

Predation-Competition Interactions for Seasonally Recruiting Species

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ABSTRACT: We investigate the interacting effects of predation and competition on species coexistence in a model of seasonally recruiting species in a constant environment. For these species, life-history parameters, such as maximum productivity and survival, have important roles in fluctuation-dependent species coexistence in that they introduce nonlinearities into population growth rates and cause endogenous population fluctuations, which can activate the coexistence mechanism termed “relative nonlinearity.” Under this mechanism, different species must differ in the nonlinearities of their growth rates and must make different contributions to fluctuations in competition and predation. Both of these features can result from life-history trade-offs associated with seasonal recruitment. Coexistence by relative nonlinearity can occur with or without predation. However, predation can undermine coexistence. It does this by reducing variance contrasts between species. However, when competition is not sufficient to cause endogenous population fluctuations, predation can enable fluctuation-dependent coexistence by destabilizing the equilibrium. This model also reproduces the classic finding that coexistence can occur with selective predation provided that it causes a trade-off between competition and predation. Our model is formulated for competition between annual plant species subject to seed predation, but it also applies to perennial communities where competition and predation limit recruitment to the adult population.

Keywords: predation, competition, species coexistence, relative nonlinearity, selective predation.

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Predation is often assumed to promote coexistence of competing species, but theoretical models imply that the role of predation can vary greatly with the circumstances (Chase et al. 2002). Recent theoretical work has focused on equilibrium coexistence arising from a trade-off between competition and predation, often using differential equation models (e.g., Grover and Holt 1998). Our chief concern is not with equilibrium conditions but with how predation modifies coexistence mechanisms that depend on endogenous fluctuations in population densities, a much neglected area of study. This question is most conveniently considered for species with seasonal recruitment where both competition and predation affect the final number of offspring contributing to the next generation. Discrete-time models apply, leading to endogenous fluctuations in many circumstances.

To make the discussion concrete, we frame it in terms of annual plants in arid regions, showing later how the results apply to seasonally recruiting species generally. For annual plant species, environmental variation (Chesson 1994) and predation (Davidson et al. 1985) have figured most prominently in hypotheses for species coexistence. The idea that environmental variation promotes species coexistence has much theoretical support (Chesson 1994; Chesson et al. 2004) and some empirical support (Pake and Venable 1995; Facelli et al. 2005; Sears and Chesson 2007). However, the importance of predation has not been examined in theoretical models of annual plant communities. Rodent and ant predation on seeds is a major feature of desert communities and has been studied empirically for its potential role in maintenance of the diversity of annual plants (Inouye et al. 1980; Davidson et al. 1985), but the absence of theoretical developments has impeded a better understanding. To redress this imbalance, the focus in this article is on predation in the absence of environmental variation, leaving the important question of the interaction between predation and environmental variation to future publication (J. J. Kuang and P. Chesson, unpublished manuscript).

We study predation that is selective, but not frequency dependent, and consider both fluctuation-independent and

fluctuation-dependent coexistence mechanisms (Chesson 2000). Fluctuation-independent coexistence means that the mechanism does not require fluctuations over time for its operation, and the addition of fluctuations need not destroy the mechanism. In the past, such mechanisms have more commonly been called “equilibrium mechanisms,” which usually indicates coexistence at a stable equilibrium point. Stability of the equilibrium means that the addition of fluctuations, provided they are not too large, does not destroy the prediction of coexistence (e.g., Turelli 1981). Fluctuation-dependent mechanisms, on the other hand, require fluctuations over time for their operation. Because we focus on constant environmental conditions, we study fluctuation-dependent coexistence arising from limit cycles and chaotic dynamics.

Our study of fluctuation-independent coexistence reproduces the classic requirement of a predation-competition trade-off, but it is exhibited here in a particularly precise and intuitive form. This trade-off is not necessary for fluctuation-dependent coexistence. Instead, life-history trade-offs suffice. Fluctuation-dependent coexistence occurs in our model with or without predation. The effect of predation on fluctuation-dependent coexistence may be positive, negative, or neutral depending on the circumstances. Importantly, we are able to explain the circumstances that allow each of these various outcomes.

