The interaction between predation and competition

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Competition and predation are the most heavily investigated species interactions in ecology, dominating studies of species diversity maintenance. However, these two interactions are most commonly viewed highly asymmetrically. Competition for resources is seen as the primary interaction limiting diversity, with predation modifying what competition does[1], although theoretical models have long supported diverse views[1–5]. Here we show, using a comprehensive three-trophic-level model, that competition and predation should be viewed symmetrically: these two interactions are equally able to either limit or promote diversity. Diversity maintenance requires within-species density feedback loops to be stronger than between-species feedback loops. We quantify the contributions of predation and competition to these loops in a simple, interpretable form, showing their equivalent potential to strengthen or weaken diversity maintenance. Moreover, we show that competition and predation can undermine each other, with the tendency of the stronger interaction to promote or limit diversity prevailing. The past failure to appreciate the symmetrical effects and interactions of competition and predation has unduly restricted diversity maintenance studies. A multitrophic perspective should be adopted to examine a greater variety of possible effects of predation than generally considered in the past. Conservation and management strategies need to be much more concerned with the implications of changes in the strengths of trophic interactions.

We focus on the middle trophic level in a three-trophic-level system (Fig. 1), and address how both competition for resources (the trophic level below) and predation (the trophic level above) affect species coexistence in the middle trophic level. Several decades ago, MacArthur[6] formulated the definitive model for resource competition in the Lotka–Volterra form. This model leads to a measure of niche overlap, ρ, between any pair of species[7], and also measures κ_j (originally k_j)[8] defining the fitness of any species, j. Coexistence occurs in two-species Lotka–Volterra competition if the competitive effect that a species has on the other species (interspecific competition, α_{ij}) is less than the competitive effect that it has on itself (intraspecific competition, α_{jj})[8]. Notably, the ratio of these competitive effects can be expressed in terms of fitnesses and niche overlap[8]:

$$\frac{\alpha_{ij}}{\alpha_{jj}} = \frac{\kappa_j}{\kappa_i}\rho \qquad (1)$$

Species j dominates over species i, and excludes it from the system, if expression (1) is greater than one. When niche overlap is complete, ρ equals one and the species with the larger fitness excludes the other. Otherwise, ρ is less than one and the relative fitness (κ_j/κ_i) must be discounted by ρ (how much the species interact) to see if exclusion occurs (that is, to see if interspecific competition exceeds intraspecific competition). Neither species can exclude the other when expression (1) is less than one for both $(i,j) = (1,2)$ and $(i,j) = (2,1)$, a condition equivalent to[9]

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho} \qquad (2)$$

When condition (2) holds, the species coexist. Thus, niche overlap, ρ, constrains the fitness differences compatible with coexistence. Low overlap (ρ near to zero) means that the species can differ greatly in fitness and still coexist with each other, whereas large overlap (ρ near to one) means fitnesses must be nearly equal for coexistence to occur (Fig. 2).

The new finding with a three-trophic-level Lotka–Volterra system is that these same conditions continue to hold, including predation in the same terms as resource competition (Box 1). To achieve this outcome, however, a new assumption is necessary: the focal species in the middle trophic level must not be the sole food source for the predators. Prey outside the focal group prevent the predators from becoming extinct when the focal species are at zero density. Although this is not the usual assumption made in models, it is not an unreasonable case to consider: often the focal group is not the entirety of a predator's prey, and predators often range more widely than their prey so that the predator is not solely supported by the region in which the focal group resides[10]. When this assumption is removed, the main conclusions here are retained (see Supplementary Information). We make a similar assumption with respect to resource competition: focal species must not drive their resources to extinction. The key conclusions are retained when this assumption is violated (Supplementary Information), but ρ is no longer a constant, complicating coexistence conditions[11].

