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THE PRINCIPLE OF COMPETITIVE SURVIVAL

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ABSTRACT

We present a model for an arbitrary number of populations that compete for an arbitrary number of resources, whose consumption is monitored by the model. We show that the state of mutual coexistence of all populations is always stable, in contrast to the classical model, in which sufficiently strong competition promotes extinction of all but one population. We suggest that the distinction in outcome reflects that the classical model is not actually one of competition, but of antagonism, aggression and warfare.

1. Introduction

Mass extinction events refer to periods in which a large number of species are lost from the geological record over a relatively short period of time. Traditionally, there have been five major mass extinction events. The largest of these was that of the End-Permian, which saw about 90% of marine species and $\sim 70\%$ of land species go extinct (see [7]). Extinction events differ in duration, intensity, diversity of affected species and even in cause. Common causes include extraterrestrial impacts, ocean acidification, temperature shifts, ocean anoxia and large igneous province volcanism (e.g., [4], [6] and [18]). All of these factors cause stress on the environment. In the modern day, human behaviour is undeniably having an impact on species and their habitats, thus bringing about extinction.


Sudakow *et al.* [14] review how mathematical models may be utilised to further our understanding of extinction. They highlight several potential approaches. We

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here focus on continuous differential equation models. The most obvious way in which extinction occurs in such models is through competition. In essence, it is theorised that if the environment is stressed from a state of stable coexistence, then extinction of the species less able to adapt occurs. The normal way to consider this is via the theory of competitive exclusion.

The classical model for n competing populations is

$$\dot{N}_i = r_i \left[1 - \frac{N_i}{K_i} - \sum_{j \neq i} \frac{\alpha_{ij} N_j}{K_j} \right], \quad i = 1, \dots, n, \quad (1.1)$$

where we have supposed the density of a population, N_i , has growth rate r_i , species carrying capacity K_i , and that the α_{ij} terms represent the competitive effect of population N_j on population N_i . The parameters r_i , K_i and α_{ij} are all positive (e.g., [13]). We make the model dimensionless by scaling $t \sim t_0$, $N_i = K_i u_i$, whence

$$\dot{u}_i = \rho_i u_i \left[1 - \sum_j \alpha_{ij} u_j \right], \quad (1.2)$$

where $\rho_i = r_i t_0$ and we define the diagonal elements $\alpha_{ii} = 1$. We could, for example, choose $t_0 = \min r_i^{-1}$, so that $\rho_i \leq 1$ for each i .

Steady states U_i of (1.2) satisfy

$$U_i = 0 \quad \text{or} \quad \sum_j \alpha_{ij} U_j = 1. \quad (1.3)$$

We are interested in the possible coexistence state in which $U_i \neq 0$ for each i . In general, such a state is unique; this occurs if $\det A \neq 0$, where $A = (\alpha_{ij})$. In the exceptional cases where $\det A = 0$, there is either no coexistence state or there is a continuum, as exemplified in the two-dimensional case by the case $\alpha_{12}\alpha_{21} = 1$, where no coexistent state occurs unless $\alpha_{12} = \alpha_{21} = 1$, when there is a continuum. Steady states for which some of the $U_i = 0$ are not of concern; if they are unstable then they are not realised, and if they are stable, the corresponding null populations can be removed from the model.

The basic result of the classical two-population model is that when the (off-diagonal) α 's are small, there is a coexistence state and it is stable, but when the α 's are large, there is also a coexistence state but it is unstable (and thus extinction of one of the populations occurs). This basic result also applies in the n -population model.

To study the linear stability of the coexistence state, we put $u_i = U_i + w_i e^{\sigma t}$, whence it follows that

$$\sum_j B_{ij} w_j = -\sigma w_i, \quad B_{ij} = \rho_i U_i \alpha_{ij}. \quad (1.4)$$

Note that the matrix $B = DA$, where $D = \text{diag}(\rho_i U_i)$.

If all the off-diagonal α 's are small, then $U_i = 1 + O(\alpha)$, and $B_{ij} \approx \rho_i \delta_{ij}$,

with δ_{ij} being the Kronecker delta. We thus find $\sigma \approx -\rho_i$ gives the n eigenvalues, $i = 1, \dots, n$; hence the coexistence state exists and is stable.

