

IS SPACE NECESSARY? INTERFERENCE COMPETITION AND LIMITS TO BIODIVERSITY

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Abstract. A single trade-off between competitive ability and mortality has been shown to support an arbitrarily large number of species in models of interference competition in spatially structured populations. We show that this results not from spatial structure, but instead from the assumption that a small difference in mortality translates into a large difference in competitive ability. We present graphical criteria for recognizing functions that support one, two, or more species. High levels of coexistence in models of this form depend on a steep slope or a discontinuous second derivative of the function relating mortality to competitiveness. These criteria are identical to those in models of interference competition that lack explicit spatial structure.

Key words: *biodiversity; coexistence; interference competition; spatial subdivision; superinfection.*

INTRODUCTION

In some guilds of organisms, there is a trade-off between density-independent components of fitness (survivorship, fecundity, or colonization ability) and competitiveness (Tilman 1994). Organisms with a high mortality rate might be able to competitively displace those with a lower rate if they allocate little energy to defense and a great deal to rapid growth (Adler 1999). Plants with few large seeds might be able to outcompete those with many small seeds (Geritz 1995, Rees and Westoby 1997a, Geritz et al. 1988). Highly virulent pathogens might be able to take over hosts from less virulent strains (May and Nowak 1994). Recent theoretical work has demonstrated that a high degree of coexistence is possible in groups of species that share trade-offs of this sort (May and Nowak 1994, Tilman 1994, Geritz 1995).

In an influential paper, Tilman (1994) extended earlier work (Hastings 1980) and showed that an arbitrarily large number of competing species can coexist in a spatially structured habitat. Identical results hold in a model of disease competition (May and Nowak

1994). We show that the high degree of coexistence is due to a simplified model of interference competition and not to spatial structure.

In particular, assume there is a trade-off between mortality and competitive ability. Picture a species with a higher mortality rate competing with a species with a lower mortality rate. In the simplified model, a species that has only a slightly higher mortality rate than its competitor displaces that competitor just as fast as a species with a much higher mortality rate (May and Nowak 1994, Tilman 1994). More mathematically, the function describing competitive ability as a function of mortality rate is discontinuous (Mosquera and Adler 1998; Pugliese, *in press*).

We show that smoothing out this competitiveness function eliminates much of the coexistence. If the function has the particularly nice property of being analytic (meaning that it has an infinite number of derivatives and is equal to its Taylor series), only a discrete set of species can coexist. We use bifurcation analysis and simulation to indicate that the transition from infinite coexistence to a discrete number of species occurs when the competitiveness function acquires a continuous second derivative.

Furthermore, the same results hold in a model without explicit spatial structure, where interference competition is modeled as frequency dependence (Rees and Westoby 1997). Again, the smoothness of the trade-off curve relating mortality (or other density-independent

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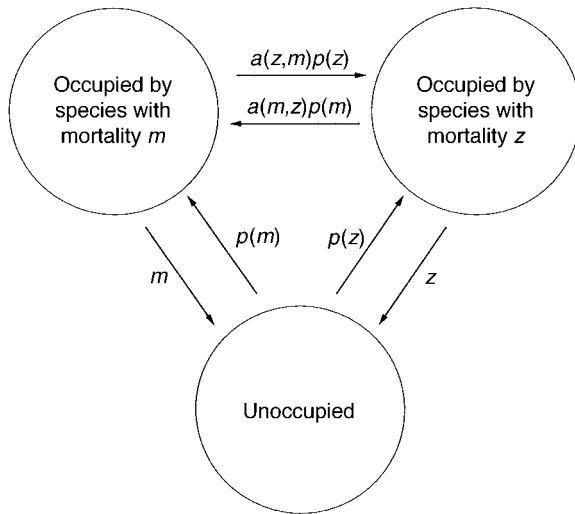


FIG. 1. Per capita transition rates for the basic model. The dynamics of two species with mortality rates m and z . The arrows are labeled with the per-patch transition rates.

components of fitness) to success in interference competition determines the extent of coexistence.

Mathematical niceties like the existence of a second derivative would be impossible to detect in data. We argue that stochasticity tends to smooth out functions, implying that the trade-off between mortality and competition will tend to support only a few species in real systems, with or without spatial structuring.

