa pimpinellifolia</i>	Ros_pim		
<i>Rubus fruticosus ag.</i>	Rub_fru		
<i>Rumex acetosa</i>	Rum_ace		
<i>Rumex acetosella</i>	Rum_aSel		
<i>Rumex conglomeratus</i>	Rum_con		
<i>Rumex crispus</i>	Rum_cri		
<i>Rumex obtusifolius</i>	Rum_obt		
<i>Rumex sanguineus</i>	Rum_san		
<i>Rumex species</i>	Rumex_spp		
<i>Sagina nodosa</i>	Sag_nod		
<i>Senecio aquaticus</i>	Sen_aqu		
<i>Senecio jacobaea</i>	Sen_jac		
<i>Solidago virgaurea</i>	Sol_vir		
<i>Stellaria graminea</i>	Ste_gra		
<i>Stellaria holostea</i>	Ste_hol		
<i>Stellaria media</i>	Ste_med		
<i>Succisa pratensis</i>	Suc_pra		
<i>Taraxacum species</i>	Taraxac_spp		
<i>Teucrium scorodonia</i>	Teu_sco		
<i>Thymus polytrichus</i>	Thy_pol		
<i>Trifolium dubium</i>	Tri_dub		

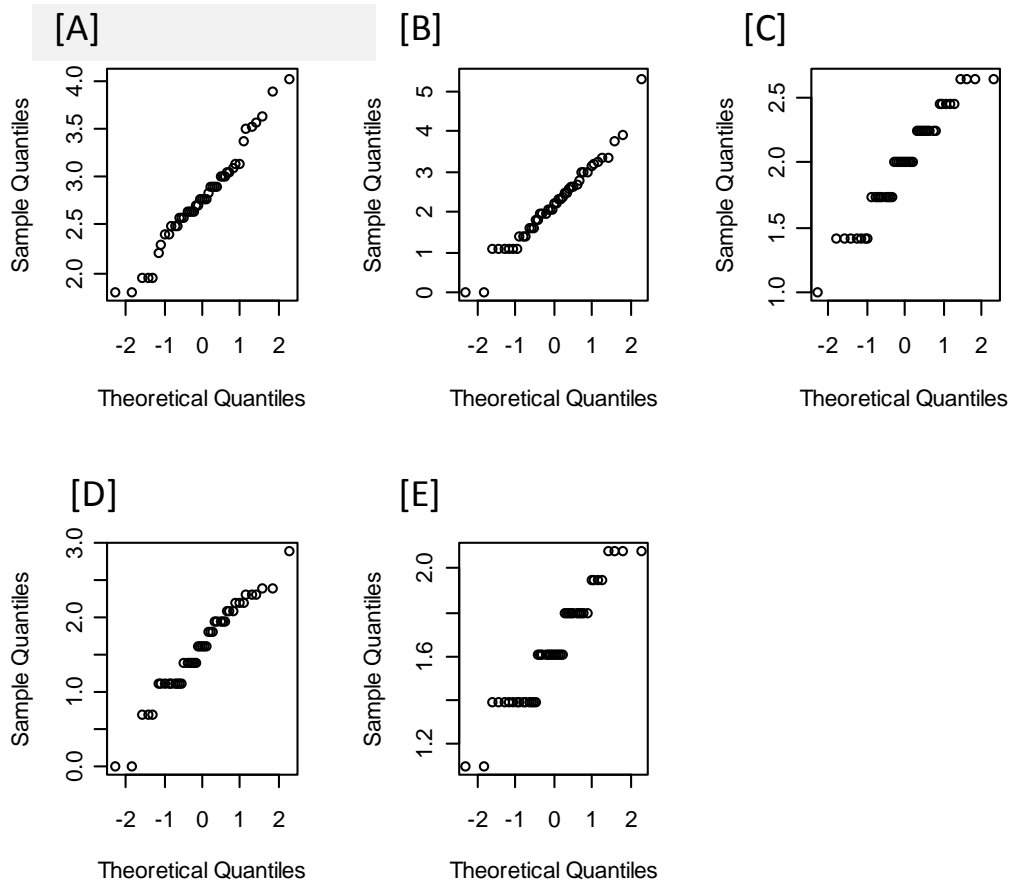
APPENDIX 17. Variance explained and significance on permutation testing of models used in the decomposition of variance of assemblages of all wild bees.

Model Number	Explanatory variables	Conditional variables	Sum of canonical eigenvalues	% of all variance in dataset	p-value
M1	All environmental sets	None	0.072	15.6	0.02
M2	All environmental sets	Spatial set	0.057	12.4	0.18
M3	Spatial set	All environmental sets	0.042	9.0	0.005

Solitary bees					
Model Number	Explanatory variables	Conditional variables	Sum of canonical eigenvalues	% of all variance in dataset	p-value
M1	All environmental sets	None	0.119	19.4	0.02
M2	All environmental sets	Spatial set	0.072	11.8	0.53
M3	Spatial set	All environmental sets	0.05	8.2	0.02

Bumblebees					
Model Number	Explanatory variables	Conditional variables	Sum of canonical eigenvalues	% of all variance in dataset	p-value
M1	All environmental sets	None	//	//	//
M2	All environmental sets	Spatial set	//	//	//
M3	Spatial set	All environmental sets	0.03	9.1	0.0

APPENDIX 18. Checking the distribution of response variables using QQ Plots



QQ plots for transformed response variables, to check if sufficiently normal in distribution for use of parametric methods. The response variables and their transformations were [A]= $\text{Ln}(\text{Bumblebee abundance} + 4)$; [B] = $\text{Ln}(\text{Solitary bee abundance} + 1)$; [C] = $\text{Square-root}(\text{Number of bumblebee species})$; [D] = $\text{Ln}(\text{Number of solitary bee species} + 1)$; [E] = $\text{Ln}(\text{Number of genera of wild bees} + 1)$

APPENDIX 19. Preliminary data exploration, checking distributions and correlations of explanatory variables

Distribution of explanatory variables (histograms), plots of explanatory variables against each other and Spearman's correlations between them, after standardisation.



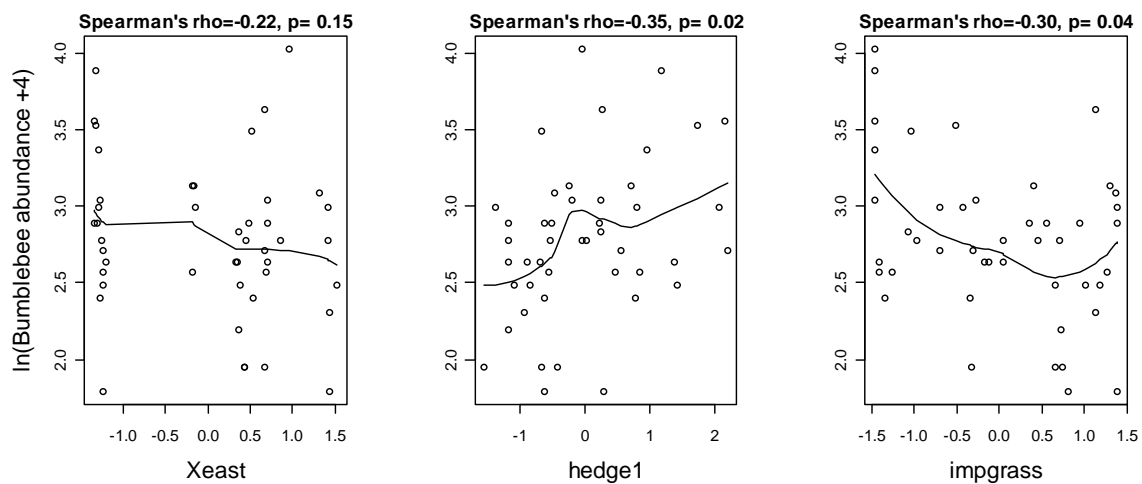
APPENDIX 20. Variance Inflation Factors of explanatory variables

Variance Inflation Factors of variables after standardisation: Xeast =3.05; Ynorth = 2.07; sward1 = 3.55; sward2 = 1.38; hgSimp = 1.67; index = 1.69; hedge1 =2.55; manage = 16.46; dairy =2.56; reseed =11.19; impgrass =1.94; wood =2.06.