Critical to fluctuation-dependent coexistence is nonlinearity of the population growth rates as functions of the key limiting factors, competition and predation. For coexistence, these nonlinearities must differ between species, as first elucidated in resource competition models by Armstrong and McGehee (1980) and investigated more recently by Adler (1990), Abrams and Holt (2002), and Abrams (2004). This mechanism is termed “relative nonlinearity” by Chesson (1994). Nonlinearity differences mean that the different species are affected differently by temporal fluctuations in their common limiting factors, with some species being favored by large variance and others by small variance. Moreover, these same nonlinearity differences mean that different species generate different variances through the feedback loops with their limiting factors. These considerations can lead to the situation where some species are favored by fluctuations but tend to dampen fluctuations (they are “consumers of variance” in the parlance of Levins [1979]). Others are relatively disadvantaged by variance but tend to generate it. The net outcome is to favor coexistence of these two sorts of species.

Although our development is framed in terms of annual plants, the model can be considered more generally as representing the dynamics of species with seasonal recruitment, that is, with recruitment concentrated at a particular time of year, a common situation in nature. For annual plants, we mean recruitment of seed to the seed bank. For perennial

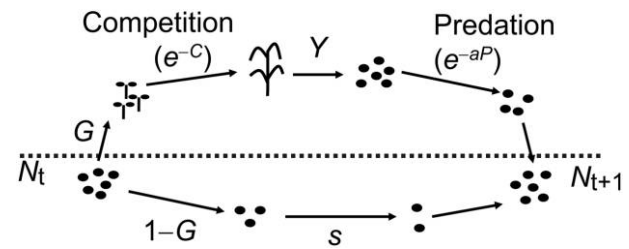


Figure 1: Life cycle of desert annuals, showing production of new seed (Y) from seeds that germinate (at rate G) subject to competition (C), predation (P), and survival (s) of dormant seed in the seed bank.

organisms, we mean recruitment to the adult population. Critical to our findings is the idea that the process of recruitment is potentially strongly affected by competition and predation, while survival of recruited organisms (seeds or adults) is not. Life-history trade-offs then lead to relatively nonlinear growth rates that enable fluctuation-dependent species coexistence. Thus, our results are dependent on distinctions between processes of production and persistence, with broad implications.

Model and Methods

Figure 1 illustrates the key features of an annual plant community subject to seed predation. Plants compete but also interact through a seed predator. These interactions occur at different stages in the life cycle. For an individual species, at the beginning of each season, some fraction G of the seeds (N) in the seed bank germinate. Each seedling produces Y seeds in the absence of competition and predation. Actual seed production is reduced by competition and predation. We quantify competition by a number, C , linearly dependent on the densities, GN , of the seedlings of each of the competing species. We assume that competition is of the Ricker form (Ricker 1954), reducing actual seed production to Ye^{-C} . A fraction of the newly produced seed is removed by predation, and the rest is incorporated into the soil seed bank. Using the Nicholson-Bailey formulation (Hassell 2000), the fraction surviving predation (and hence incorporated into the seed bank) is e^{-aP} , where P is predator density and a is the attack rate.

The nongerminating (dormant) fraction ($1 - G$) of the seed bank is subject to mortality and has the survival rate s to the beginning of the next germination season. Thus, for a system of n species with species-specific parameters, we obtain the following system of difference equations:

$$\begin{cases} N_j(t+1) = N_j(t)[s_j(1 - G_j) + G_j Y_j e^{-C(t) - a_j P(t)}] \\ P(t+1) = \sum_{j=1}^n b_j G_j Y_j N_j e^{-C(t)} [1 - e^{-a_j P(t)}] + s_p P(t) \end{cases} ; j = 1, \dots, n, \quad (1)$$

where $C(t) = \sum_{j=1}^n d_j G_j N_j(t)$. Here, b is the conversion between seed and predator, s_p is the survival rate of the predator, and d is the competition coefficient. This same set of equations can be used to model perennial organisms, with some changes in definitions (app. F). A complete list of notation is included in appendix A.