On the other hand, if all the off-diagonal α 's are large, then

$$\sum_{j \neq i} \alpha_{ij} U_j \approx 1, \tag{1.5}$$

since $U_i = O\left(\frac{1}{\alpha}\right)$, and the stability criterion is approximately

$$\det(C + \sigma I) = 0, \tag{1.6}$$

where C is the matrix with off-diagonal entries B_{ij} , but the diagonal elements are zero. The polynomial in (1.6) can in general be written as

$$\det(C + \sigma I) = \sigma^n + \text{tr } C \sigma^{n-1} + \left[\sum_{i < j} (C_{ii} C_{jj} - C_{ij} C_{ji}) \right] \sigma^{n-2} + \dots \tag{1.7}$$

If the roots of (1.7) are $\sigma_1, \dots, \sigma_n$, then

$$-\sum \sigma_i = \text{tr } C = 0, \tag{1.8}$$

and thus in general at least one value of σ_i has $\text{Re } \sigma_i > 0$, so that the coexistence state is unstable at high α . The alternative possibility is that for each i , $\sigma_i = 0$ or $\sigma_i = i\Omega$. Since the complex roots occur as complex conjugates, this implies that (1.7) must be of the form

$$\det(C + \sigma I) = \sigma^{n-2k} \prod_1^k (\sigma^2 + \Omega_i^2) = \sigma^n + \left(\sum_1^k \Omega_i^2 \right) \sigma^{n-2} + \dots, \tag{1.9}$$

which is impossible on comparison with (1.7), since $C_{ii} = 0$. Therefore the two-population result is repeated in the n -dimensional case.

The coexistence state is unstable if the off-diagonal α 's are large enough. Using the general result in (1.7), the eigenvalues σ_i satisfy

$$\sum_{i < j} \sigma_i \sigma_j = \sum_{i < j} (B_{ii} B_{jj} - B_{ij} B_{ji}) = \sum_{i < j} \rho_i \rho_j U_i U_j (1 - \alpha_{ij} \alpha_{ji}), \tag{1.10}$$

and thus a sufficient condition for instability is that $\alpha_{ij} \alpha_{ji} > 1$ for each pair i, j . As indicated earlier, a simple direct instability in which σ passes through zero requires $\det B = 0$ at the transition point, and thus also $\det A = 0$ (since $B = DA$). Such a transition requires either the complete degeneracy where a continuum of steady states occurs, or more generally $\sigma \rightarrow 0$ if one of the populations $U_i \rightarrow 0$. In that case there is a transcritical bifurcation. The two-dimensional case provides an illuminating example. In the case that no other bifurcation has occurred, we then expect that the large α case will lead to extinction.

What is unclear in our analysis is whether a Hopf bifurcation of the coexistence

state can occur for $n \geq 3$. Were that to occur, and a limit cycle solution exist, it is possible that the unstable large α coexistence state could simply lead to continuous oscillations without extinction. Our analysis does not find any simple reason whereby this possibility can be excluded. Indeed, it has been shown previously that periodic limit cycle solutions may occur in this system for $n \geq 3$ (see [9]). A well-studied example of this periodic limit cycle behaviour is the three species model of May and Leonard [12]. They study the special case in which the parameters $\alpha_{12} = \alpha_{23} = \alpha_{31} = \alpha$ and $\alpha_{13} = \alpha_{21} = \alpha_{32} = \beta$ with the growth rates $\rho_1 = \rho_2 = \rho_3$. It then follows that when $\alpha + \beta = 2$ (and $\alpha \neq \beta$) the system exhibits periodic limit cycles. Further study of limit cycle solutions of the three species case has been outlined by, for example, Zeeman [19], Chi *et al.* [5] and Zhang and Chen [20].

