

SUPPLEMENT

Justification of the logistic predator growth term

The model of the text (box 1) has a logistic growth term for alternative prey. A predator with dynamics that are slow relative to those of a self-limited prey will itself appear self-limited according to the logistic equation, justifying the use of the logistic here to represent the effects of nonfocal prey species on the predator. This fact follows from the technique used by MacArthur⁶ to derive Lotka-Volterra competition equations from his consumer-resource equations, under the assumption that resource dynamics are fast relative to those of the consumers. See the next section for explicit application of this technique.

Justification for the density-dependent interaction coefficients, α_{ij} and α_{jj} .

Equating the resource and predator equations (box 1) to 0 leads to formulae for R_i and P_m in terms of the N_j . Substituting these formulae into the focal species equations leads to the following differential equations for the focal species:

$$\frac{1}{N_j} \frac{dN_j}{dt} = r_j \left(1 - \sum_k \alpha_{jk} N_k \right), \quad (\text{S1})$$

where $\alpha_{jk} = \rho s_k / \kappa_j$, and $r_j = \kappa_j s_j$, with ρ calculated for the species pair, j, k . According to this differential equation, α_{jk} defines the interspecific density dependence of species j on species k , except when $k = j$, when it is intraspecific density dependence. However, this equation is not fully justified under most circumstances that we have in mind. First consider a case where it would be justified. This would occur in the case where the dynamics of both the resources and the predators were fast relative to the focal species. Thus, the N_j would behave essentially as constants in the predator and resource equations, and so predators and resources would converge on equilibria as functions of the N_j , justifying substituting these equilibrium values into the focal species equations. The predators in that case would need to be parasitic or disease organisms rather than species with similar or longer generation times than the focal species. In other cases, equations (S1) are not generally correct, but do give the correct results in a number of situations. The most general situation is when focal species dynamics are temporarily suspended. Resources and predators again converge on equilibria as functions of focal species. Focal species growth at that time is then given by (S1). Most important for considerations of species coexistence, however, equations (S1) give the correct equilibrium relationships for resident species, and the correct invasion rates for invaders, regardless of timescale assumptions for resource, focal and predator species. In the two-species case, we ask if species i (the invader) can increase from low density in the presence of species j , which has converged on equilibrium. Equations (S1) show that the equilibrium density is $1/\alpha_{jj}$. The invasion rate of species i is then $r_j(1 - \alpha_{ij}/\alpha_{jj})$, which means for invasion, $\alpha_{ij}/\alpha_{jj} < 1$.

When predators do not have alternative prey

For the case where predators do not have alternative prey outside the focal species, the term $r_m^P (1 - \alpha_m^P P_m)$ for the predator in equations (3) is replaced simply by $-d_m$, where d_m is the prey maintenance requirement for predator m . To define the relative predation rates θ_{ij} , we first define the predation rate relative to sensitivity to competition. This is the attack rate a_{jm} divided by a measure of sensitivity to competition for species j — the joint sensitivity measure of box 1

without the predation terms^{9, appendix D} — and equals

$$a'_{jm} = \frac{a_{jm}}{\sqrt{\left(\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} \right)}}. \quad (\text{S2})$$

Then $\theta_{ij} = a'_{ij} / a'_{jj}$, where the predators are given the same subscript as the prey species supporting them.

In this case, each of the focal species, when present alone, can support just one predator, and provided the predators do differ in their parameters, this predator would normally be unique to the prey species among the pool of predators that might potentially be present¹⁰. When both focal species are present, two predators might be supported if these predators depended most heavily on different prey species. The focal coexistence conditions now become

$$\rho_1 < \frac{\kappa_1^R}{\kappa_2^R} < \frac{1}{\rho_2}, \quad (\text{S3})$$

where the fitnesses κ reflecting predation and competition jointly are now replaced by κ^R , which means fitness based on resources alone, not accounting for predation. Predation is accounted for fully in the measures ρ_i , which differ between species, and depend on three quantities: ρ^R , resource overlap; the relative predation, θ_{ij} , on focal species i , compared with focal species j , by the predator supported by focal species j ; and Δ_j , the fractional depression of the equilibrium density of focal species j by the predator that it supports². Thus,

$$\rho_i = \rho^R (1 - \Delta_j) + \theta_{ij} \Delta_j. \quad (\text{S4})$$

In this formula, when competition is dominant, Δ_j is near zero, ρ_i is near ρ^R , and the outcome of focal species interactions reduces to the situation without predation, giving coexistence or exclusion essentially according to conditions (2) without predation. On the other hand, as predation more effectively depresses prey, ρ_i moves toward θ_{ij} , and gives control of the outcome to predation. In the limit, the absence of predator partitioning between prey, $\theta_{12} = 1/\theta_{21}$, which ensures exclusion, but with predator partitioning, the focal species can coexist, for then both θ_{12} and θ_{21} can be less than 1. Intermediate values of Δ_j mean again that the outcome is joint between predation and competition. Thus, the full essence of the conclusions of the discussed in the text are upheld.

When resources may go extinct

In deriving the coexistence diagram in the text, the assumption is made that resource species do not go extinct as the circumstances change. However, resource extinction might occur if focal species have maintenance requirements μ that are too low¹¹. The work of Abrams¹¹ emphasizes that the ρ values will not accurately predict coexistence from the formulae given here under these circumstances. There is a critical question as to how this set of resource species is defined. An unrestricted set of resource species makes no sense. No difficulties arise when resource species are restricted to only those that persist regardless of which focal species are present. Should some resources persist in the presence of one focal species, but not with the other, then equation (2) of the text would not hold, but the fundamental condition that expression (1) be greater than 1 for exclusion would remain correct provided that each of the quantities used in the formula were

calculated for those resources that are present when focal species j is in the resident state (i.e. present without species i). Thus, our key analysis of how the niche overlap measure changes with the strengths of the various feedback loops, in particular, the relative strengths of predation and competition, continues to be relevant to this question of exclusion. Thus, fundamental conclusions on the nature of the competition-predation interaction remain valid in the context of the inverse of coexistence, viz how species are excluded from a community. In the usual case where the failure of each species to exclude the other means they coexist, conclusions about coexistence remain intact also with the additional complication that ρ must be analyzed separately for each resident state.