In the original MacArthur model, fitness (κ_j) is proportional to the net excess resource intake of a species over its maintenance requirements[9]. With three trophic levels, subtracted from this net excess is the mortality due to predation when predators are at their equilibrium densities in the absence of the focal species. These new fitnesses, κ_j, are maximal quantities representing the abilities of focal species to gather resources and avoid predation. These quantities have the
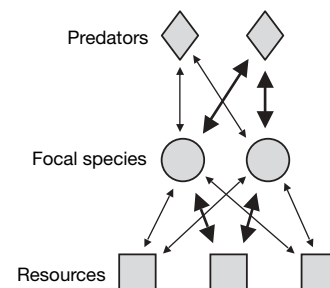
Figure 1 | Simplified three-trophic-level food web. The heavy lines highlight linkages between focal species through a shared resource and a shared predator. Double-headed arrows indicate that linkages are bidirectional, creating feedback loops. For example, high focal density of a species increases predator density, which then feeds back to greater predation on both the same focal species and the other focal species (apparent competition). Similarly, feedback loops through resources create resource competition. Each bidirectional linkage by itself is an intraspecific feedback loop for a focal species. Linkages between focal species through a shared predator or shared resource are interspecific feedback loops.

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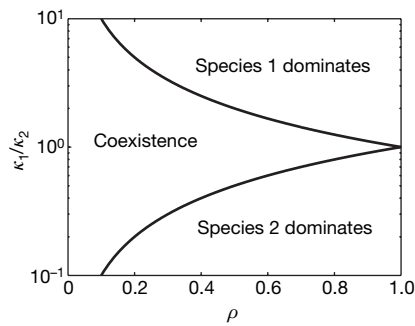
Figure 2 | Coexistence and exclusion regions. Two species coexist when the niche overlap, ρ, and fitness ratio, κ_1/κ_2, lie within the central wedge, in which condition (2) is satisfied. Exclusion occurs outside this wedge. The log scale for the κ_1/κ_2-axis preserves symmetry.

essential property of predicting the winning species in cases in which there is no resource or predator partitioning (that is, in situations in which there is no possibility of coexistence[8,12]).

The quantities α_{jj} and α_{ij} now represent the total strengths of intraspecific and interspecific density dependence, combining both competition and predation. Thus, α_{jj} measures the combined strengths of the feedback loops from species j to species j through both resources and predators, whereas α_{ij} measures the combined strengths of all such loops from species j to species i (Fig. 1). The fact that feedback loops through predators lead to mutually negative indirect interactions between prey, analogous to competition, is the important insight of Holt[2,13], who coined the term "apparent competition" for this outcome (Fig. 1). The simple idea that competitive coexistence requires intraspecific competition to exceed interspecific competition is now generalized to the idea that intraspecific density dependence must exceed interspecific density dependence. The critical ratio of interspecific density dependence to intraspecific density dependence is again given by expression (1), showing that the ability of a species to exclude another depends simply and intuitively on its relative fitness, κ_j/κ_i, discounted by niche overlap, ρ. Niches now involve how the species relate to their predators in addition to how they relate to their resources (Fig. 3). Niche overlap once again determines the breadth of the opportunities for coexistence according to condition (2), illustrated in Fig. 2. This condition is derived from the requirement that $(\kappa_j /\kappa_i)\rho$ must always be less than one for coexistence (that is, α_{jj} should always be greater than α_{ij}).

The measures α_{jj}, α_{ij} and ρ depend on each feedback loop according to its strength. This fact is intuitive but of profound consequence: competition and predation can each undermine the predicted effects of the other (either coexistence or exclusion) depending on which is stronger. Niche overlap jointly represents the overlap between species in their patterns of resource dependence and their patterns of predator susceptibility (Fig. 3), but the dependence of ρ on predators and resources reflects the tendencies of these trophic levels to dominate focal species interactions. If resources strongly dominate, ρ approaches the limiting value ρ^R based on resource overlap alone. If predators strongly dominate, ρ approaches the predator overlap value ρ^P. Which of these dominates depends on the relative strengths of the density-dependent feedback loops through resources and through predators (that is, on which of these more strongly regulates the densities of the focal species). A complex of factors determine which feedback loops are strongest, but, simply put, resource loops are strong if resources regenerate slowly, and predation loops are strong if predators are primarily controlled by prey in the focal group (Box 1).