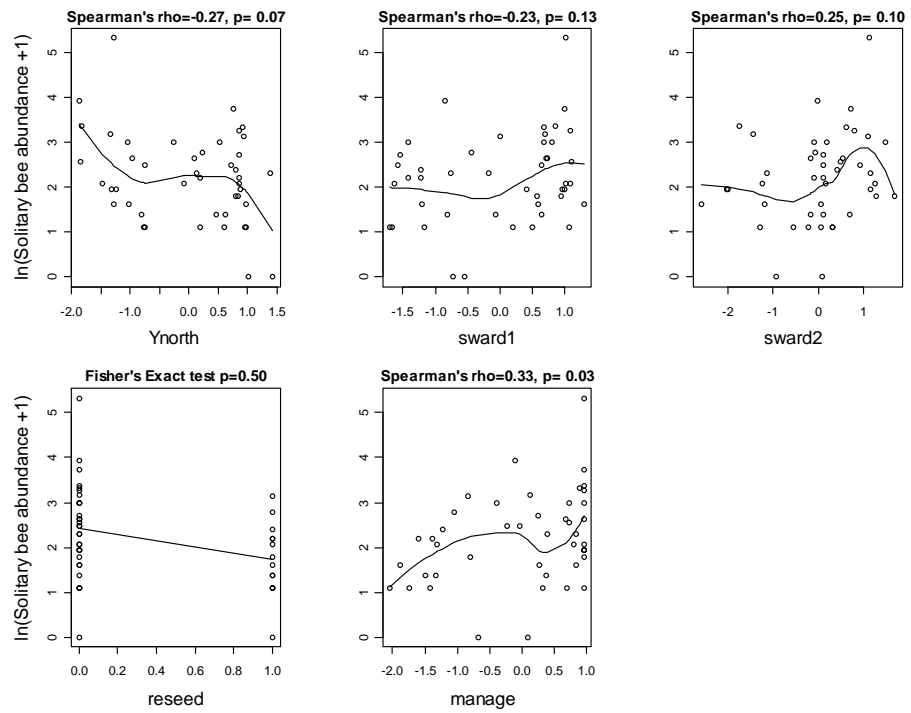
APPENDIX 21. Preliminary data exploration: Associations between bee response variables and environmental variables

Associations between bee abundances and the most strongly correlated environmental variables for which Spearman's $\rho > 0.20$. (NB p-values are approximate due to tied values and are the probability that $\rho \neq 0$).

