

Increased competition may promote species coexistence

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It is a mainstay of community ecology that local exclusion of species will result if competitive pressures become too large. The pattern of exclusion may be complicated, but the qualitative orthodoxy has changed little since the pioneering work of Lotka, Volterra, and Gause—no two species can occupy the same niche. Stated in a more precise form, the higher the intensity of interspecific competition in an assemblage of species, the fewer the number of species that can coexist in perpetuity. We suggest that this orthodoxy results from “linear” thinking, and that if the classical equations are formulated more realistically with attendant nonlinearities, the orthodoxy breaks down and higher levels of competition may actually increase the likelihood that species will avoid competitive exclusion. Furthermore, this increased probability of coexistence at higher levels of competition is accompanied by characteristic dynamic patterns: (i) at lower levels of competition, after all extinction events have occurred, remaining species follow irregular chaotic patterns; (ii) at higher levels of competition, when most species coexist, all species are entrained in a single large limit cycle; (iii) the transient behavior appears to correspond to a special case of chaos, uniform phase chaotic amplitude.

It has become increasingly evident that nonlinear phenomena may play an important role in structuring ecosystems (1–3). Most modeling frameworks have come to the general conclusion that patterns of dynamic behavior become more complex as more components are added to the system (4–7), although the pattern of addition of the components may have a substantial impact on system behavior (8). This acknowledged complexity has not had substantial impact on certain classical ideas, which persist as generalities even though their realization is clouded by this complex behavior. One of these ideas is the notion of competitive exclusion. If two species overlap too much in their resource use, they cannot both persist indefinitely. This result was originally shown by Lotka and Volterra (refs. 9 and 10, see also ref. 11) and subsequently became something of a central organizing principle for community ecology (12, 13). Demonstrations of its failure when nonlinearities were added to theoretical models (14–16) did not seem to dampen enthusiasm for the basic paradigm.

Here we use the consumer/resource approach pioneered by MacArthur (17), with the added factor of functional response (18) to investigate the consequences of adding this key nonlinearity to the classical system in a multispecies context. We specifically investigate the consequences of increasing competitive pressure on the maintenance of the species richness of the system. Our expectation, from the classical theory, is that species coexistence should generally decline as overall competitive pressure is increased.

The Model

We presume that each consumer is partially specialized on a primary resource, but may use alternative resources at some level that is smaller than the use of its specialized resource. Thus, a system of many consumers and many resources may be thought of as a series of predators using a suite of weighted resources Θ ,

$$\Theta_i = R_i + \sum_{j \neq i} f_{ij} R_j$$

where the summation is over all $j \neq i$, R_i is the biomass of the i th resource, f_{ij} is the conversion factor that converts a unit of resource j into a unit of consumer i . In the present communication, we study in detail the specialized case where $f_{ij} = c$ (for $i \neq j$), where $0 < c < 1.0$. In other words, the resources used by a given consumer are a collection composed of a principle resource plus a series of other resources that are consumed in proportion to the consumption of the principle resource (i.e., c). Relaxing the assumptions of this special case does not seem to affect the qualitative generalizations.

If Θ_i represents the resources for the i th consumer, the dynamic equations can be written in standard Lotka–Volterra (with density dependence and type II functional response) form as,

$$\frac{dC_i}{dt} = \frac{a\Theta_i C_i}{1 + b\Theta_i} - mC_i \quad [1a]$$

$$\frac{dR_i}{dt} = r_i R_i (1 - R_i) - \frac{aR_i C_i}{1 + b\Theta_i} - \sum_{j \neq i} \frac{aR_i c C_j}{1 + b\Theta_j} \quad [1b]$$

where a is the rate of consumption, m is the mortality rate of the consumer, b is the parameter of the functional response, and r_i is the intrinsic rate of natural increase of the i th resource. This way of writing the functional response for multiple species is chosen as a direct extension of the form normally used for a single species, where, instead of a single resource generating the response, we use the “effective” resource (i.e., Θ), and employ a type II functional response (18). If b is set to zero, system 1 becomes equivalent to the extended Lotka–Volterra system as studied by many authors (e.g., refs. 14, 17, and 19) with simple density dependence—all solutions are simple focal point attractors and, assuming that $a < m$, extinction is impossible for any c (in the range 0–1), reflecting the well-known dictum that coexistence is realized whenever intraspecific competition is greater than interspecific.