Whether coexistence or exclusion is promoted is determined by whether partitioning of the dominant interaction occurs—be that competition or predation. As the relative intensity of predation and competition is changed, niche overlap, ρ, changes as depicted in Fig. 4. Cases in which there is resource partitioning, but no predator

Box 1 | Model and analysis

Lotka–Volterra equations for three trophic levels (focal species, N_j, resources, R_l, and predators, P_m) are

$$\frac{1}{N_j}\frac{dN_j}{dt} = \sum_l c_{jl}v_l R_l - \sum_m a_{jm}P_m - \mu_j$$

$$\frac{1}{R_l}\frac{dR_l}{dt} = r_l^R\left(1-\alpha_l^R R_l\right) - \sum_j N_j c_{jl}$$ (3)

$$\frac{1}{P_m}\frac{dP_m}{dt} = r_m^P\left(1-\alpha_m^P P_m\right) + \sum_j w N_j a_{jm}$$

with parameters c_{jl} (consumption of resource l by focal species j), a_{jm} (attack rate of focal species j by predator m), r_l^R and r_m^P (predator and resource intrinsic rates of increase), α_l^R and α_m^P (resource and predator intraspecific competition—reciprocals of carrying capacities), v_l (unit value of resource l), μ_j (resource maintenance requirement of focal species j), and w (value of a unit of prey to a predator).

For any pair, j and k, of focal species, methods previously described[7] give the overlap measure

$$\rho=\frac{\sum_l \dfrac{c_{jl}v_l c_{kl}}{r_l^R \alpha_l^R} + \sum_m \dfrac{a_{jm}w a_{km}}{r_m^P \alpha_m^P}}{\sqrt{\left(\sum_l \dfrac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} + \sum_m \dfrac{a_{jm}^2 w}{r_m^P \alpha_m^P}\right)\left(\sum_l \dfrac{c_{kl}^2 v_l}{r_l^R \alpha_l^R} + \sum_m \dfrac{a_{km}^2 w}{r_m^P \alpha_m^P}\right)}}$$ (4)

To obtain ρ^R and ρ^P, the predator and resource terms, respectively, are set to zero.

Joint sensitivity to predation and competition is measured as

$$s_j = \sqrt{\left(\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} + \sum_m \frac{a_{jm}^2 w}{r_m^P \alpha_m^P}\right)}$$ (5)

following Appendix D of ref. 9.

Fitness measures,

$$\kappa_j = \frac{1}{s_j}\left(\sum_l \frac{c_{jl}v_l}{\alpha_l^R} - \sum_m \frac{a_{jm}}{\alpha_m^P} - \mu_j\right)$$ (6)

are focal species per capita growth rates at zero densities of all focal species, divided by s_j (Appendix D of ref. 9).

Intraspecific and interspecific coefficients of density dependence are

$$\alpha_{jj} = s_j/\kappa_j \text{ and } \alpha_{ij} = \rho s_j/\kappa_i$$ (7)

as explained in Supplementary Information. The invasibility criterion for coexistence of two species[8] leads to condition (2). See Supplementary Information for details.

Competition is strong if resources regenerate slowly (that is, if r_l^R is small). Density dependence due to predation is strong if predators depend only weakly on prey outside the focal group (that is, if r_m^P is small). The importance of predation or competition is thus inverse to r_l^R or r_m^P. Figure 4 represents a common linear increase from left to right in each $1/r_m^P$ with a corresponding linear decrease in each $1/r_l^R$.