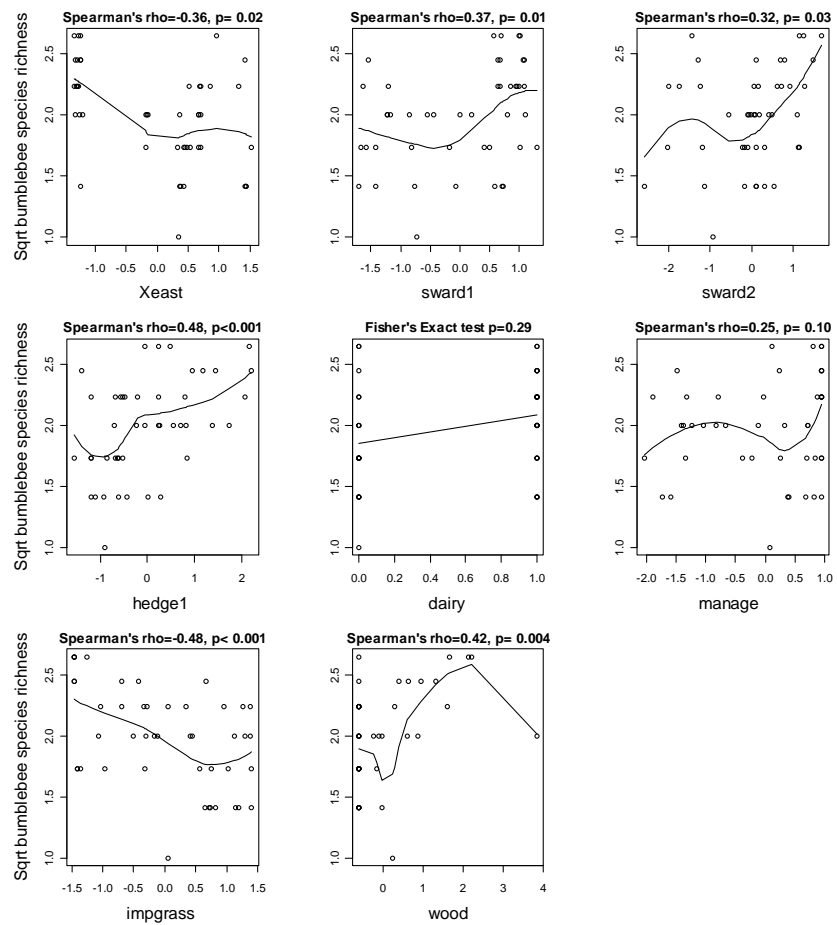
Bumblebee abundance



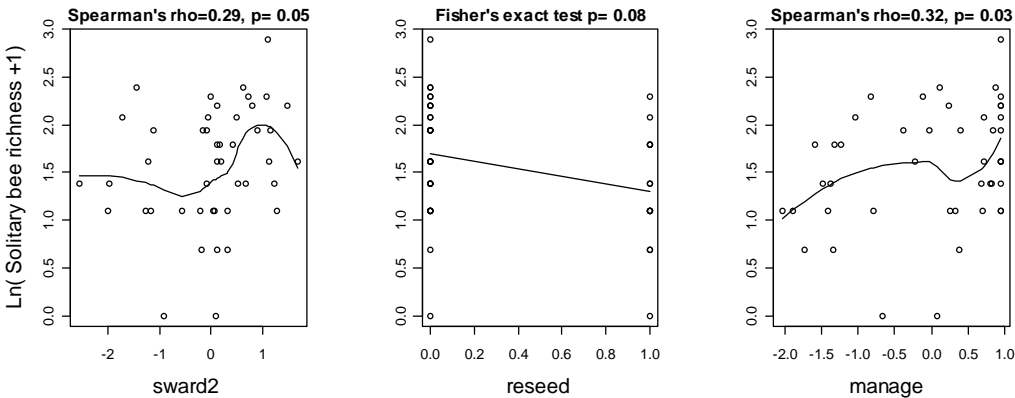
Solitary bee abundance



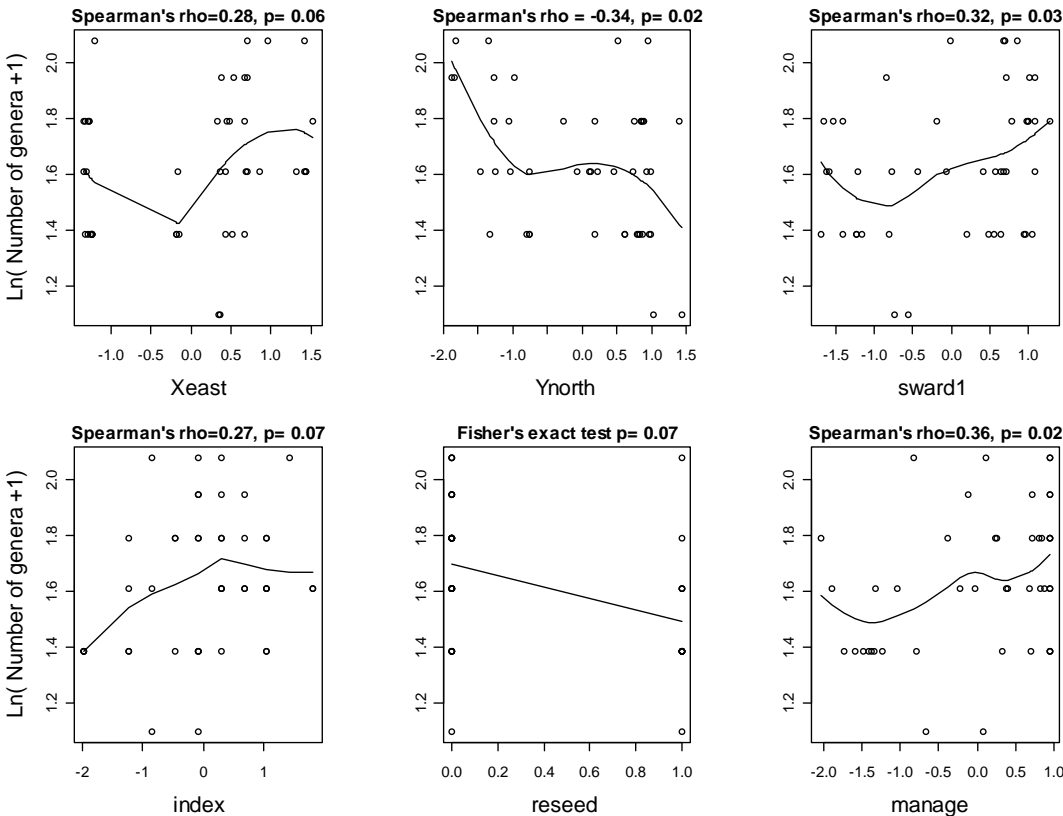
Bumblebee species richness



Number of Solitary bee species

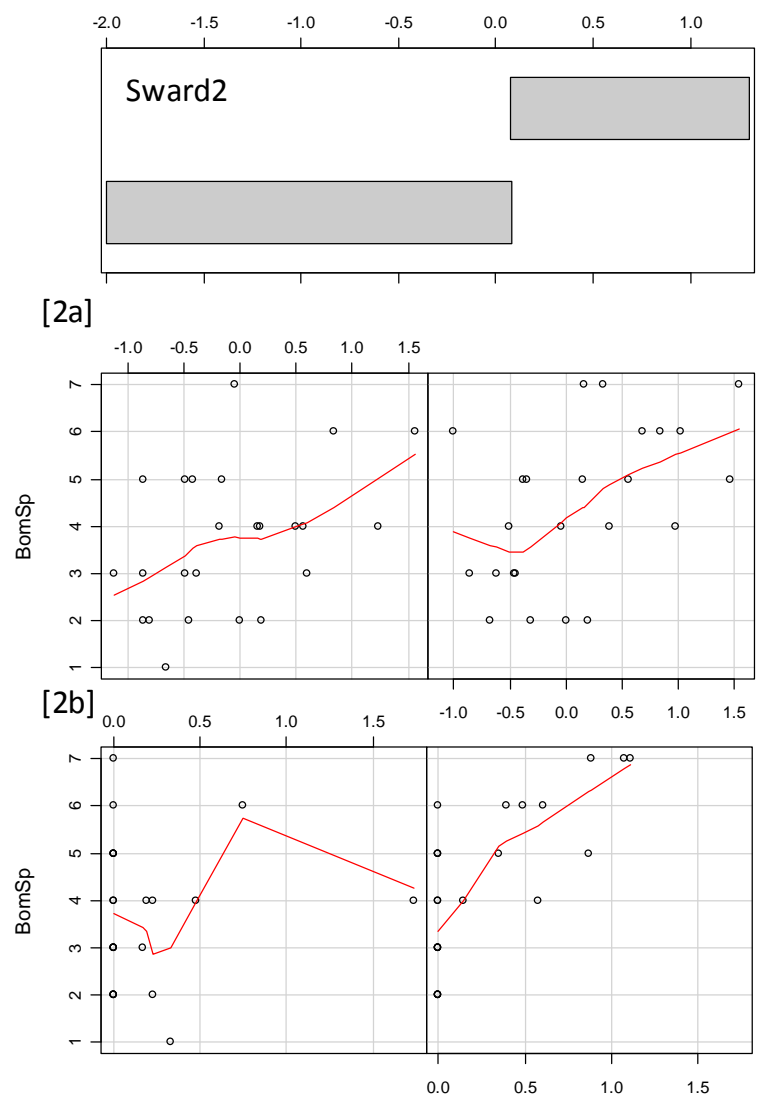


Number of genera



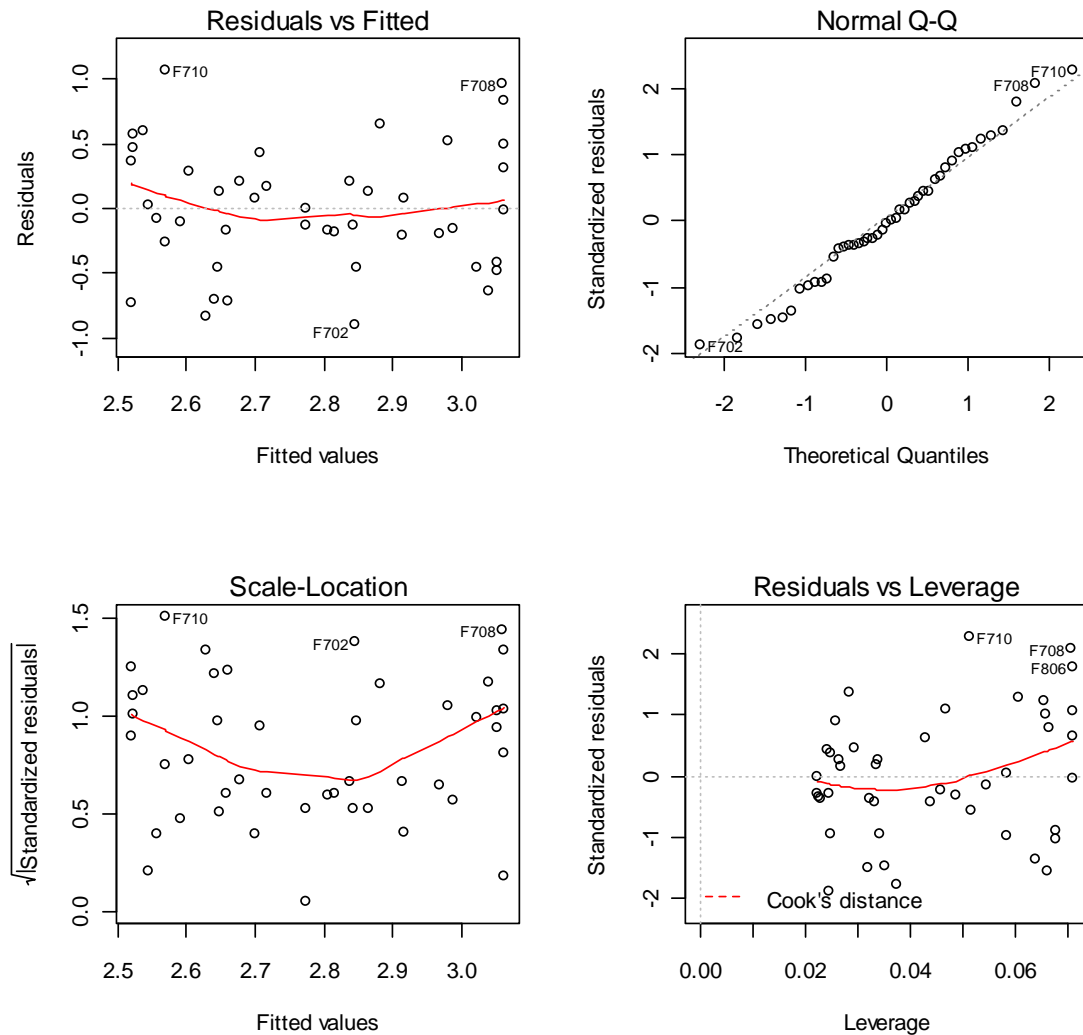
APPENDIX 22. Preliminary data exploration: Conditional plots examining potential interactions

Conditional plots showing potential interaction between grassland composition as it reflects calcareous conditions (sward2>0) to neutral-acidic conditions (sward2<0) and [2a] a gradient in hedgerow vegetation, from dominated by *Crataegus monogyna* (hedge1 <0) to dominated by *Prunus spinosa* (hedge1 >0) and [2b] a gradient in area of woodland/scrub/young forestry in landscape on the numbers of bumblebee species



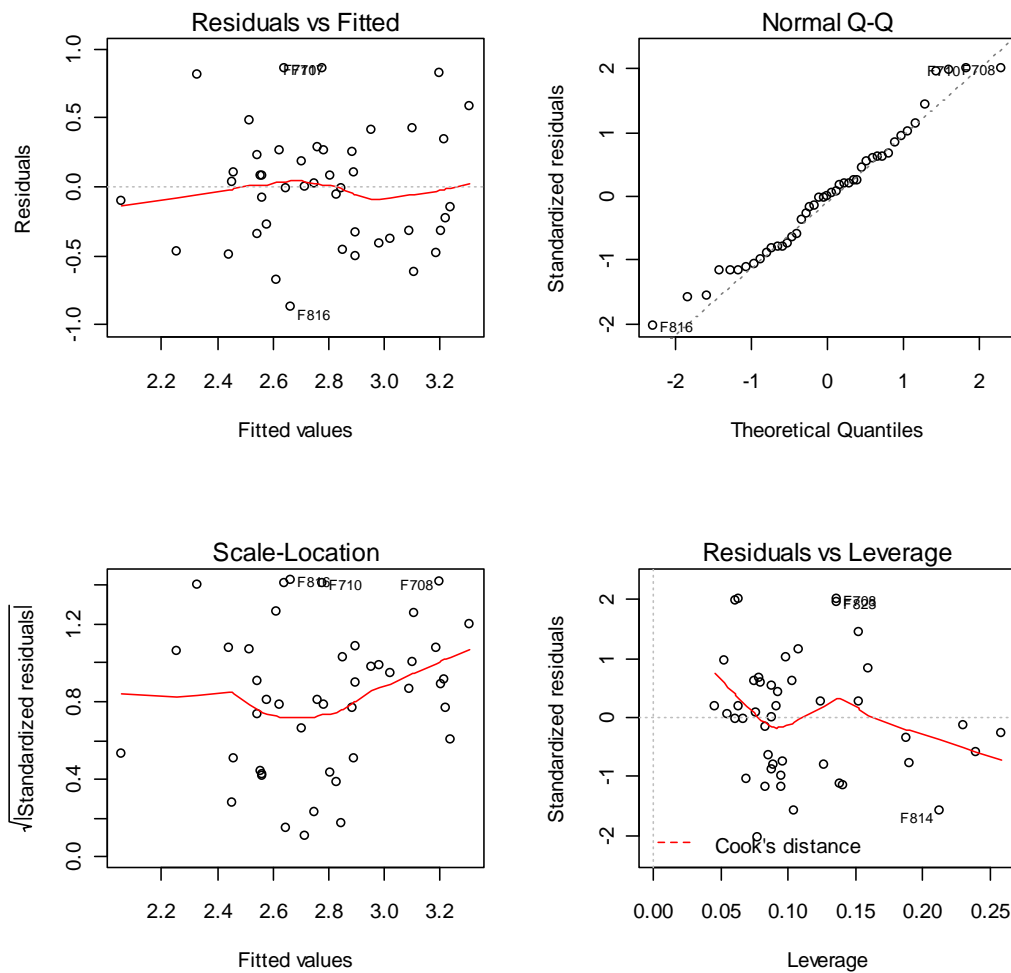
APPENDIX 23. Residuals of stepwise regressions