However, if b is set sufficiently large that all uncoupled two-dimensional subsystems (any consumer/resource pair) exhibit limit-cycle behavior, a substantially different pattern is observed. For most parameter settings all species are maintained in the system, but both resource and consumer may become so small that their extinction from the system is virtually assured through a very small stochastic effect. To simulate this extinction force, we set the critical lower limit at which a population was regarded as extinct at 10^{-20} . Thus, on the one hand, the classic form of the equation (i.e., $b = 0$, with only a single consumer and a single resource) cannot generate extinctions as long as $m < a$. On the other hand, if functional response is included (i.e., $b > 0$), extinction is possible in the sense that oscillations come arbitrarily close to zero, even when the mortality rate is small relative to the consumption rate [extinction is inevitable in any

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Abbreviation: UPCA, uniform phase chaotic amplitudes.

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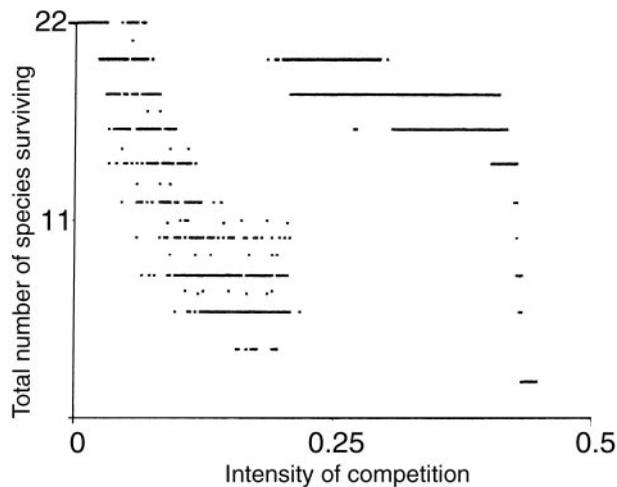


Fig. 1. Species remaining in community after 5,000 iterations as a function of the intensity of competition. Data based on three different initiation values of C_i and R_i . Parameter values, $a = 12$, $r = 1.1 + 0.01i$, $b = 5.5$, $m = 0.9$, with 10^{-20} the critical lower value below which populations were set to zero.

two dimensional subsystem if $m > a/(b + 1)$, but all simulations reported herein were with $m < a/(b + 1)$].

The coefficient c is a measure of competition among the consumers in the system. Thus, according to the classical ideas of competitive exclusion, we expect that as c increases consumers will begin to eliminate resources and then go extinct themselves. That is, competitive exclusion will eventually eliminate all but one pair of consumer/resources as the parameter c increases. This is the expectation from classical ecological theory.

Basic Model Behavior

We find that the pattern expected from classical ecological theory occurs, but only when competition is relatively weak. As long as competition intensity remains generally weak, when competition increases, species are eliminated from the system, as anticipated. This reduction in species number with increasing competitive intensity continues until only a few species remain. However, the pattern is different when competition intensity is generally strong. Consider the set of parameters, $a = 12$, $r_i = 1.1 + 0.01i$ (where i is the index of the i th resource), $b = 5.5$, $m = 0.9$ and allow i to range from 0 to 10 (i.e., a total of 22 species, 11 consumers and 11 resources, in the system). We numerically solved the system for 5,000 time steps for three different initiation points of the C_i and R_i (Fig. 1). As expected, the number of species coexisting declines with increasing competition when the intensity of competition is relatively low (i.e., from $c = 0$ to about $c = 0.19$). However, when the intensity of competition increases further (i.e., from about 0.19 to 0.3), almost all species are maintained in the system until competition increases yet further, when exclusion occurs again. Finally, at a coupling of about 0.43 or greater, the entire system collapses (Fig. 1).

In the range $0.03 < c < 0.19$, competitive exclusion removes some of the species, leaving the rest to coexist. The pattern whereby the species are removed is generally consistent, as illustrated in Fig. 2. The time series before the extinctions occur are, of course, transients. However, the transients illustrate a fundamentally chaotic pattern (20). These chaotic transients are also phase coordinated (21) and illustrate a pattern most recently referred to as uniform phase chaotic amplitudes (UPCA) (1), where the phases of the consumers are entrained on one another, but the amplitudes appear to form a chaotic pattern. The extinction illustrated in Fig. 2 is typical of the way in which