THE MODEL

The basic model is outlined schematically in Fig. 1. The world is broken up into patches or safe sites (Tilman 1994) that can be occupied by a single individual at a time. The fraction of sites occupied by a species with mortality rate m will be denoted by $p(m)$. The total fraction of sites occupied is

$$T = \int p(m) dm. \quad (1)$$

A species with mortality rate m can lose or gain a site in four ways (Fig. 1):

- 1) lose occupied sites through death (per site rate m);
- 2) lose occupied sites by being taken over by any another species (per site rate $\int a(z, m)p(z) dz$);
- 3) take over sites occupied by any other species z (net rate $\int a(m, z)p(z)p(m) dz$);
- 4) take over empty sites (net rate $(1 - T)p(m)$, where the colonization rate of empty sites has been scaled to 1).

The function $a(m, z)$ describes the rate at which m takes over from z relative to the colonization rate of

empty sites and has been called the superinfection function in an epidemiological context (Mosquera and Adler 1998). If a higher mortality rate leads to higher competitive ability, as we assume here, $a(m, z)$ will be an increasing function of m . The fraction of sites occupied by species m obeys the differential equation

$$\frac{dp(m)}{dt} = \left(1 - T - m + \int a(m, z)p(z) dz - \int a(z, m)p(z) dz \right) p(m). \quad (2)$$

For simplicity, we assume that $a(m, z) = a(m - z)$, meaning that the rate of takeover is a function only of the difference between the two mortality rates. In this case, we can rewrite Eq. 2 as

$$\frac{dp(m)}{dt} = \left(1 - T - m + \int b(m - z)p(z) dz \right) p(m) \quad (3)$$

where

$$b(m - z) = a(m - z) - a(z - m). \quad (4)$$

The competitiveness function b describes the net rate of takeover of sites occupied by species z by individuals from species m . It is necessarily true that

$$b(0) = 0 \quad b(z) > 0 \quad \text{if } z > 0 \quad b(-z) = -b(z).$$

We assume that b has a negative (or zero) second derivative for positive values of its argument, meaning that higher competitiveness produces diminishing returns. Various versions of the competitiveness function b are shown in Fig. 2. We scale $\lim_{z \rightarrow \infty} b(z) = 1$ to match the rate at which species take over empty sites.

Our goal is to find stable equilibria, consisting potentially of a coalition of species (those species present at positive frequency), that cannot be invaded by any other species. At equilibrium, the per capita reproduction of each member of the coalition must be zero. For the equilibrium to be uninvadable, the per capita reproduction of every species absent from the coalition must be nonpositive. Denoting the coalition as the set Ω , the per capita reproduction of any species m is given by the invasion function $f(m)$:

$$f(m) = 1 - T - m + \int_{z \in \Omega} b(m - z)p(z) dz. \quad (5)$$

The coalition is uninvadable if

$$\begin{aligned} f(m) &= 0 & \text{if } m \in \Omega \\ f(m) &\leq 0 & \text{if } m \notin \Omega. \end{aligned} \quad (6)$$

RESULTS

How many species will be members of a stable coalition for different forms of the competitiveness func-