Abundance of bumblebees (model 1)



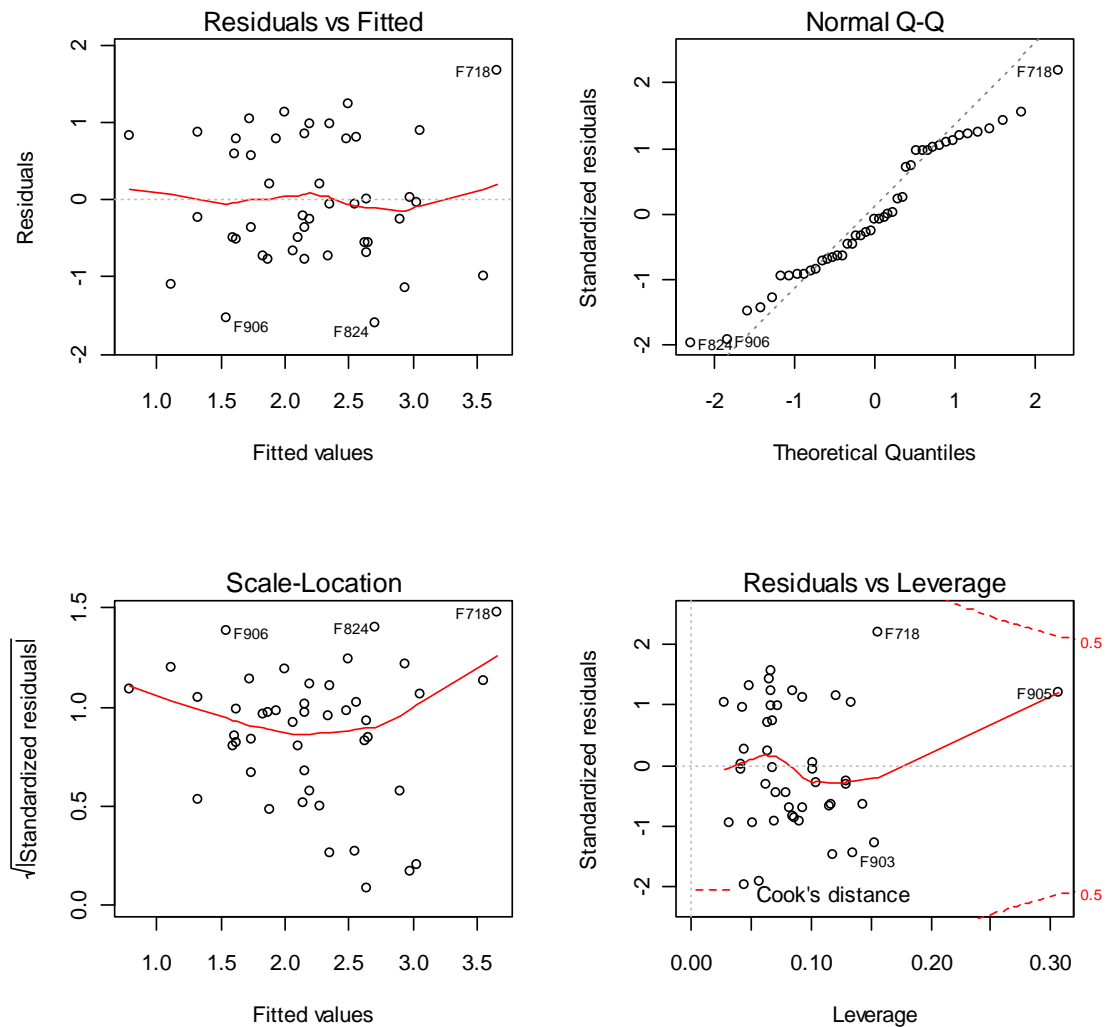
Residuals from the model: $\text{Ln}(\text{bumblebee abundance} + 4) = 2.78 - (0.19 \cdot \text{impgrass}) + \epsilon$

Abundance of bumblebees (model 2)



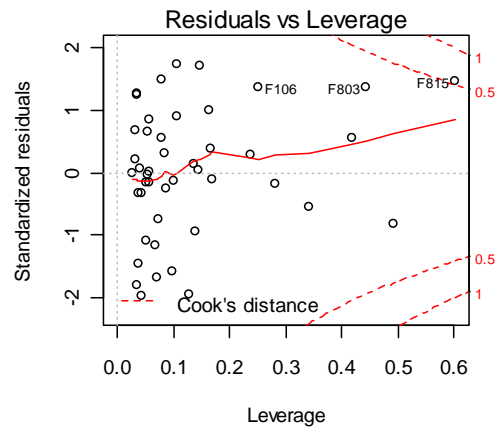
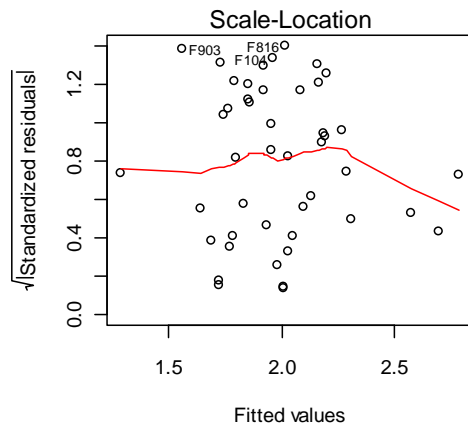
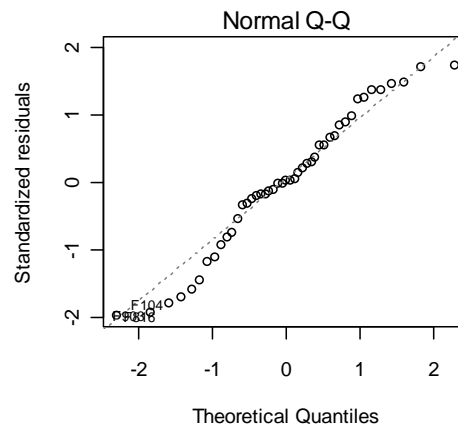
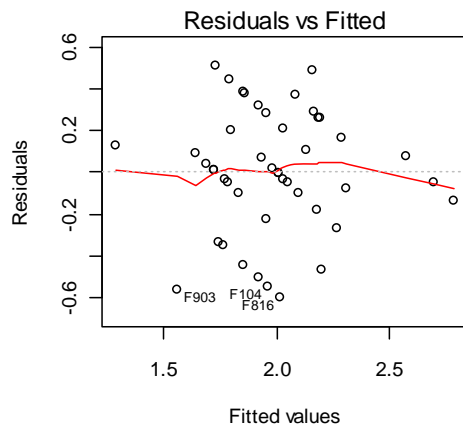
Residuals from the model: $\text{Ln}(\text{bumblebee abundance} + 4) = 2.75 + (0.19 \cdot \text{hedge1}) + (0.32 \cdot \text{index}) + (0.02 \cdot \text{dairy}) + (-0.34 \cdot \text{index} \cdot \text{dairy}) + \epsilon$