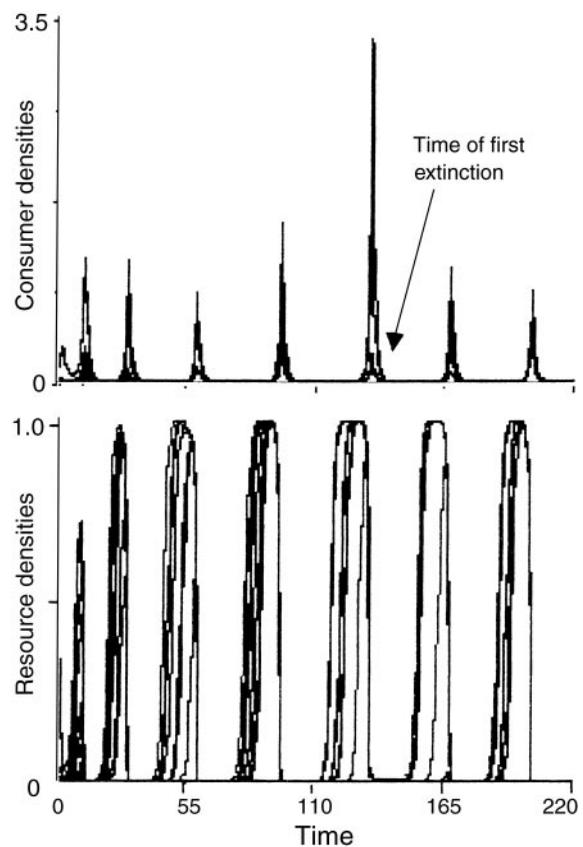


Fig. 2. Time series of all consumers and resources for the first 220 time steps. Note the dramatic flush of a single population of consumer just before the first extinction. Parameter values as in Fig. 1.

extinctions occur at the beginning of a time series, with a single consumer flushing and driving its resource to extinction (in the case of Fig. 2 the first species to go extinct is R_{10}). Subsequent extinctions may follow a different pattern, as illustrated in Fig. 3. Here, the phase coordination is temporarily lost, but the system remains in chaos (although is still in a transient stage), and rapidly readjusts to a phase coordinated pattern again after the two rapid extinctions.

After all transients have died out, the remaining species coexist in perpetuity (at least for 100,000 time steps), in a chaotic state with no apparent phase coordination, as illustrated by the four surviving species in Fig. 4. A sample phase portrait and a peak to peak return map are illustrated in Fig. 5, strongly suggesting chaos. Although the number of species that are driven to extinction increases with increasing competition over this range ($\approx 0.03 < c < 0.19$), the general behavior of the system is qualitatively similar to that shown in Figs. 2–4 for all other values of competition in that range. It is worth noting that we find many examples, in this range of parameter values, of more consumers than resources in the equilibrium state, a point of obvious ecological interest, and probably an extension of the behavior of the three-dimensional system studied by Armstrong and McGehee (15) and similar to the work of Huisman and Weissing (22, 23).

For $0.19 < c < 0.3$ almost all of the species coexist, apparently as a phase coordinated limit cycle (Fig. 6). It is worth noting that phase coordination is characteristic for both the chaotic transients before extinctions occur in the range of species loss ($0.03 < c < 0.19$) and for the attractor itself in the range where most species coexist ($\approx 0.19 < c < 0.38$). The difference is that all