It is well known that coexistence is possible if intraspecific competition dominates interspecific competition (Volterra 1926; Lotka 1932). However, to study how coexistence arises in the presence of predation or endogenous fluctuations, we consider only situations where fluctuation-independent coexistence is not built into assumptions about competition. Thus, we assume that intra- and interspecific competition are the same, which is consistent with the idea that the annual plant species are limited by just one resource or are limited in the same way by several resources. Limitation by relatively few factors is a common expectation for plants (Grubb 1977), and this feature of our model allows the magnitude of competition to be represented by the single quantity C .

Another simplification is the Type I functional response of the predator to prey density implicit in the formula e^{-aP} for the fraction of seed lost to predation. Type II functional responses are more realistic in general but are difficult to implement realistically in discrete-time models because these functional responses represent behavior on a shorter timescale than the annual timescale of the model (Nunney 1979). A Type II functional response might promote population fluctuations (Abrams 1999), but the Ricker and Nicholson-Bailey components of the model also do this (May and Oster 1976; Hassell 2000).

For mathematical simplicity, we assume that the ratio b_j/d_j is the same for each species. This means that the plant species with more effect on plant resources (per seed) has larger seeds, which provide more nutrition to the predator. The ratio b_j/d_j affects predator density and disappears from the nondimensionalized equations used for the analysis (app. B). These equations may exhibit deterministic fluctuations, such as cycles or chaos, or settle on an equilibrium point.

Coexistence Conditions

Throughout this article, we focus on stable coexistence defined by the invasibility criterion, in other words, requiring each species to recover from rarity. This is an ecological notion of stability suitable for situations where populations may fluctuate over time (Chesson 2000) and

is not to be confused with stability of an equilibrium point. Also, this is not the coexistence of neutral models (Hubbell 2001) where recovery from rarity need not occur. The invasibility criterion has been developed for stochastic models (Turelli 1978; Chesson and Ellner 1989; Ellner 1989), but it is also applicable to deterministic models (Armstrong and McGehee 1980), as first suggested by MacArthur and Levins (1964). It is necessary but not sufficient for coexistence in the sense of permanence (Hutson and Schmitt 1992). In practice, the full conditions for permanence are difficult to calculate, and mutual invasibility is often used in its place, backed up by simulation to ensure that all persisting species remain bounded away from zero. This is the approach we adopt here. See appendix C for further discussion.

In a mutual invasion analysis, one species (the invader) is perturbed to effectively zero density, and the densities of the $n - 1$ other species (the residents) are allowed to converge on a joint equilibrium or steady fluctuations (e.g., as defined by a limit cycle or ergodic chaos; Matsu-moto 1996) that they have in the absence of the invader. The success of invasion is measured by the invader's long-term low-density growth rate (\bar{r}_i), as explained in appendix C. If \bar{r}_i is positive, we conclude that the invader increases in the long run, and the invasion is successful. If \bar{r}_i for each species is positive, we say the species coexist.

Fluctuation-Independent Coexistence

Because there is no distinction between intraspecific and interspecific competition in this model, the most competitive species excludes all others in the absence of predation and population fluctuations (Armstrong and McGehee 1980). Similarly, in the absence of competition, there would be no equilibrium coexistence because the species most tolerant of predation would exclude all others (Holt et al. 1994). With competition and predation both present, we ask when their interaction promotes coexistence. We consider first the case where resident species come to equilibrium so that the invader encounters constant conditions and coexistence is of the fluctuation-independent form.

Fluctuation-independent coexistence requires selective predation, that is, $a_1 \neq a_2$ (app. D), but several quantities are important in defining when coexistence will occur. The first is the productivity, η_j , of each species j before accounting for predation and competition. It is defined as the log total seed production per unit of seed loss for each species j , in other words, $\ln \{G_j Y_j / [1 - s_j(1 - G_j)]\}$. Next we need the equilibrium values, P_j^* and C_j^* , of predation and competition for each prey species j when present alone (i.e., in its single-species resident state). Third, we need

equilibrial predation and competition when the species are jointly present. These are

$$P_{12}^* = \frac{\eta_2 - \eta_1}{a_2 - a_1} \quad (2a)$$

and

$$C_{12}^* = \frac{a_2\eta_1 - a_1\eta_2}{a_2 - a_1} \quad (2b)$$

(see app. D).