partitioning (Fig. 3b), make ρ an increasing function of relative predation intensity, having a low value when competition is dominant, increasing to a value of one when predation dominates (Fig. 4, curve b). Thus, broad opportunities for coexistence in terms of potentially broad differences in κ values are permitted when competition dominates, but not when predation dominates. Notably, the opposite pattern of predator partitioning without resource partitioning (Fig. 3c) provides the strongest opportunities for coexistence (lowest ρ) under dominance by predation (Fig. 4, curve c). When there is no partitioning at either level, coexistence is still possible if there is a trade-off across species between resource sensitivity and predation sensitivity (Fig. 3d). In this case, opportunities for coexistence arise for a broad region of intermediate values of relative competition and predation intensities (Fig. 4, curve d). However, in the absence of the trade-off between competition and predation, ρ is instead one for all predation and competition intensities (Fig. 4, curve e).
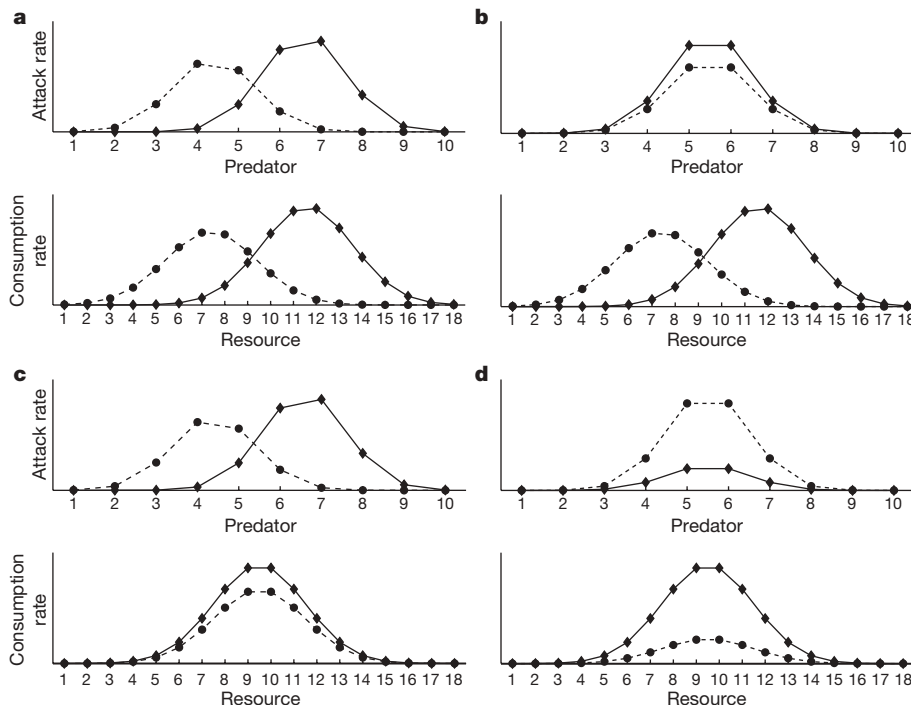
Figure 3 | Niches of two focal species in terms of resources and predators. The *x* axis labels identify predator and resource species. The filled circles and filled diamonds define focal species. The *y* axes are the rates a_{jm} and c_{jl} of Box 1. **a**, Niches separated by resource consumption ($\rho^R = 0.33$) and predation ($\rho^P = 0.31$). **b**, N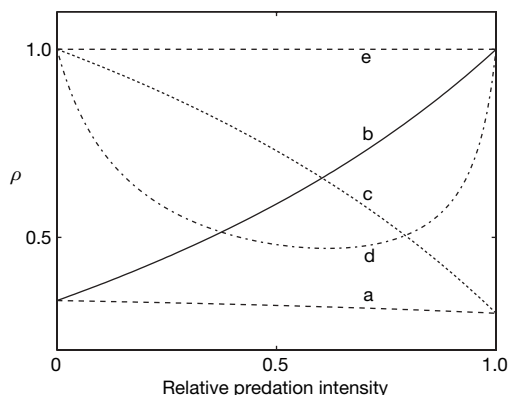iches separated by resources ($\rho^R = 0.33$), but not predators ($\rho^P = 1$). **c**, Niches separated by predators ($\rho^P = 0.31$), but not resources ($\rho^R = 1$). **d**, No separate predator or resource niche differences ($\rho^R = \rho^P = 1$). In **a**–**c**, overall niche overlap, ρ, is intermediate between ρ^R and ρ^P. In **d**, ρ is less than 1 whenever neither predators nor resources dominate focal species interactions.