The classical competitive exclusion model (1.1), though often interpreted in terms of resources, does not explicitly consider the mechanism by which competition takes place. The model is written in the fashion that one species acts to actively remove another. Other versions of this competitive exclusion model have been proposed which do consider explicit resource dependence; examples include the works of León and Tumpson [10], Armstrong and McGehee [1, 2, 3] and Tilman [15, 16, 17] – with more discussed in the review of Grover [8]. Such models follow a general formulation and, depending on the choice of resource growth and interaction terms, may be converted back to that of classical competitive exclusion if the resource rapidly reaches a steady state (see, for example, the appendix of the second chapter of MacArthur [11]).

Here we create a simple model of a different formulation in which we allow competition purely in the form of resource depletion, and we show with such a model that mutual coexistence of all populations is always stable.

2. Resource competition model

We consider a model in which each population has a carrying capacity which depends on the availability of resources that are consumed by them. In general for n species and m resources we write

$$\begin{aligned} \dot{N}_i &= r_i N_i \left[1 - \frac{N_i}{K_i} \right], & i = 1, 2, \dots, n, \\ \dot{R}_i &= I_i \left(1 - \frac{R_i}{M_i} \right) - R_i \sum_{j=1}^n s_{ij} N_j, & i = 1, 2, \dots, m, \\ K_i &= \sum_{j=1}^m g_{ij} R_j. \end{aligned} \tag{2.1}$$

In this we have supposed that the density of a population, N_i , is given by a logistic equation with growth rate r_i and carrying capacity K_i . Similarly, the resources R_i satisfy equations with growth rates I_i and limit capacities M_i . In addition, each resource R_i is consumed by the population N_j with a specific consumption rate coefficient s_{ij} . The carrying capacities for the populations are given in terms of the parameters g_{ij} , which represent the rate at which population i favours (or

can consume) resource j . Note that a reasonable presumption might be that the appetite s_{ji} of population i for resource j might be similar or proportional to the importance of this resource for the population, i. e., g_{ij} . We have assumed that the resource supply rate is non-zero when the resource itself is not present; we have in mind, for example, growth of vegetation from seed. We non-dimensionalise the equations (2.1) by choosing scales

$$t \sim \frac{1}{r_1}, \quad N_i \sim K_i^*, \quad R_i \sim M_i, \quad K_i = K_i^* \kappa_i, \quad (2.2)$$

and thus we obtain

$$\begin{aligned} \dot{N}_i &= \rho_i N_i \left[1 - \frac{N_i}{\kappa_i} \right], \quad i = 1, 2, \dots, n, \\ \dot{R}_i &= \lambda_i (1 - R_i) - R_i \sum_{j=1}^n \beta_{ij} N_j, \quad i = 1, 2, \dots, m, \\ \kappa_i &= \sum_{j=1}^m \gamma_{ij} R_j, \end{aligned} \quad (2.3)$$

where the parameters are defined by

$$\rho_i = \frac{r_i}{r_1}, \quad \lambda_i = \frac{I_i}{r_1 M_i}, \quad \beta_{ij} = \frac{K_j^* s_{ij}}{r_1}, \quad \gamma_{ij} = \frac{g_{ij} M_j}{K_i^*}; \quad (2.4)$$

the carrying capacity scales K_i^* could be chosen so that $\max_j \gamma_{ij} = 1$, for example.

Steady states of the system are given by

$$\begin{aligned} N_i = 0 \quad \text{or} \quad N_i = \kappa_i &= \sum_j \gamma_{ij} R_j, \\ R_i &= \frac{\lambda_i}{\lambda_i + \sum_j \beta_{ij} N_j}. \end{aligned} \quad (2.5)$$

It is clear for this system that all the partially extinct states (where at least one population is zero) are unstable, so we confine our attention to the coexistent state given by

$$N_i = N_i^* = \sum_j \gamma_{ij} R_j^*, \quad R_i^* = \frac{\lambda_i}{\lambda_i + \sum_{j,k} \beta_{ij} \gamma_{jk} R_k^*}. \quad (2.6)$$

At least in the case of a single resource, this coexistent state is unique. It is less obvious that this is the case for more than one resource, but we shall assume so.