Assuming that species 2 is the species with the larger value of a , appendix D shows that the coexistence condition is

$$P_1^* < P_{12}^* < P_2^* \quad (3)$$

Thus, the predator equilibrium, when both species are present, must lie between the two equilibria with only one prey species. Moreover, the species more vulnerable to predation (with larger a) has to support higher predator density when it is present alone. In addition, since P_{12}^* must be positive, this species must be the more productive species ($\eta_2 > \eta_1$). Appendix D shows that condition (3) is equivalent to

$$C_2^* < C_{12}^* < C_1^*, \quad (4)$$

that is, the species supporting less predation (with lower P^*) has to support more competition (higher C^*). Together, expressions (3) and (4) precisely represent the idea that coexistence results from a trade-off between competition and predation, as has been discussed in a variety of circumstances (Grover and Holt 1998; Holt et al. 1994; HilleRisLambers and Dieckmann 2003). There are some subtleties, however. Higher support of competition in the presence of predation requires

$$\frac{\eta_2}{a_2} < \frac{\eta_1}{a_1}, \quad (5)$$

that is, higher productivity per unit predation rather than higher productivity in absolute terms ($\eta_2 < \eta_1$), which would more normally apply in the absence of predation (app. D). No more than two species can coexist by this mechanism. The proof is similar to Levin's (1970) demonstration that the number of coexisting species cannot exceed the number of limiting factors in a differential equation model when these factors combine linearly. The coexistence region in terms of η_1 and η_2 values is given in figure 2.

An interesting special case occurs when one species does

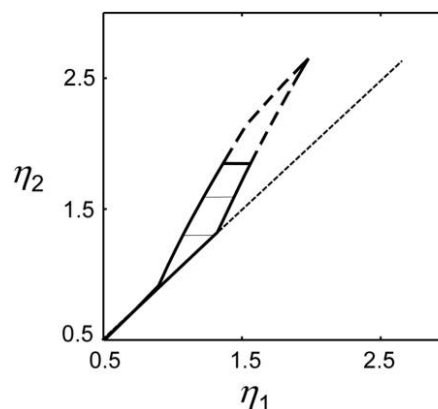


Figure 2: Coexistence region for two prey species with a competition-predation trade-off as the only coexistence mechanism. In the region enclosed by solid lines, resident species come to equilibrium. Above that, in the dashed-line region, at least one resident has endogenous fluctuations, but coexistence by a competition-predation trade-off still occurs. Species 1 excludes species 2 to the right of the coexistence region, and species 2 excludes species 1 to the left. $G_1 = G_2 = 0.5$, $s_1 = s_2 = 0.8$, $a_1 = 0.5$, $a_2 = 0.75$, and $s_p = 0.2$. See table A1 for definitions of symbols.

not support the predator. Condition (3) still holds, but the requirement $P_1^* < P_{12}^*$ simplifies to $\eta_2 > \eta_1$. This means that coexistence is possible when species 2 has only a slight advantage in net productivity, even though it may have a large disadvantage in predation. This effect is shown in figure 2 as the portion of the coexistence boundary corresponding to $\eta_2 = \eta_1$, continued as a dashed line. Species 1 does not support the predator when present alone, but species 2 enters the system because it is a superior competitor. The predator can then enter the system and ensure that species 2 does not become so abundant as to eliminate species 1. Hence, coexistence occurs.