Abundance of solitary bees



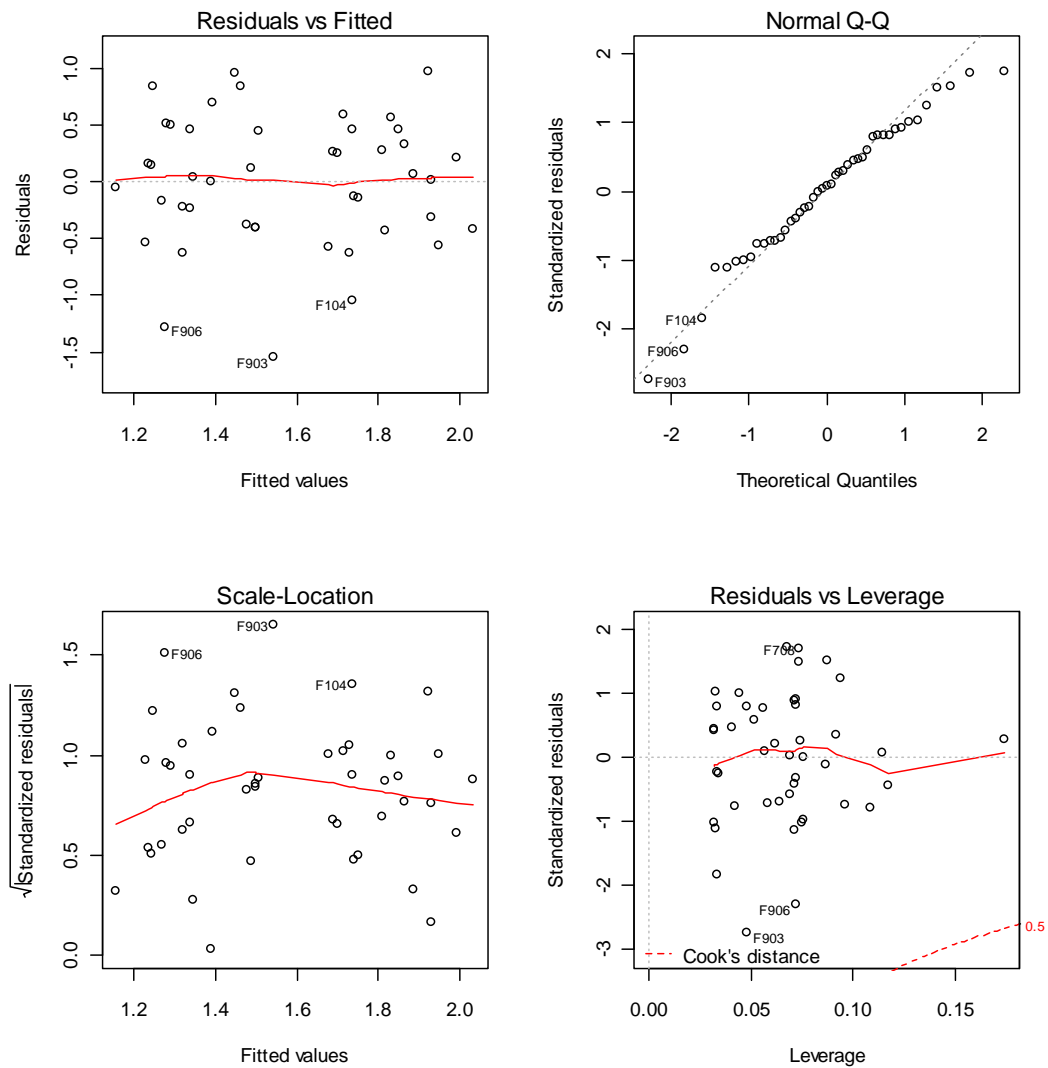
Residuals of $\ln(\text{solitary bee abundance} + 1) = 2.20 + (-0.48 \cdot Y_{\text{north}}) + (0.47 \cdot \text{sward2}) + (0.32 \cdot \text{manage}) + \epsilon$

Number of bumblebee species



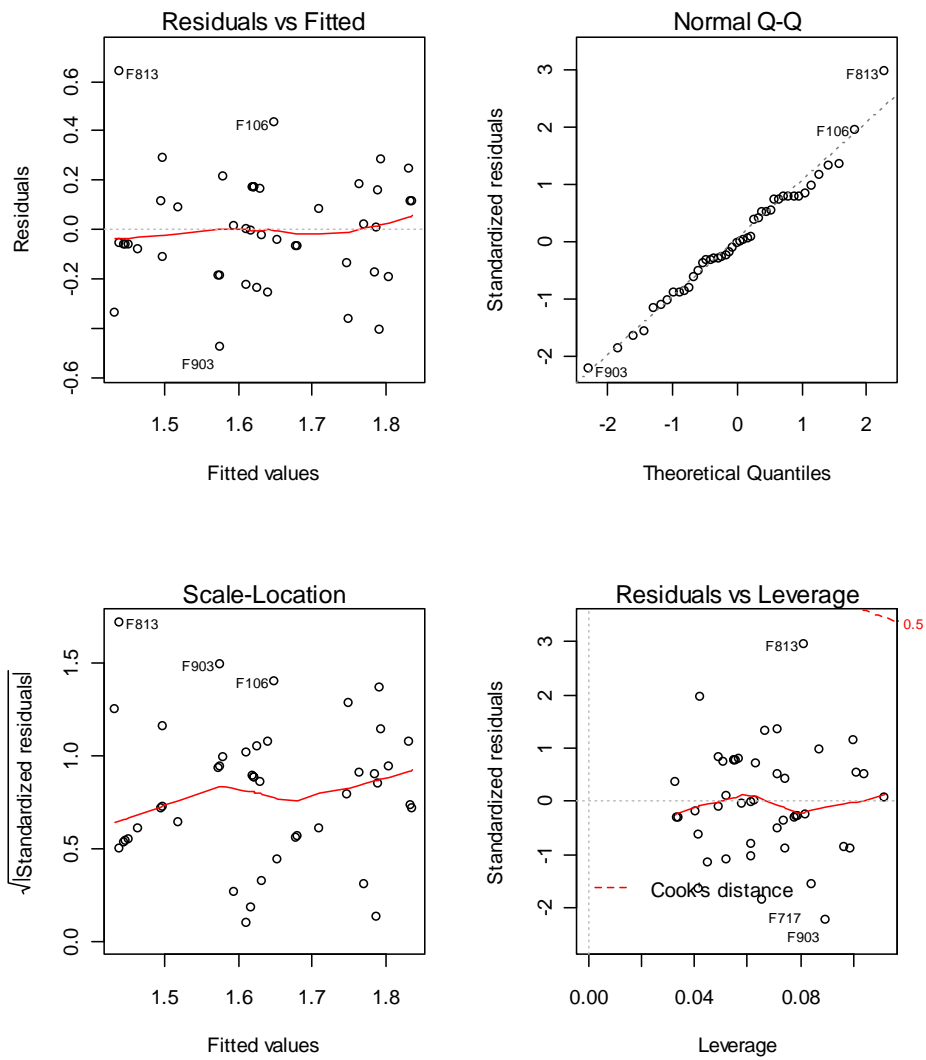
$$\text{Sqrt}(\text{Number of bumblebee species}) = 1.94 + (0.03 * \text{sward2}) + (0.21 * \text{hedge1}) + (-0.05 * \text{wood}) + (0.28 * \text{sward2} * \text{wood}) + (-0.12 * \text{sward2} * \text{hedge1}) + \epsilon$$