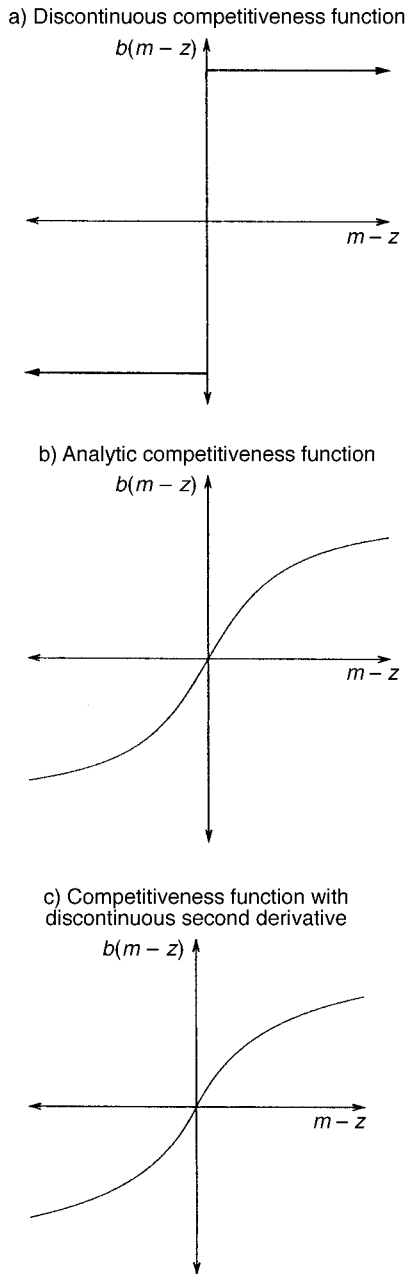


FIG. 2. Three versions of the competitiveness function b : (a) discontinuous, wherein a species with a slight advantage takes over as readily as a species with a large advantage; (b) analytic, using the form $b(z) = 2/\pi \tan^{-1}(\pi/2 z)$ [the factors of $\pi/2$ normalize the slope at $z = 0$ and $\lim_{z \rightarrow \infty} b(z)$ to be equal to 1]; (c) discontinuous second derivative, using the form $b(z) = z/(1 + |z|)$.

tion b ? We verify that discontinuous forms for the competitiveness function b support a coalition that consists of a whole continuum of species (May and Nowak 1994, Tilman 1994). In contrast, coalitions supported by an analytic (very smooth) form of the competitiveness function b cannot include such a continuum of species. For such functions, we identify the conditions under which one or two species can form a coalition. In contrast, a competitiveness function with a discontinuous second derivative never supports a coalition with exactly two species. Finally, we show that the same results hold when the competitiveness function describes frequency-dependent competition in a non-spatial model.

Infinite coexistence with a discontinuous competitiveness function

Previous papers (May and Nowak 1994, Tilman 1994) have analyzed one particularly simple form for the function b , the step function

$$b(m-z) = \begin{cases} s & \text{if } m > z \\ -s & \text{if } m < z \end{cases} \quad (7)$$

(Fig. 2a). In this case, a species with high mortality takes over at rate s even when it is only slightly different. It is straightforward to show that the coalition with

$$p(m) = \frac{1}{2s} \quad \text{for } 0 \leq m \leq \frac{2s}{1+s}$$

is stable (Appendix A). This discontinuous competitiveness function b produces a continuum of species in the coalition.

Finite coalition with an analytic competitiveness function

In contrast to this discontinuous function, analytic functions are extremely smooth. Not only do they have an infinite number of continuous derivatives, but they have a Taylor series that is equal to the function at all points (Rudin 1974). A coalition that includes a continuum of species is impossible with any nonlinear analytic function (the linear case is degenerate). The proof is sketched in Appendix B. There could, however, be a coalition consisting of a large number of discrete species.

Condition for a single-species coalition

When will a single species repel all invasions? We show in Appendix C that such a species must have the mortality rate $m = 0$ (the lowest possible mortality). A species with mortality m cannot invade the species with mortality 0 if it gains sites (rate $b(m)$) at a lower rate than it loses sites (rate m). Because we have as-

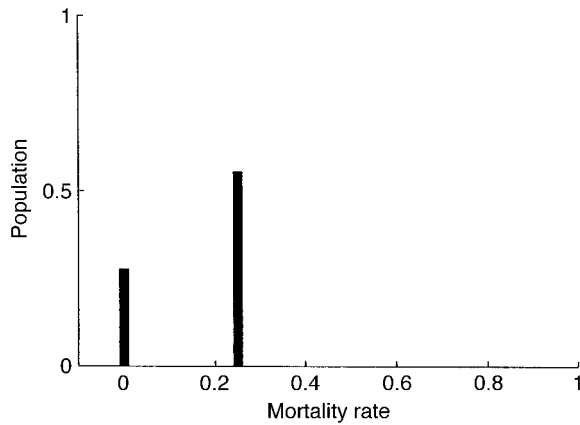


FIG. 3. Coalition of two coexisting species after the initial bifurcation. Here the competitiveness function has a continuous third derivative at $z = 0$ and slope $b'(0) = s = 1.2$. The species with higher mortality is approximately twice as common (Eq. 17).

sumed that the competitiveness function b is concave down, $b(m) < m$ for all $m > 0$ if and only if

$$b'(0) < 1. \tag{8}$$

The slope of the competitiveness function b at 0 determines whether a single species, the least competitive, can repel all others. If the benefits of higher competitiveness are high enough, species with higher mortality and higher competitiveness can invade.