The Fluctuation-Dependent Case

When the resident equilibrium is unstable, endogenous fluctuations arise, creating the potential for the long-term low-density growth rate, \bar{r}_i , and hence the conditions for invasion, to depend on these fluctuations. The quantity \bar{r}_i is the average over time of the appropriate discrete-time growth rate, r_i , which is given by the formula

$$r_i = \ln [s_i(1 - G_i) + G_i Y_i e^{-C(t) - aP(t)}]$$

(app. C), where we have assumed for simplicity that predation is nonselective ($a_i \equiv a$). The quantities that vary with time, C and P , can be combined into one, $F = C + aP$, and the growth rate is then a nonlinear function of this varying quantity, or a "limiting factor," in the terminology of Chesson (2000). Figure 3 illustrates the out-

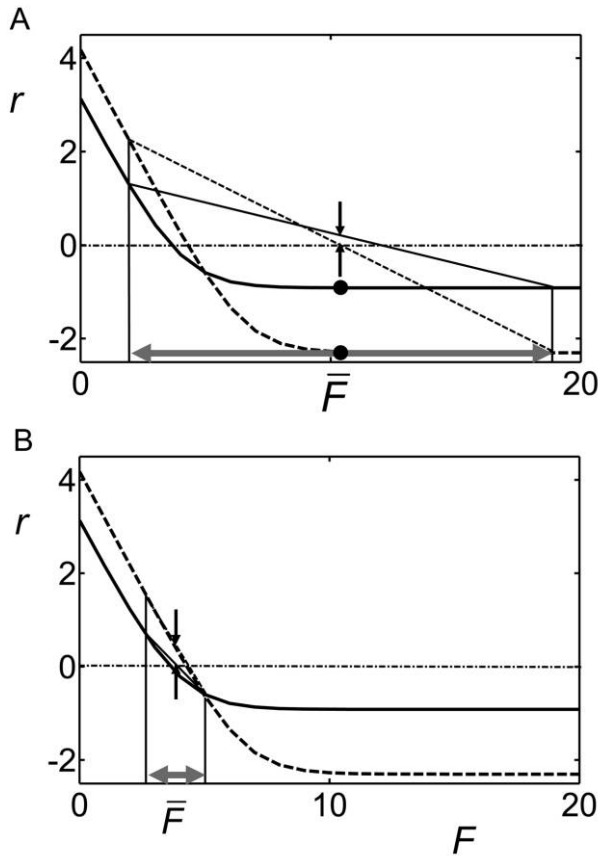


Figure 3: How relative nonlinearity allows mutual invasibility. Each species generates two-point cycles as resident, indicated in each panel by the double-headed arrow. Each species also has convex nonlinearities. The values of $\bar{r}(F)$ are indicated by the vertical arrows and lie on the straight lines joining the curve, $r(F)$, at the two points of the cycle determined by the resident species, as explained by scale transition theory (Chesson et al. 2005). Hence, the fluctuations in F increase the $\bar{r}(F)$ values over the growth rates at the mean of F , namely, $r(\bar{F})$ (indicated by black circles in A). The species with the solid line has the stronger nonlinearity and so benefits more from these fluctuations. As invader in A, fluctuations raise $\bar{r}(F)$ values of the solid-line species above the zero value experienced by the other species as resident, allowing invasion. In B, the solid-line species is resident and causes only small fluctuations in the limiting factor F , and so only small differences between $\bar{r}(F)$ and $r(\bar{F})$ result. In particular, the benefit the resident gains from these fluctuations is insufficient to give it a higher $\bar{r}(F)$ than the invader, despite its stronger nonlinearity. Resident $\bar{r}(F)$ is zero by necessity, and so the invader (dashed line) has positive $\bar{r}(F)$, allowing invasion.

come in the simple case of a two-point limit cycle for which F fluctuates equally between two values. Since $r(F)$ is a convex (concave up) function of F , $\bar{r}(F) > r(\bar{F})$. Thus, the actual long-term growth rate is greater than the growth rate evaluated at the mean of the limiting factor, that is, at the mean of the predator and prey densities. The degree of difference between $\bar{r}(F)$ and $r(\bar{F})$ depends on the mag-

nitude of the fluctuations ($\text{Var}(F)$), which can change depending on which species is the resident, as shown in figure 3. The right combination of nonlinearity differences and variance differences promotes coexistence by relative nonlinearity, as discussed in the introduction to this article. Nonlinearity depends on the rate at which seeds are lost from the seed bank, which is the quantity $\beta = 1 - s(1 - G)$. Appendix E derives the following approximate coexistence conditions, assuming $\beta_2 > \beta_1$:

$$\frac{\text{Var}(F_1)}{2} < \frac{\eta_2 - \eta_1}{\beta_2 - \beta_1} < \frac{\text{Var}(F_2)}{2}, \quad (6)$$

where $\text{Var}(F_j)$ means the variance of F with species j as resident and the other species as invader.