Number of solitary bee species



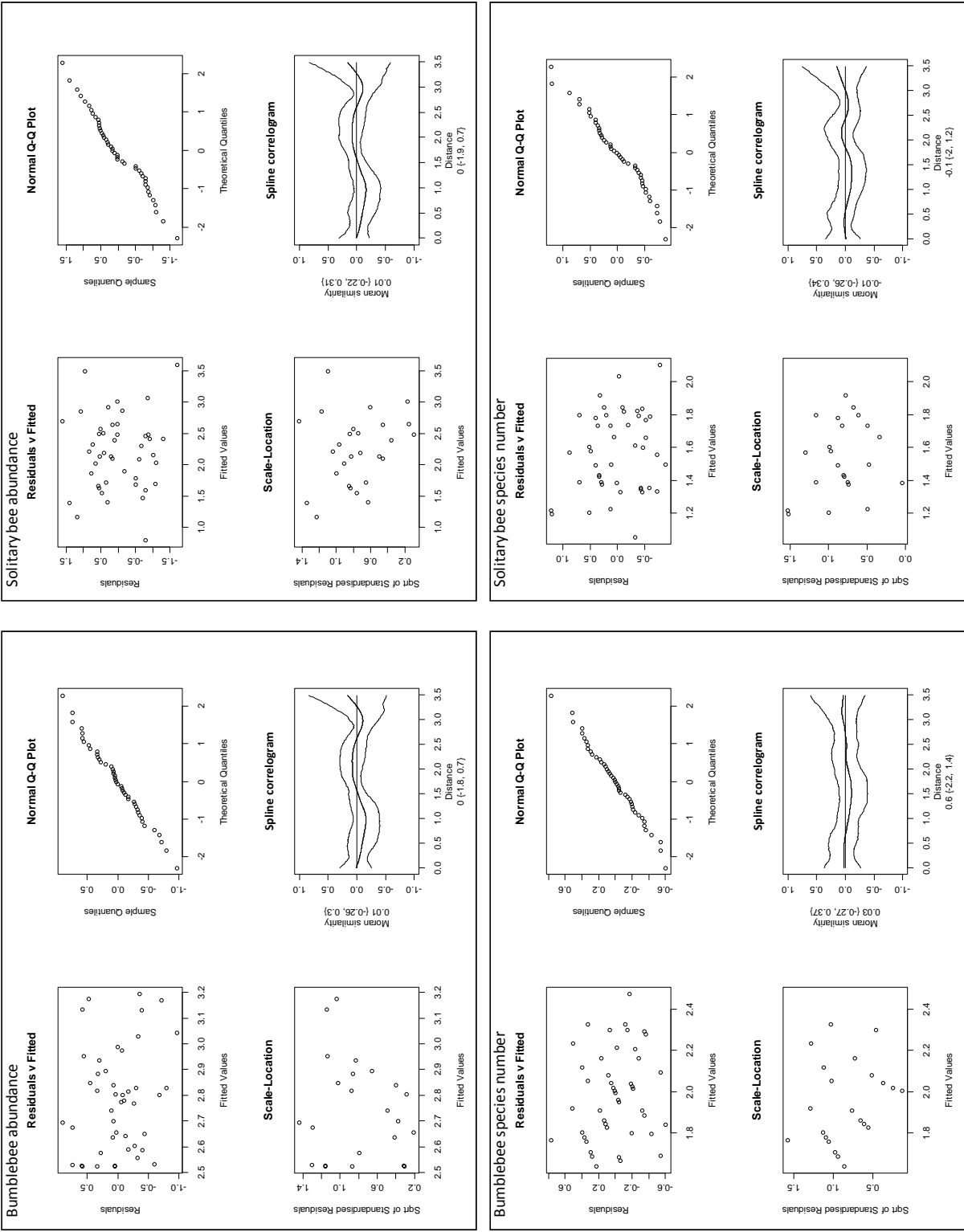
$$\text{Ln}(\text{Number of solitary bee species} + 1) = 1.72 + (-0.45 \cdot \text{reseed}) + (0.19 \cdot \text{sward2}) + \epsilon$$

Number of genera of wild bees

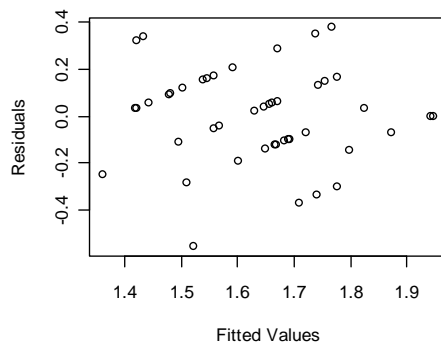


Residuals of $\text{Ln}(\text{number of genera}+1) = 1.69 + (-0.09 \cdot Y_{\text{north}}) + (-0.17 \cdot \text{reseed})$

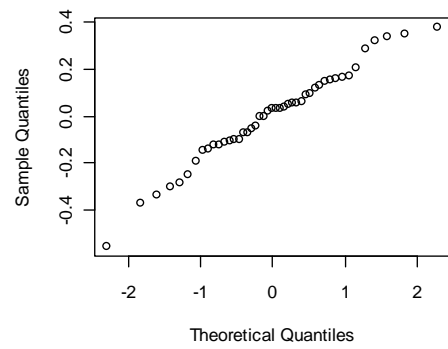
APPENDIX 24. Post Hoc residual analyses of Bayesian averaged models



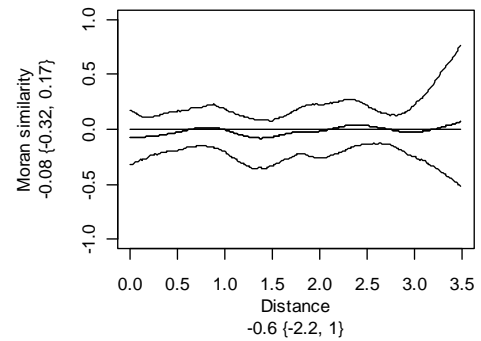
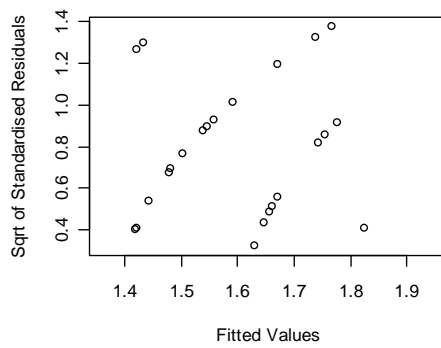
Number of wild bee genera Residuals v Fitted