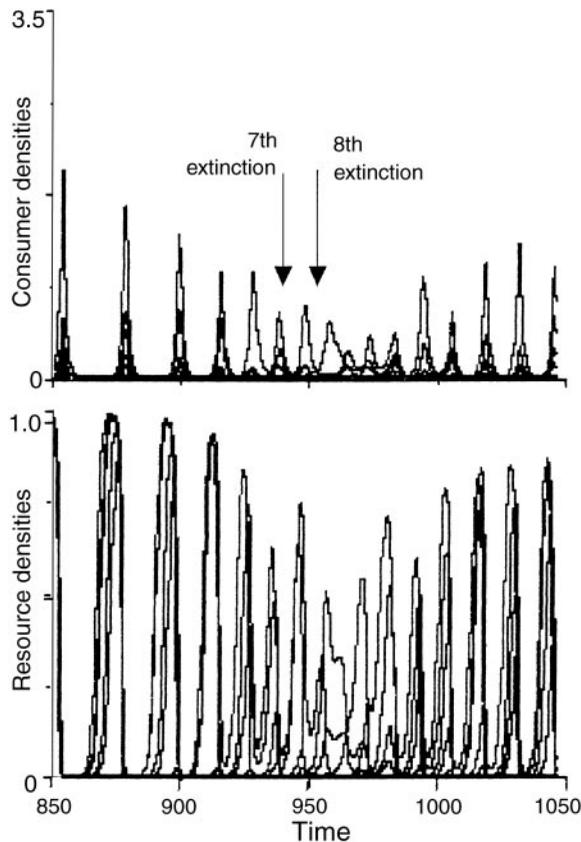


Fig. 3. Time series of all remaining consumers and resources during the time of the seventh and eighth extinction. Note how the dynamic pattern is distinct from the first extinctions (Fig. 2). At about the time of the extinction events the system loses its phase coherence for a short time, but gains it rapidly after the extinctions. Parameter values as in Fig. 1.

resources in the later range peak at their carrying capacity (1.0), whereas some of the resources never reach their carrying capacity in the former range (compare Fig. 2 with Fig. 6). The qualitative interpretation of this phenomenon seems related to the fact that resources in the range of species coexistence ($\approx 0.19 < c < 0.38$) all reach carrying capacity quickly (see Fig. 6). All of the resources thus are briefly maintained at their carrying capacity while the consumers display a sort of demographic lag before they peak simultaneously. Thus, in this zone (i.e., the zone of competition that leads to coexistence, which is $\approx 0.19 < c < 0.38$) the consumer pressure peaks after all resources have actually reached carrying capacity. In contrast, when in the species exclusion range ($\approx 0.03 < c < 0.19$), the point of maximum pressure from the consumers occurs when one or more of the resources has not yet reached its carrying capacity. The resources with lower than carrying capacity population densities can easily be driven to extinction by the combined pressure of the phase-coordinated consumers (see Fig. 2).

Finally, when competition becomes very strong ($\approx c > 0.38$) extinctions again occur as expected. But here, the surviving species exhibit a phase-coordinated limit cycle.

Model Behavior with Changing Consumption Rates

It is instructive to explore changes in overall behavior of the model with different values of the parameter a , which reflects the rate of predation (consumption). In the above simulations that rate was $a = 12$. With a much smaller predation rate ($a = 8$), the pattern is quite different, as shown in Fig. 7 *Top*. Increasing competition does little to force extinctions until relatively large

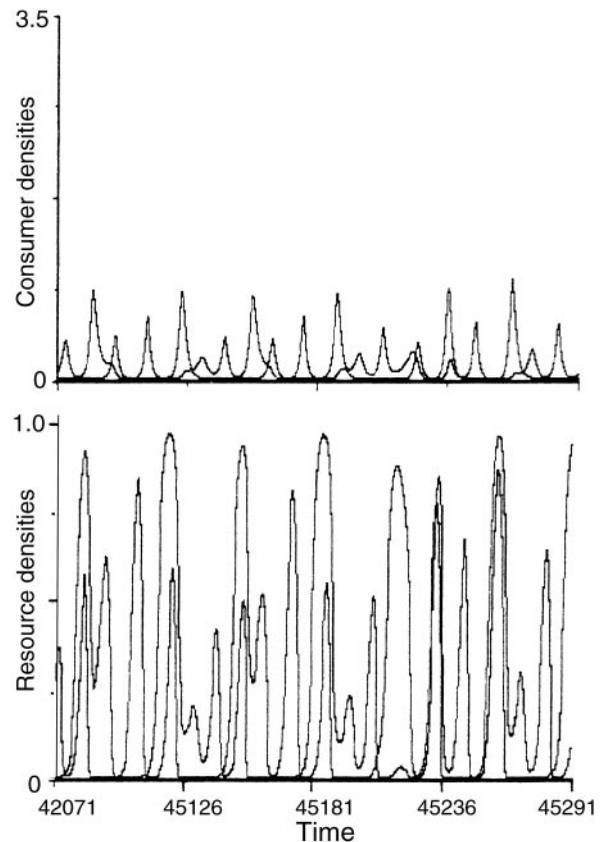


Fig. 4. Time series for remaining four species after 42,000 iterations. The system remains apparently chaotic, but the phase coordination is no longer evident as it was in the chaotic transient stage (Figs. 2 and 3). Parameter values as in Fig. 1.

values of competition, at which time there is rapid loss of species with small increases in competition. Throughout, in Fig. 7 *Top*, the solutions are phase coordinated limit cycles at the attractor and UPCA chaotic transients leading up to the attractor. With a much larger predation rate ($a = 25$), the pattern is again qualitatively quite different (Fig. 7 *Bottom*), with a rapid loss of species with increasing competition, when competition is relatively low. In this case, all attractors are chaotic (not phase coordinated), but again the chaotic transients leading to the attractors are UPCA.