According to these conditions, trade-offs in life-history parameters remain important for fluctuation-dependent coexistence. The species with the higher net rate of seed loss from the seed bank (higher β) must be compensated with higher net productivity (higher η) and must generate higher variance. However, expression (6) may hold regardless of the presence of predation, and in contrast to the fluctuation-independent case, coexistence is possible without predation, as we shall see below. Thus, coexistence in the fluctuating system can arise by mechanisms other than competition-predation trade-offs.

A variety of conditions, including different Y values (fig. 3), can lead to different levels of fluctuations as residents. When a species with higher productivity has larger seed loss rate and causes larger fluctuations as a resident (fig. 3A), it gives an advantage to the inferior competitor as invader, which can lead to coexistence. Condition (6) can hold even if only one species generates fluctuations as a resident, but that species must be species 2, that is, the species with the larger productivity and seed loss rate. Under these circumstances, the invasion requirement for species 2 becomes $\eta_2 > \eta_1$, and coexistence condition (6) applies with $\text{Var}(F_1) = 0$. Thus, coexistence is possible when species 2 has only a slight advantage in net productivity, even though it may have a large disadvantage in seed persistence (fig. 4A).

Expression (6) gives a specific form of the standard approximate condition (Chesson 1994, eq. [68]) for coexistence by relative nonlinearity. The term $\eta_2 - \eta_1$ is a comparison of the fitnesses of the species in their common environment and is independent of fluctuations. The term $\beta_2 - \beta_1$ measures relative nonlinearity as defined by Chesson (1994). Thus, it measures how the nonlinearity of the growth rate of species 2 differs from the nonlinearity of the growth rate of species 1. As shown in figure 3, an invader species i with a negative value of $\beta_i - \beta_j$ gains a boost on average at low density from fluctuations from a

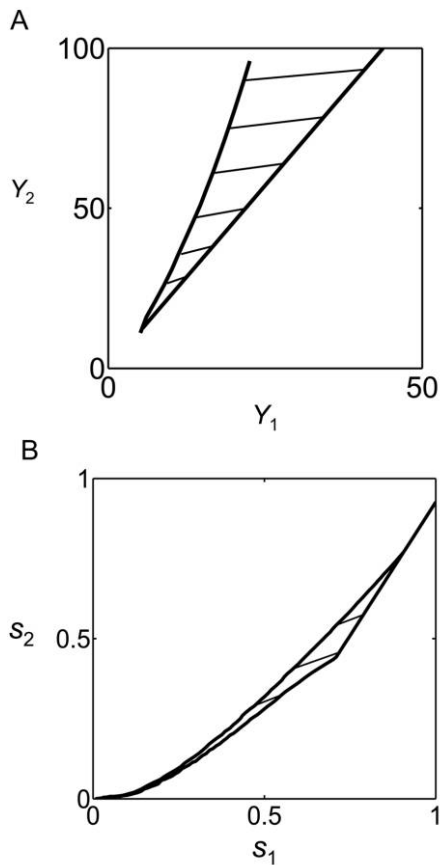


Figure 4: Coexistence with predation and s - Y trade-offs. There is no coexistence without predation because fluctuations are purely predation driven. *A*, Coexistence region in Y_1 - Y_2 space. Note that the right boundary coincides with the neutral coexistence line without predation. $G_1 = G_2 = 0.1$, $s_1 = 0.8$, $s_2 = 0.4$, $a_1 = a_2 = 1$, $s_p = 0.5$. *B*, Coexistence region in s_1 - s_2 space. The straight portion of the right boundary coincides with the neutral coexistence line without predation. $G_1 = G_2 = 0.1$, $Y_1 = 30$, $Y_2 = 50$, $a_1 = a_2 = 1$, $s_p = 0.5$. See table A1 for definitions of symbols.