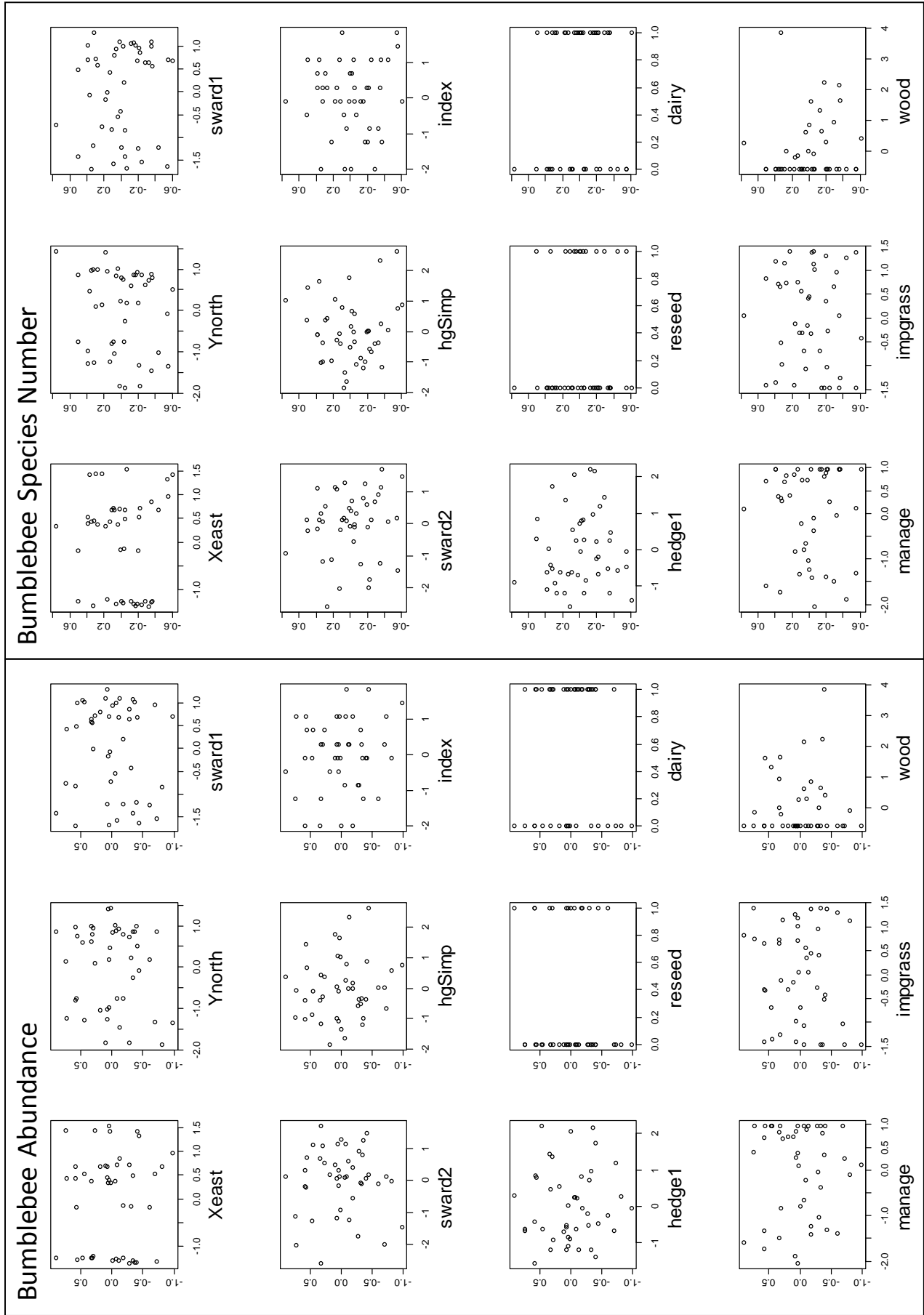


Normal Q-Q Plot

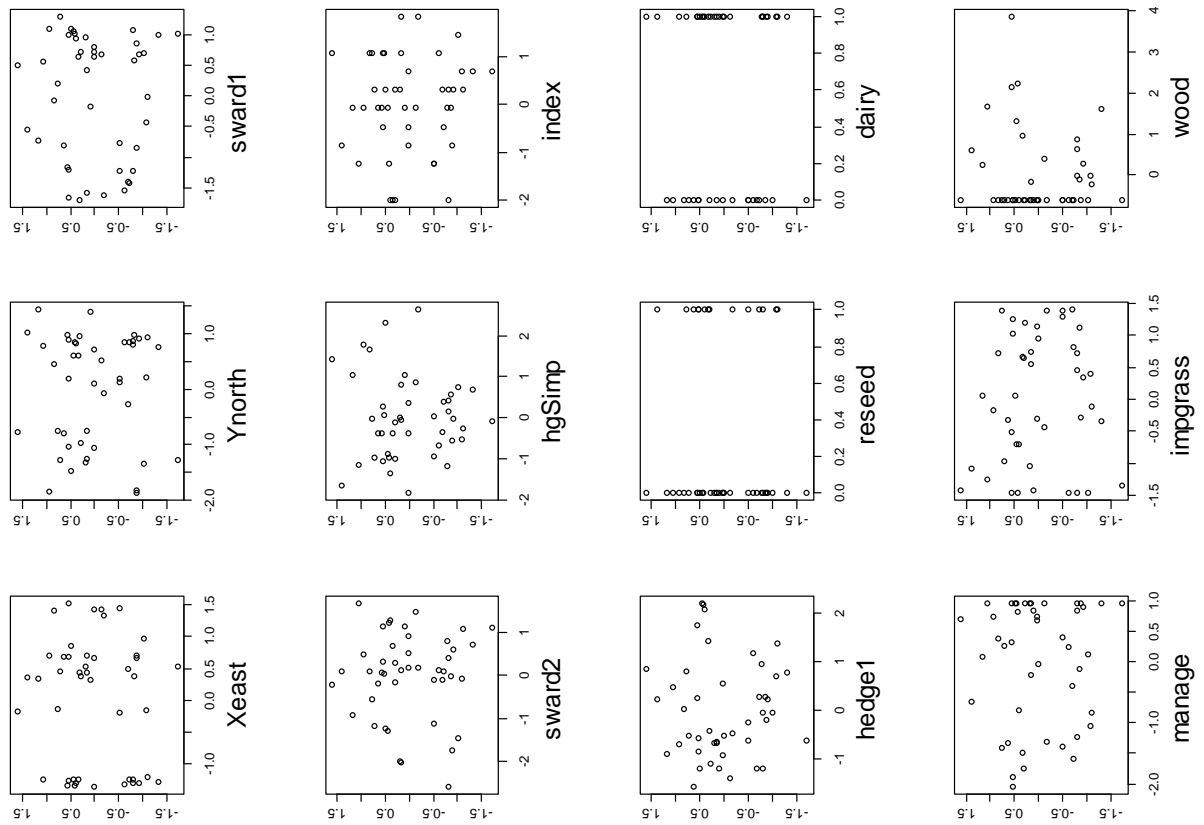


Scale-Location

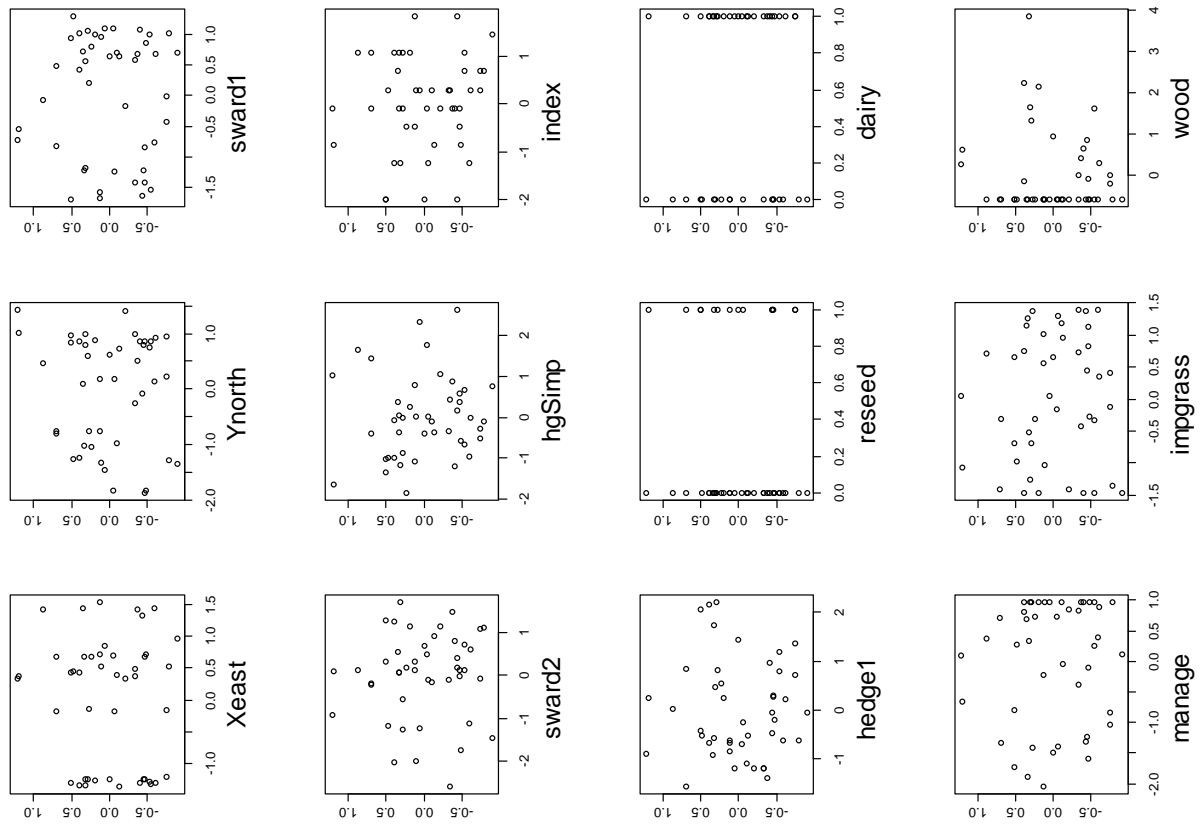




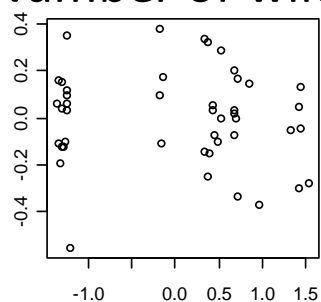
Solitary Bee Abundance



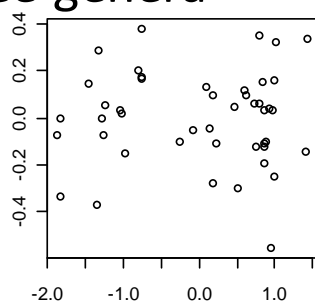
Solitary Bee Species Number



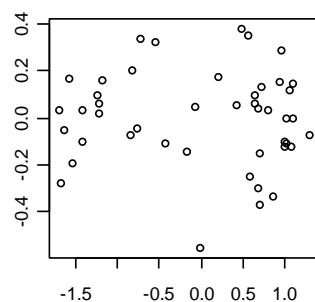
Number of wild bee genera



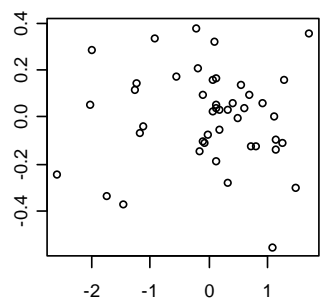
Xeast



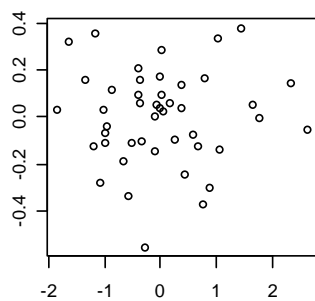
Ynorth



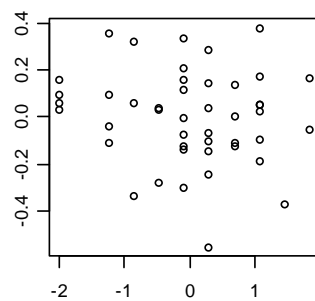
sward1



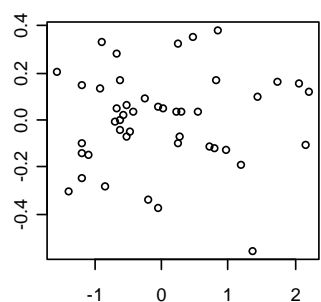
sward2



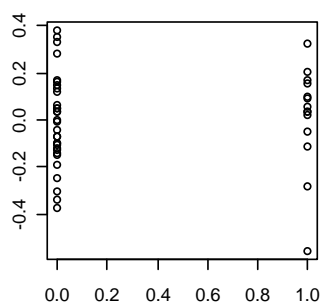
hgSimp



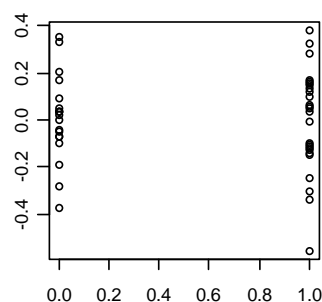
index



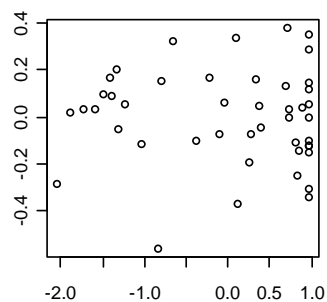
hedge1



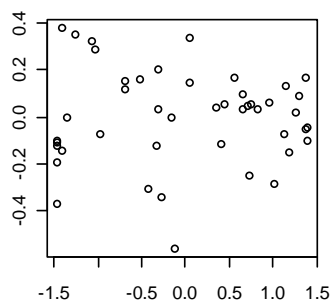
reseed



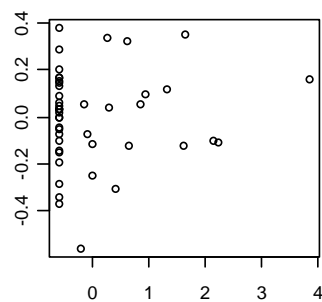
dairy



manage



impgrass



wood

APPENDIX 25. Calculating the pure and shared effects of important variables with geographical location

Bumblebee abundances

Pure and shared effects of grid reference and hedgerow structural index on bumblebee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{Index } \beta_3 + \epsilon$	$[a+b+c]$	0.17
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.10
$x = \text{Index } \beta_3 + \epsilon$	$[b+c]$	0.05

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	-0.02
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.10
Pure hedge index effect, c	$= [b+c] - b$	0.05

Pure and shared effects of grid reference and hedgerow vegetation composition on bumblebee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{hedge1 } \beta_3 + \epsilon$	$[a+b+c]$	0.23
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.10
$x = \text{hedge1 } \beta_3 + \epsilon$	$[b+c]$	0.17

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.04
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.06
Pure hedge1 effect, c	$= [b+c] - b$	0.13

Pure and shared effects of grid reference and reseed on bumblebee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{reseed } \beta_3 + \epsilon$	$[a+b+c]$	0.15
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.10
$x = \text{reseed } \beta_3 + \epsilon$	$[b+c]$	0.05

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.00
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.10
Pure reseed effect, c	$= [b+c] - b$	0.05

Pure and shared effects of grid reference and proportion of improved grassland in landscape on bumblebee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{impgrass } \beta_3 + \epsilon$	[a+b+c]	0.19
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.10
$x = \text{impgrass } \beta_3 + \epsilon$	[b+c]	0.18

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.06
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.04
Pure impgrass effect, c	$= [b+c] - b$	0.12

Solitary bee abundances

Pure and shared effects of grid reference and Sward2 on solitary bee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{Sward2} * \beta_3 + \epsilon$	[a+b+c]	0.30
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.15
$x = \text{Sward2} * \beta_3 + \epsilon$	[b+c]	0.06

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	-0.09
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.15
Pure Sward2 effect, c	$= [b+c] - b$	0.06

Pure and shared effects of grid reference and reseed on solitary bee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{reseed } \beta_3 + \epsilon$	[a+b+c]	0.22
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.15
$x = \text{reseed } \beta_3 + \epsilon$	[b+c]	0.11

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.04
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.11
Pure reseed effect, c	$= [b+c] - b$	0.07

Pure and shared effects of grid reference and manage on solitary bee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{manage } \beta_3 + \epsilon$	[a+b+c]	0.23
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.15
$x = \text{manage } \beta_3 + \epsilon$	[b+c]	0.11

Effect	Algorithm	Proportion of
--------	-----------	---------------

		variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.03
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.12
Pure manage effect, c	$= [b+c] - b$	0.08

Pure and shared effects of grid reference and proportion of wood in landscape on solitary bee abundance

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{wood } \beta_3 + \epsilon$	$[a+b+c]$	0.16
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.15
$x = \text{wood } \beta_3 + \epsilon$	$[b+c]$	0.03

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.02
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.13
Pure wood effect, c	$= [b+c] - b$	0.01

Number of bumblebee species

Pure and shared effects of grid reference and hedgerow vegetation composition on number of bumblebee species