In the particular case of a phase-coordinated limit cycle, the model can be approached somewhat more analytically because there is full synchrony of all of the populations. Given the synchrony, we can approximate by presuming $C_i = C_j$ and $R_i = R_j$ for all i and j . Then, Eqs. 1a and 1b become,

$$\frac{dC}{dt} = \frac{\alpha CR}{\beta + R} - mC \quad [2a]$$

$$\frac{dR}{dt} = rR(1 - R) - \frac{\alpha RC}{\beta + R} \quad [2b]$$

where N is the total number of pairs of species in the system, and

$$\alpha = \frac{a}{b}$$

$$\beta = \frac{1}{b[1 + c(N - 1)]}$$

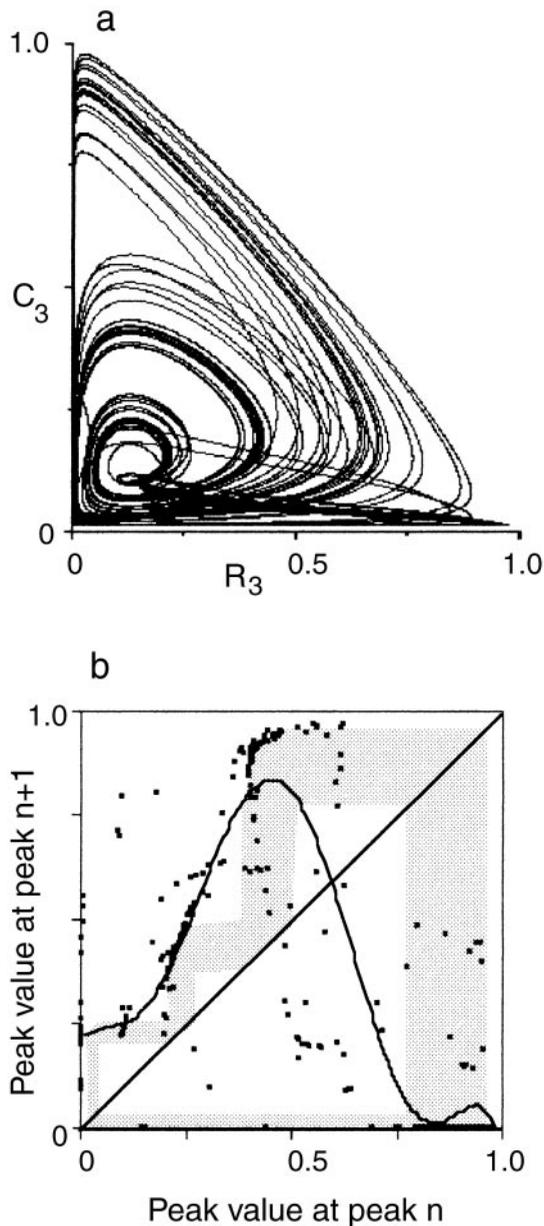


Fig. 5. Data from Fig. 4 plotted as **a.** phase portrait of C_3 and R_3 and **b.** as peak-to-peak map of C_3 . Fitted curve is a 6° polynomial fit. Note that the eigenvalue is < -1 (i.e., the slope of the fitted curve at the point where it crosses the 45° line). Other polynomial fits (degree 3–7) all gave eigenvalues < -1 . The shaded region illustrates qualitatively where most of the trajectories are located for this attractor.

These equations are, in form, the classic Lotka–Volterra equations with density dependence and a type II functional response. The isoclines of this system are diagrammed in Fig. 8 for various situations. The peak of the prey isocline occurs at $R = (1 - \beta)/2$ and the predator isocline occurs at $R = \beta m / (\alpha - m)$. A glance at Fig. 8 reveals the particular analytical formulations leading to each of the pictured cases. These are:

Cases **a** and **b**:

$$\frac{1 - \beta}{2} > \frac{\beta m}{\alpha - m}$$

Case **c**:

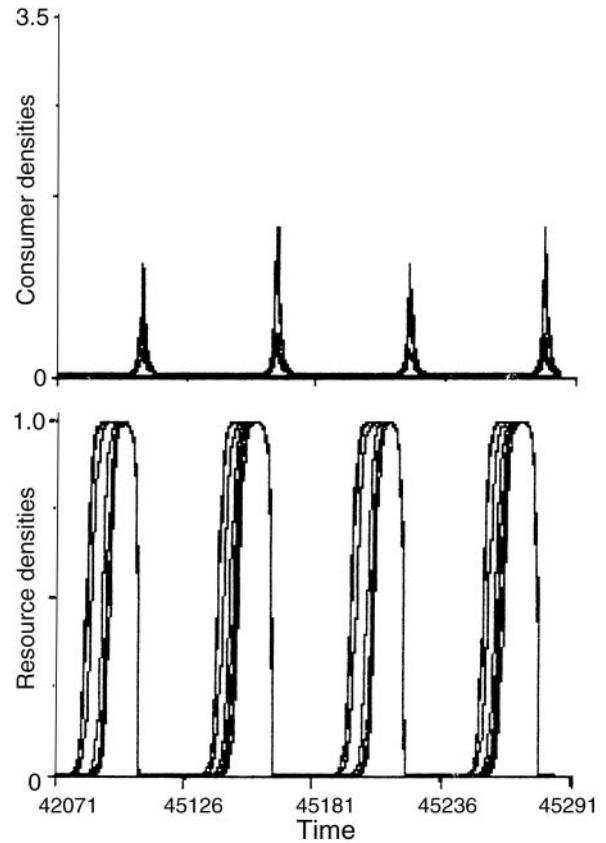


Fig. 6. Phase coordinated limit cycle in the region of coexistence of 20 species.

$$\frac{1 - \beta}{2} < \frac{\beta m}{\alpha - m} < 1.0$$

Case **d**:

$$\frac{\beta m}{\alpha - m} > 1.0$$

From these relationships it is a simple matter to demonstrate that as the predation rate (α) increases, the predator isocline moves to the left (i.e., we move from case **d** toward case **a**), whereas as the number of species and/or the competition coefficient (N and/or c) increases the predator isocline moves to the right (i.e., we move from case **a** to case **d**), because both c and N are negatively associated with β . With this approximate model (recall it is only an approximate model when there is complete synchrony of all populations) we can speculate on the origin of the behaviors discussed above. For small predation rate (small a) we are constrained to cases **c** and **d** of Fig. 8 (small “ a ” meaning that the predator isocline will be at a relatively large value of R) and as competition increases we expect the isocline to move from case **c** to case **d**. Case **d** is such that some species has to go extinct, which reduces the value of N and thus causes the isocline to jump to the left (toward the case **c**). This process continues such that the value of C and R tend to be buffered away from very small values (compare cases **c** and **d** in Fig. 8). This pattern is exactly what is observed in the behavior of the actual model (Fig. 7 *Top*).

For large predation rate (large a) we are constrained to cases **a** and **b** of Fig. 8 (large “ a ” meaning that the predator isocline will be at a relatively small value of R) and, as competition increases we expect the prey isocline to move from case **a** to case