resident species r . However, an invader with a positive value of $\beta_i - \beta_r$ suffers a penalty relative to its competitor. For coexistence, this penalized species must be the one with the higher net productivity, η , but the penalty it receives must be less than the boost that the other species gains. This difference between the penalty and the boost requires the invader with the negative value of $\beta_i - \beta_r$ to experience a larger $\text{Var}(F)$ from the resident, as depicted in figure 3.

Since $\eta = \ln(GY/\beta)$ and $\beta = 1 - s(1 - G)$, there are potentially three pairwise trade-offs between the three parameters, G , Y , and s , associated with relative nonlinearity. However, as shown in figure 1, the germination rate (G) affects the prey dynamics through two paths in the life

cycle: production of new seed and persistence in the seed bank. So by itself, the germination rate generates trade-offs between these two pathways. Thus, we focus on two kinds of trade-offs: s - Y trade-offs and self-trade-offs of G values. In the coexistence regions graphed below (figs. 4–8), numerical evaluation of the long-term low-density growth of the original equations, not the quadratic approximations, is used to define coexistence boundaries. The general features of these regions, however, are explained by the quadratic approximations.

Figures 4 and 5 consider cases in which fluctuations are absent without predation, precluding coexistence. Because predation is nonselective, equilibrium coexistence with predation is impossible. However, the predator can introduce fluctuations, and these do lead to coexistence in these particular examples with s - Y trade-offs. In figure 4*A*, the right boundary coincides with the neutral coexistence line where the species have equal fitness. Species 2 is disadvantaged by fluctuations, but species 1 does not generate fluctuations when present alone, and so species 2 can invade with even a slight fitness advantage over species 1. However, species 2 generates fluctuations, which disadvantage it and prevent it from excluding species 1, explaining coexistence.

In figure 4*B*, the coexistence region in the s_1 - s_2 plane shows nonmonotonic behavior in the center of the realistic range of s values, first increasing in width and then decreasing with increasing s . This occurs because the variance of the system changes nonmonotonically with s . Simulations show that larger s values have a direct effect on variation by stabilizing prey dynamics. Larger s values also have an indirect effect by increasing prey and predator

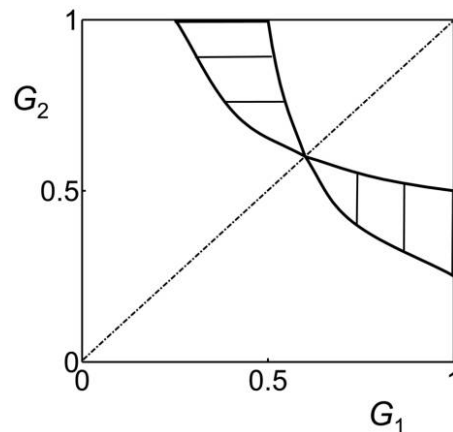


Figure 5: Coexistence shown in G_1 - G_2 space, with predation illustrating the G self-trade-off. $s_1 = s_2 = 0.8$, $Y_1 = Y_2 = 8$, $a_1 = a_2 = 1$, $s_p = 0.5$. See table A1 for definitions of symbols.