R2 rather than adjusted r2 used becos values for adjusted R2 were suspiciously large.

$x = \text{sqrt}(\text{number of bumblebee species})$

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{hedge1 } \beta_3 + \epsilon$	$[a+b+c]$	0.32
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.27
$x = \text{hedge1 } \beta_3 + \epsilon$	$[b+c]$	0.23

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.18
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.09
Pure hedge1 effect, c	$= [b+c] - b$	0.05

Pure and shared effects of grid reference and proportion of improved grassland in landscape on the number of bumblebee species

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{impgrass } \beta_3 + \epsilon$	$[a+b+c]$	0.37
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.27
$x = \text{impgrass } \beta_3 + \epsilon$	$[b+c]$	0.21

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.11
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.16
Pure impgrass effect, c	$= [b+c] - b$	0.10

Pure and shared effects of grid reference and proportion of scrub and woodland in landscape on the number of bumblebee species

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{wood } \beta_3 + \epsilon$	[a+b+c]	0.34
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.27
$x = \text{wood } \beta_3 + \epsilon$	[b+c]	0.17

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.10
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.17
Pure wood effect, c	$= [b+c] - b$	0.07

Number of solitary bee species

$x = \log_{10}(\text{number of solitary species} + 1)$

Pure and shared effects of grid reference and management intensity of grassland on the number of solitary bee species

R² rather than adjusted r² used becous values for adjusted R² were suspiciously large.

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{manage } \beta_3 + \epsilon$	[a+b+c]	0.18
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.11
$x = \text{manage } \beta_3 + \epsilon$	[b+c]	0.09

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.02
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.09
Pure manage effect, c	$= [b+c] - b$	0.07

Pure and shared effects of grid reference and reseeding on the number of solitary bee species

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{reseed } \beta_3 + \epsilon$	[a+b+c]	0.18
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.11
$x = \text{reseed } \beta_3 + \epsilon$	[b+c]	0.09

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.02
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.09
Pure reseed effect, c	$= [b+c] - b$	0.07

Pure and shared effects of grid reference and grassland composition (sward2) on the number of solitary bee species

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{sward2}^* \beta_3 + \epsilon$	[a+b+c]	0.21
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	[a+b]	0.11
$x = \text{sward2}^* \beta_3 + \epsilon$	[b+c]	0.06

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	-0.04
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.11
Pure sward2 effect, c	$= [b+c] - b$	0.06

Number of wild bee genera

R² rather than adjusted r² used becos values for adjusted R² were negative.

Pure and shared effects of grid reference and grass management intensity on the number of bee genera

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{manage } \beta_3 + \epsilon$	$[a+b+c]$	0.24
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.14
$x = \text{manage } \beta_3 + \epsilon$	$[b+c]$	0.12

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.02
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.12
Pure manage effect, c	$= [b+c] - b$	0.10

Pure and shared effects of grid reference and reseeding on the number of of bee genera

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{reseed } \beta_3 + \epsilon$	$[a+b+c]$	0.24
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.14
$x = \text{reseed } \beta_3 + \epsilon$	$[b+c]$	0.15

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	0.05
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.09
Pure reseed effect, c	$= [b+c] - b$	0.10

Pure and shared effects of grid reference and grassland composition (sward2) on the number of of bee genera

Model	Component of algorithm	R ²
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \text{sward2}^* \beta_3 + \epsilon$	$[a+b+c]$	0.24
$x = \text{Xeast } \beta_1 + \text{Ynorth } \beta_2 + \epsilon$	$[a+b]$	0.14
$x = \text{sward2}^* \beta_3 + \epsilon$	$[b+c]$	0.02

Effect	Algorithm	Proportion of variance explained
Shared effect, b	$= [a+b] + [b+c] - [a+b+c]$	-0.08
Pure Xeast and Ynorth effect, a	$= [a+b] - b$	0.14
Pure sward2 effect, c	$= [b+c] - b$	0.02