We linearise about the steady state by writing

$$N_i = N_i^* + n_i, \quad R_i = R_i^* + r_i, \quad (2.7)$$

which leads to the pair

$$\begin{aligned}\dot{n}_i &= \rho_i \left[\sum_k \gamma_{ik} r_k - r_i \right], \\ \dot{r}_i &= -\frac{\lambda_i r_i}{R_i^*} - R_i^* \sum_j \beta_{ij} n_j.\end{aligned}\tag{2.8}$$

We put

$$n_i = a_i e^{\sigma t}, \quad r_i = b_i e^{\sigma t},\tag{2.9}$$

and then, after eliminating a_i , we obtain the eigenvalue problem

$$\left(\sigma + \frac{\lambda_i}{R_i^*} \right) b_i = -R_i^* \sum_{j,k} \frac{\beta_{ij} \gamma_{jk} \rho_j}{(\rho_j + \sigma)} b_k.\tag{2.10}$$

If λ_i is large, then (2.6) implies $R_i \approx 1$, and then (2.10) implies that the eigenvalues are $\sigma \approx -\lambda_i$, so that the coexistent state is stable (and incidentally unique). If instability occurs, it is either through an exchange of stability when $\sigma = 0$, or through a Hopf bifurcation when $\sigma = i\Omega$. The first case requires

$$\frac{\lambda_i}{R_i^*} b_i = -R_i^* \sum_{j,k} \beta_{ij} \gamma_{jk} b_k;\tag{2.11}$$

the second requires (equating real parts)

$$\frac{\lambda_i}{R_i^*} b_i = -R_i^* \sum_{j,k} \frac{\beta_{ij} \gamma_{jk} \rho_j^2}{(\rho_j^2 + \Omega^2)} b_k.\tag{2.12}$$

It is straightforward to see that for a single resource (but any number of populations), neither of these is possible, hence the coexistent state is stable, but it is less obviously the case in general. If we follow our earlier comment by taking $\gamma_{ij} \propto \beta_{ji}$, however, then the matrix C with

$$C_{ik} = \sum_j \frac{\beta_{ij} \gamma_{jk} \rho_j^2}{(\rho_j^2 + \Omega^2)}\tag{2.13}$$

is of the form $C = BB^T$, and hence C is non-negative. It follows in this particular case that neither (2.12) nor (similarly) (2.11) is possible, so stability is assured with this assumption.

The more general case can be analysed as follows. It suffices to consider (2.12). We write $b_i = R_i^* v_i$, and can normalise the arbitrarily scaled v_i by choosing $\max |v_i| = 1$. From (2.12) there follows

$$\lambda_i |v_i| \leq R_i^* \sum_{j,k} \beta_{ij} \gamma_{jk} R_k^*,\tag{2.14}$$

bearing in mind on the right hand side that $|v_i| \leq 1$ for all i . Equation (2.6) implies, however, that the right hand side is just $\lambda_i(1 - R_i^*)$, and therefore (2.14) implies

$$|v_i| \leq 1 - R_i^* < 1 \quad (2.15)$$

for all i , which conflicts with our requirement that $\max |v_i| = 1$. So neither (2.12) nor (with $\Omega = 0$) (2.11) are possible, and the coexistent state remains stable.

An associated consequence is that the coexistent state is unique. It is unique at large λ_i , by explicit calculation, and suffers no bifurcation as λ_i is reduced, so the only way another such state could occur in the hyper-quadrant $R_i \geq 0$ is by passing through one of the hyper-axes $R_i = 0$, and this is clearly not possible.

3. Conclusions

Here we have presented a model for which an arbitrary number of populations compete for an arbitrary number of resources, upon which the populations are explicitly dependent. We show that in this model formulation, the mutual coexistence state is always stable. In contrast to this, the classical theory of competitive exclusion typically leads to extinction of all but one dominant species if the competitive effects are sufficiently strong.

This distinction leads to a semantic dichotomy: classically, strong competition causes extinction, whereas we suggest this is not the case. The difference can be resolved by a more subtle consideration of how competition is modelled. In our view, competition for resource is a passively effected property: the competitors might starve, but they do not fight. In contrast, the classic competition model portrays the result of competition as an active removal of the competitors. These classical competitors are not benign foragers, they are vicious assailants who fight over their depleted resources. The classical competition model is not one of diminished appetite, but of antagonism, aggression and warfare.

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