These results show that predation and resource competition have the potential to affect diversity in the same way, and each may either promote coexistence or promote exclusion. Each promotes exclusion when it does not differentiate between species; conversely, each promotes coexistence when it does differentiate between species. Moreover, predation and competition interact with each other. If one is much stronger than the other, the predictions of the stronger prevail. When present together, both differentiating between species, coexistence is promoted more strongly by their joint action. When only one process differentiates between species, the joint outcome is less coexistence than when only the differentiating process is present. When of similar strength, predation and competition can jointly

Figure 4 | Niche overlap as a function of relative predation intensity. Changes in niche overlap as the intensity of density dependence owing to predation is varied relative to the intensity of competition. Curves correspond to panels in Fig. 3, with the extra curve e for the case in which there is no partitioning of resources or predators and no trade-off between susceptibility to predation and sensitivity to resources (like Fig. 3d but with the symbols switched in the attack-rate graph to match the consumption-rate graph).

promote coexistence through a trade-off between competition and predation. In this last way, the predation–competition interaction differentiates between species, and creates an effective mechanism where previously there was none.

These outcomes are not restricted to the two-focal species illustrations given here, as multispecies findings for MacArthur's model[14] allow their extension. This new understanding suggests a classification of coexistence mechanisms as competition-based (when intraspecific competition exceeds interspecific competition), predation-based (when intraspecific density feedback through predators is stronger than interspecific density feedback through predators) or jointly based on competition and predation[4,15]. In his classic work on diversity maintenance, Hutchinson[16] focused coexistence studies within trophic levels, spawning an industry in the study of interspecific competition. The fact that predation may function in a very similar way in the maintenance of diversity within trophic levels means that studies of predation–competition interactions should move beyond the notion that competition is the primary interaction limiting diversity, with predation modifying what competition does. We echo the call by Holt a quarter of a century ago to treat predation and competition even-handedly[2]. The absence of an accurate sense of theoretical predictions for the role of predation in diversity maintenance has led to much confusion at the interface between theoretical and empirical work[1]. Better targeted empirical investigations should be possible with the new understanding from this and related, although more complex, work for non-Lotka–Volterra systems[1,15,17].

Maintaining predators is of increasing concern in conservation and management strategies[18–21]. Humans have had major effects on the trophic structure of terrestrial, freshwater and marine ecosystems, with implications that are yet to be fully realized[22–24]. The individual species approach to conservation often enshrined in law, such as the US Endangered Species Act, focuses on minimal populations for a species' own conservation without considering its role in an ecosystem. Our findings emphasize the profound effects that one trophic level can have on diversity maintenance in other trophic

levels. They argue for conservation strategies that seek to maintain trophic structure and the strengths of trophic links. In particular, they reinforce concerns that the decimation of carnivores that is occurring in most environments on the planet may have major impacts on diversity maintenance in lower trophic levels[18,23,24].

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Author Contributions P.C. and J.J.K. jointly developed the model. P.C. derived the coexistence conditions and wrote the first draft of the manuscript. P.C. and J.J.K. jointly prepared the figures and all revisions of the manuscript.

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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 MacArthur[6] 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_l 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:

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

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 $r_m^P\left(1 - \alpha_m^P P_m\right)$ 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

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

(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 present[10]. 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

$$\rho_1 < \frac{\kappa_1^R}{\kappa_2^R} < \frac{1}{\rho_2},$$

(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 supports[2]. Thus,

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

(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 low[11]. The work of Abrams[11] 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.