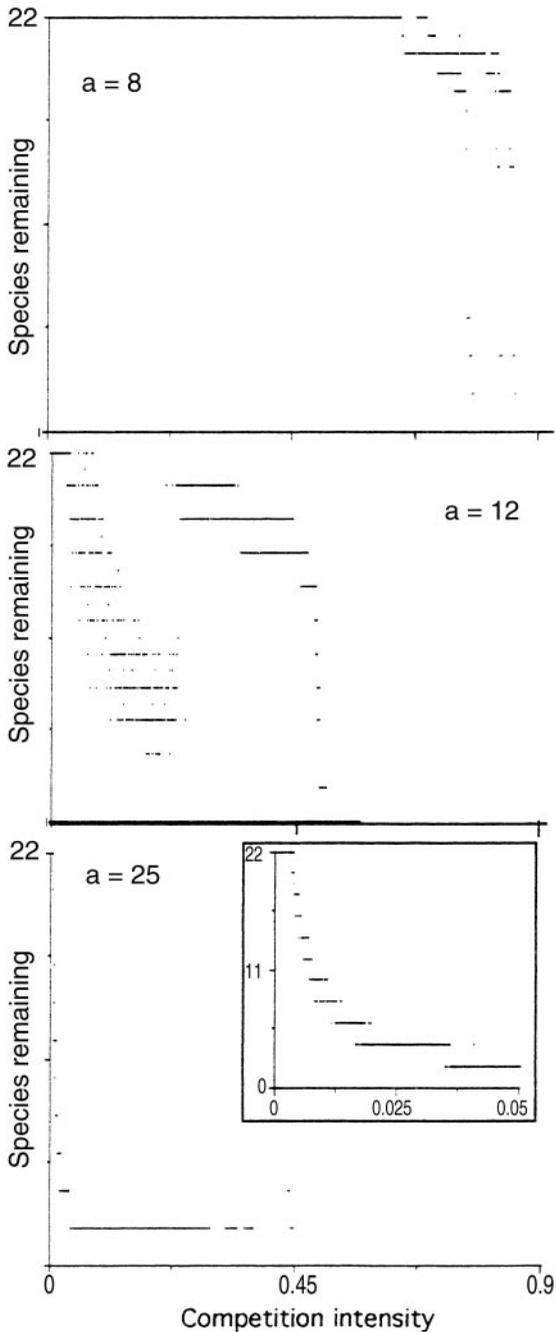


Fig. 7. Species remaining as a function of competition intensity at three different values of a (other parameters the same as in Fig. 1). For small a ($a = 8$), all species are maintained in the system until competition intensity becomes very large, at which time competitive exclusion rapidly excludes species. For intermediate a ($a = 12$) the pattern as described earlier (see Fig. 1) obtains, with more competitive exclusion for increasing competition up to a point, after which coexistence of almost all species is seen (with the pattern of phase coordinated limit cycle; see Fig. 6). For larger values of a ($a = 25$) there is rapid extinction as competitive intensity increases, and no apparent phase of coexistence through phase coordination. *Inset* is a closer view of coexistence patterns at lower values of c .

b. But as species are excluded (and thus N decreases), we expect to move from case **b** to case **a**, meaning that the oscillations would be expected to become less severe. This change is because the predator isocline crosses the prey isocline where the latter is less steep, meaning the oscillations would be of lower amplitude

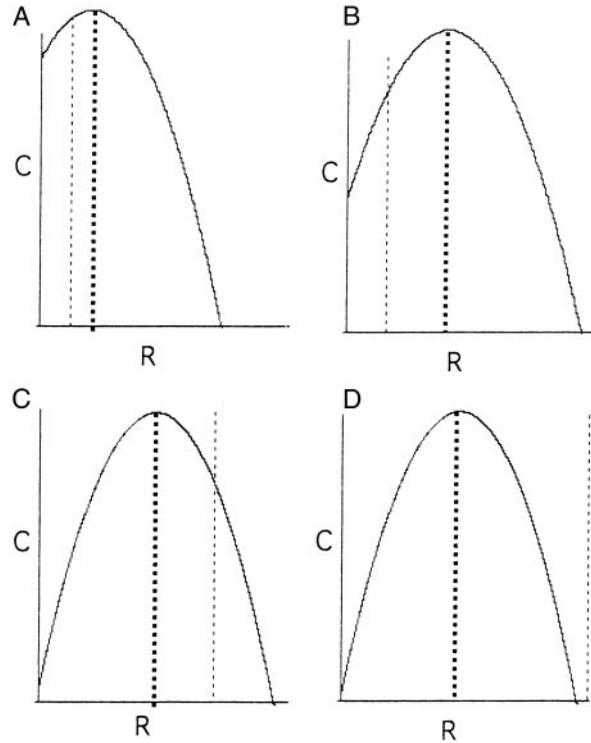


Fig. 8. Diagrammatic illustration of extinction patterns based on approximate model (Eqs. 2a and 2b) with full nonchaotic phase coordination. Heavy dashed line shows the peak of the prey isocline and light dashed line is the predator isocline.

than if the prey isocline, at the point of intersection, were more steep. Thus the system is less likely to generate extinctions because of large oscillations.

The overall pattern thus seems to be one in which there are two forms of competitive exclusion. First, the “effective” predator isocline (see Fig. 8) may be to the right of the peak of the prey isocline. This essentially means that the predation rate is relatively small, which means that the level of competition can be relatively large before competitive exclusion is generated, and furthermore the exclusion is a result of overall predator pressure directly on resources. This is the case that likely produces the pattern in Fig. 7 *Top*. Second, the “effective” predator isocline (see Fig. 8) may be to the left of the peak of the prey isocline. This means that the predation rate is relatively high, which means that the level of competition that generates competitive exclusion is relatively small, and furthermore the exclusion is a result of excessively large oscillations which result from a UPCA pattern effectively coordinating the predation pressure of a number of predators. This is the case that likely produces the pattern in Fig. 7 *Bottom*.