Conditions for a two-species coalition

Suppose that the slope $b'(0)$ of the invasion function is indeed greater than 1, meaning that no single species can be uninvadable. When will there be a coalition of two species that can repel all others? The details, laid out in Appendix D, can be summarized in the following graphical criterion.

Denote the slope $b'(0)$ by s . Define the “reduced function” $h(z)$ as

$$h(z) = \frac{1 - \frac{b(z)}{sz}}{z}. \tag{9}$$

The reduced function h will be continuous if b has a continuous second derivative because the two divisions by z effectively remove two derivatives of b .

The graphical method requires checking whether the reduced function $h(z)$ is increasing for small values of $z > 0$. If it is increasing, the number of species in the coalition increases from one to two when the slope s crosses 1. For $s < 1$, the single species $m = 0$ forms an uninvadable coalition. For s slightly greater than 1, there is an uninvadable two-species coalition (Fig. 3). In this case, the species with the higher mortality rate

has a population that is generally twice as large as that of the species with $m = 0$ (Appendix D).

As an example, consider the analytic function based on arctangent:

$$b(z) = \frac{2}{\pi} \tan^{-1}\left(\frac{\pi}{2}sz\right) \tag{10}$$

normalized to have slope of s at $z = 0$ and a limit of 1 as $z \rightarrow \infty$ (Fig. 2b). The reduced function is

$$h(z) = \frac{1 - \frac{2}{\pi sz} \tan^{-1}\left(\frac{\pi}{2}sz\right)}{z}.$$

This function is increasing for small positive values of its argument (Fig. 4a). In this case, the number of species in the coalition changes from one to two as s crosses 1 (as in Fig. 3).

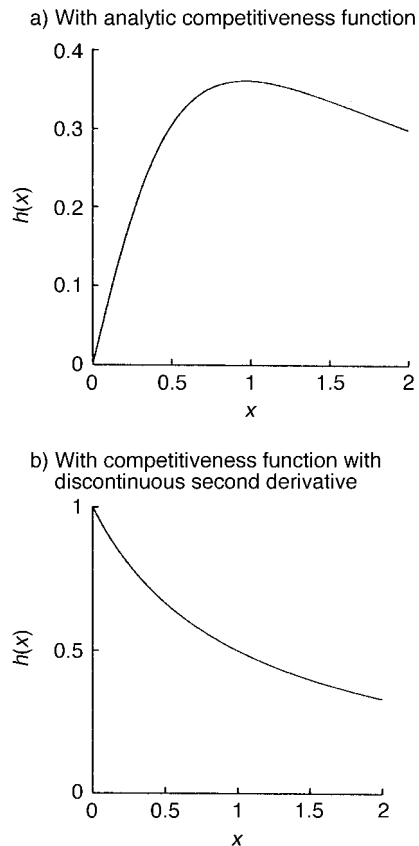


FIG. 4. The reduced function h (Eq. 9) derived from two versions of the competitiveness function b . (a) Analytic, using the form in Fig. 2b. The reduced function is increasing for $z < 0.964$, the maximum possible value of the mortality rate in a two-species coalition (the coalition breaks up for values much below this). (b) Discontinuous second derivative, using the form in Fig. 2c. The reduced function is decreasing, and there can be no two-species coalition.

Alternatively, consider the following function:

$$b(z) = \frac{sz}{1 + s|z|} \quad (11)$$

with discontinuous second derivative at $z = 0$ (Fig. 2c). The reduced function is

$$h(z) = \frac{s}{1 + sz}$$

for $z > 0$ (Fig. 4b). This function is everywhere decreasing, thus the coalition jumps from one species to more than two species when the slope s crosses 1.

Simulation results

When the competitiveness function has a reduced function $h(z)$ that is increasing for small positive values of z (meaning that it has a continuous second derivative), the uninvadable coalition bifurcates from a single species at $m = 0$ when the slope $s < 1$ to a two-species coalition when $s > 1$. Algebraic methods become too complicated for slopes far from 1. Fig. 5a shows results of a simulation of many competing species using an analytic competitiveness function. In accord with the theory, the population always includes the strategy $m = 0$. The coalition has two species over the range $s = 1$ to $s = 1.96$ (this value can be found using the theory in Appendix D), then splits to 3 (over the range of approximately $s = 2$ to $s = 2.8$), then quickly to 4 and more species as s increases further. When the function has a discontinuous second derivative, there is no stable two-species coalition. Simulation results indicate that the coalition includes many species for any $s > 1$ (Fig. 5b). Although neither our simulation nor our analysis can prove it, we believe that the coalition includes a continuum of species.

Space is not necessary

Rees and Westoby (1997) present a model for evolution and diversity of seed size that differs substantially in structure from that used here. They model a trade-off between seed size (competitiveness) and seed number (fecundity, rather than mortality). Furthermore, their model describes a well-mixed population rather than one where interactions occur in discrete sites. Mathematically, their model takes place in discrete rather than continuous time. Nonetheless, the conclusions of the present analysis apply to their model.

We use our notation to present a simplified model that follows the dynamics of the number of seeds of size s . Let $N(s)$ and $N'(s)$ represent the number of seeds size s in the present and subsequent generations respectively. Then,

$$N'(s) = \frac{\lambda(s)N(s)}{1 + a \int_0^\infty \alpha(u - s)N(u) du}. \quad (12)$$

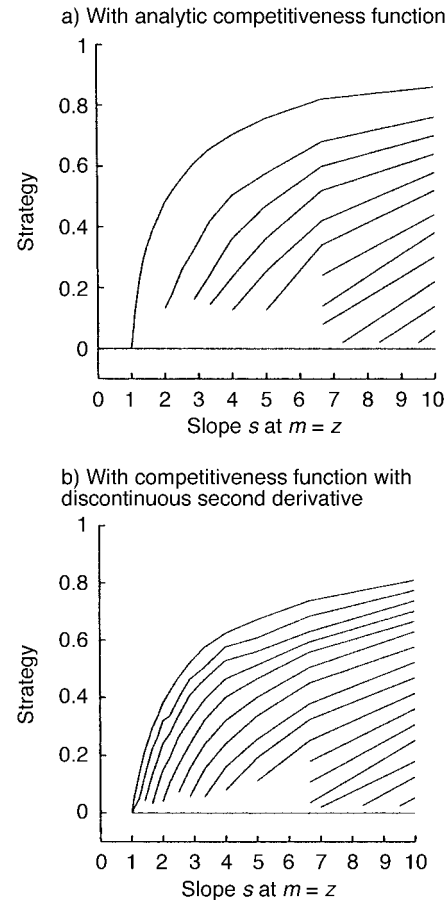


FIG. 5. Equilibrium coalitions found by simulation. The figures show a range of values of the slope s for (a) the analytic form (Eq. 10) and (b) the form with discontinuous second derivative (Eq. 11). Coalitions are read vertically for each value of s in the range from 1 to 10, with the lines indicating strategies present at equilibrium. Simulations of Eq. 2 were run up to time 100 000, starting from initial conditions of 50 evenly spaced equally common strategies.

The function $\lambda(s)$ is a decreasing function representing the lower fecundity of adult plants with larger seed size, and $\alpha(u - s)$ is an increasing function describing the competitive effect of an individual seed of size u on a seed of size s . The parameter a is chosen to scale $\alpha(0) = 1$.

All of the results derived for the spatially structured model hold when $\lambda(s)$ is decreasing, and α is suitably symmetric (Appendix E). An infinite coalition of species exists when α is discontinuous. Only a finite coalition is possible when the function α is analytic. If the competitiveness function of α is differentiable, the evolutionarily stable coalition bifurcates from a single species with the minimum seed size into a two-species coalition as the slope of α increases only if the com-

petitiveness function also has a continuous second derivative. In fact, if $\lambda(s)$ is a linear function, the conditions are identical to those for the spatially structured model.