Thus, in this very approximate special case (Eqs. 2a and 2b), we can see two extreme situations, one in which consumption rates are high and thus little niche overlap (competition) is allowable before exclusion sets in, and one in which consumption rates are low and thus more niche overlap is allowable before exclusion sets in. It is in the former case that chaotic attractors are evident once the transients have died down (i.e., once all exclusions have occurred).

Discussion

Although the expectations from classical ecological theory are reflected in the extended consumer/resource system (Eqs. 1a and 1b), for some parameter values we obtain the surprising

result that increased competition results in more species coexistence (Fig. 1). The exact ecological mechanisms as to why this pattern occurs are not transparent, but have to do with the phase coordination that occurs at this parameter combination, perhaps in a similar manner to the coexistence of two consumers on a single resource as reported elsewhere (15).

However, at a larger scale (i.e., Fig. 7), this curious pattern seems to make more ecological sense. The overall qualitative behavior illustrated in Fig. 7 concords with ecological intuition about interspecific competition. If the rate of utilization of resources (predation rate) is very small (Fig. 7 *Top*), when competitors are added to the system, as long as competition is not too severe, nothing is likely to happen. Only when the competition is strong does the expected exclusion occur. At the other extreme, with the rate of utilization of resources large (Fig. 7 *Bottom*), the addition of even the weakest competition stresses the whole system and exclusion follows rapidly. Intermediate between these two cases is the case analyzed in this paper (Figs. 1 and 7 *Middle*), where both patterns occur, depending on the intensity of competition, and where the counterintuitive result of more species at higher rates of competition is observed.

What remains enigmatic is the dramatic difference in the behavior of the system after all extinctions have occurred (i.e., when the attractor is reached). When the resource utilization rates are high (Fig. 7 *Bottom*), the attractors are all nonphase coordinated chaotic (similar to previous work, refs. 22 and 23). When the resource utilization rates are low (Fig. 7 *Top*), the attractors are all phase coordinated limit cycles, though they are approached with chaotic transients.

The relationship between these results and recent controversies over top-down versus bottom-up control in ecosystems is, we think, obvious. A system with generally small values of the predation rate (as in Fig. 7 *Top*) is similar to one in which the dominant form of control is bottom-up, whereas one with generally large values of the predation rate (as in Fig. 7 *Bottom*) is similar to one in which the dominant form of control is top-down. This observation suggests, then, that the ultimate behavior of the system will be distinctly different for cases of top-down control versus cases of bottom-up control, and furthermore implies that systems intermediate between top-down

and bottom-up may be those in which we expect the unusual pattern of increased competition resulting in higher species diversity. This speculation of course refers to control over the resource, not the consumer.

In addition to Armstrong and McGhee (15), the recent work of Huisman and Weissing (22, 23) is relevant to the present study. Although they use a different set of equations (the resources are not self-replicating and only the limiting resource controls the consumer's growth), some of their conclusions are related to our main point, and we suspect the same biological phenomena apply. In particular, they note that the coexistence of several consumers on a lesser number of resources is conditioned by competition between two competing cycles (23). Their system effectively oscillates irregularly between these two cycles, a qualitative explanation of the chaotic pattern. At distinct parameter settings this pattern breaks down to two alternative cycles with chaotic transients leading to each, with fractally interdigitating basins of attraction. Their emphasis is on the unpredictability of winners in competition, which is implicitly similar to the results herein. Our emphasis on the particular fact that more species can coexist when competition intensity is higher is different, but likely because of the same or similar ecological forces. In the zones of chaos, our model illustrates similar oscillatory dynamics as is evident in Fig. 5. Although we did not search for alternative attractors or fractal basins, based on Huisman and Weissing's work (23), we suspect they may exist.

Finally, it is tempting to speculate that the pattern shown in Fig. 7 *Middle* is the most likely pattern in nature. If resource utilization rates are generally low, there will be a tendency for consumers with higher rates of utilization to enter the community. On the other hand, if resource utilization rates are generally high, there will be a tendency for species to overexploit their resources and go extinct. This dynamic implies that communities might be assembled, on average, in a state of intermediate resource utilization rates (Fig. 7 *Middle*).

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