DISCUSSION

How many species coexist based on a trade-off between some component of density-independent fitness and competitiveness? Contrary to an expectation derived from an imprecise verbal version of the principle of competitive exclusion (Levin 1970, Levin et al. 1977, Armstrong and McGehee 1980), this number can be infinite in models with interference competition and spatial structure (May and Nowak 1994, Tilman 1994). We have checked whether that surprising conclusion holds up when the trade-off between mortality and competitive ability is modeled over a wider range of conditions, and whether it depends on spatial structure.

Smoothing the competitiveness function, which describes competitive success as a function of mortality rate, greatly reduces this coexistence. Mathematically, an analytic competitiveness function can support only a discrete set of species. In fact, unless the slope of the competitiveness function is steep, meaning that a slightly higher mortality rate leads to a much higher competitive ability, we predict that only a few species will coexist based solely on this trade-off. Similar results have been found in a model of seed size evolution where a higher degree of competitive asymmetry tends to support larger numbers of coexisting seed sizes (Geritz et al. 1998).

We have also shown that the conditions for coexistence in a spatially structured patch model match those in a randomly mixing model of interference competition, highlighting the similarity between different "theory lineages" (Fagerstrom and Westoby 1997). Space is not necessary to support high diversity in systems of this sort, only a steep or discontinuous competitiveness function.

What sort of competitiveness functions might be expected in nature? Analytic functions are visually indistinguishable from functions lacking a continuous second derivative (Fig. 2). These idealized curves, of course, would have to be derived from data plotting probability of successful takeover as a function of the mortality rates. Probability of takeover would be subject to noise, such as random differences between sites or arrival times. This stochasticity could be thought of as creating a "realized" strategy that is not equal to the "genetic" strategy. If the realized strategy differs from the genetic strategy according to a normal distribution (or any other smooth distribution), arguments similar to those in Appendix B indicate that the realized competitiveness function will be analytic, and only a small number of species will coexist.

Although stochasticity also plays a role in mediating the extent of coexistence in models of exploitation competition for a continuum of resource types, the effects of stochasticity are not consistent among models (Abrams 1983) and operate through a mechanism that seems unrelated to smoothing of the competitiveness function.

We have here considered only one trade-off, between competition and mortality, assuming that all species have equal colonization rates. The general result that the number of species depends sensitively on the smoothness of the competitiveness function carries over to cases that include trade-offs between colonization and competition or mortality (Adler and Mosquera, *in press*; Pugliese, *in press*). However, the detailed predictions about the initial bifurcation may no longer hold.

The relevance of these results depends on the shape, and indeed the existence, of the competitiveness function (Banks 1997). The results here show that the extent of coexistence depends primarily on the slope of the function for similar species. Testing would require finding species with similar mortality rates (or other density-independent components of fitness), and finding the effects of each on the other through interference competition. For example, in the case of the trade-off between seed size and fecundity, species with larger seeds do have higher establishment success, but do not necessarily win in all sites (Turnbull et al. 1999).

We suggest measuring the slope of the curve relating mortality or fecundity to the probability of success in competition. In the absence of other trade-offs, we predict that such systems will support only one species if the slope is less than 1, two species if the slope is less than ~ 2 , and more species only if the slope is larger than 2. Furthermore, these models predict that the species with the highest mortality (or largest seed size) will be most abundant.

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APPENDIX A

A formula for the continuous coalition supported by a discontinuous competitiveness function is available in ESA's Electronic Data Archive: *Ecological Archives* E081-027-A1.

APPENDIX B

Proof that an analytic function b cannot support a stable coalition with a continuum of species is available in ESA's Electronic Data Archive: *Ecological Archives* E081-027-A2.

APPENDIX C

Theoretical conditions for a single-species coalition is available in ESA's Electronic Data Archive: *Ecological Archives* E081-027-A3.

APPENDIX D

Theoretical conditions for a two-species coalition is available in ESA's Electronic Data Archive: *Ecological Archives* E081-027-A4.

APPENDIX E

Results with a nonspatial model are available in ESA's Electronic Data Archive: *Ecological Archives* E081-027-A5.