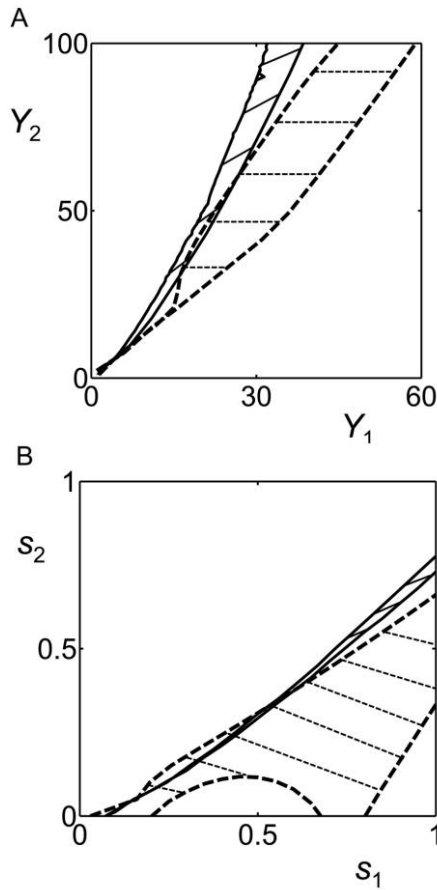


Figure 6: Comparison of coexistence with and without predation and s - Y trade-offs. A, Coexistence region in Y_1 - Y_2 space. Note that with predation, two alternative resident attractors are present in the vicinity of $Y_2 = 91$. Thus, two alternative invasion boundaries occur, as indicated, as a result of chaotic dynamics. $G_1 = G_2 = 0.5$, $s_1 = 0.8$, $s_2 = 0.4$, $a_1 = a_2 = 1$, $s_p = 0.5$. B, Coexistence region in s_1 - s_2 space. $G_1 = G_2 = 0.5$, $a_1 = a_2 = 1$, $s_p = 0.5$, $Y_1 = 30$, $Y_2 = 50$. See table A1 for definitions of symbols.

densities and the ranges of their fluctuations, thus increasing the variance of F .

As discussed above, the germination rate produces a trade-off between the benefits of productivity and persistence in the seed bank in a way that should also create the right variance relationships for species coexistence. Figure 5 illustrates this outcome for a case where fluctuations would not occur in the absence of predation, and so predation is again necessary for coexistence.

Although predation can activate the relative-nonlinearity mechanism by generating fluctuations when fluctuations would be present in the absence of predation, predation need not have a positive effect on coexistence. In the case of competition-induced fluctuations, introduction

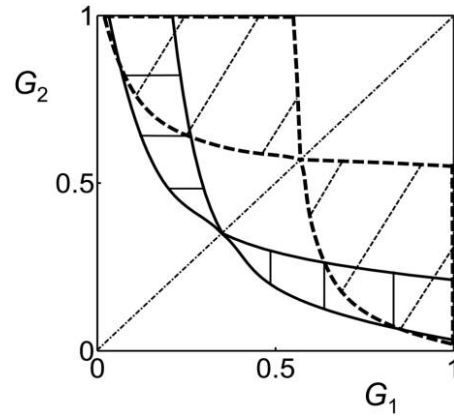


Figure 7: Comparison of coexistence regions with (solid line) and without (dashed line) predation, for the case of germination trade-offs. $s_1 = s_2 = 0.8$, $Y_1 = Y_2 = 30$, $a_1 = a_2 = 1$, $s_p = 0.5$. See table A1 for definitions of symbols.

of predation increases the magnitude of fluctuations and increases both the upper and lower boundaries of the coexistence region, leading to a narrower region overall, as illustrated in figures 6 and 7. This finding of a generally narrower coexistence region extends also to cases when selective predation is present, even though selective predation is capable of generating coexistence in its own right (fig. 8).

Discussion

This work provides a foundation for the study of the interaction between predation and competition for species

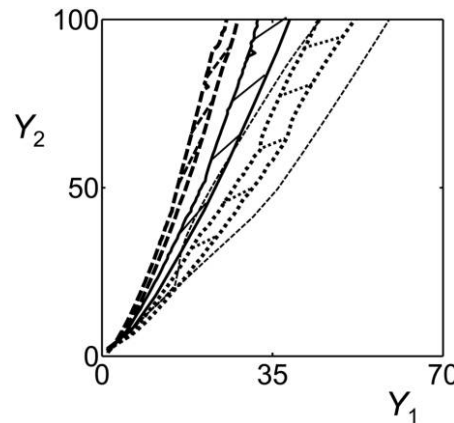


Figure 8: Comparison of coexistence regions with selective, nonselective, and no predation. Hatched regions, from left to right, denote coexistence with selective predation ($a_1 < a_2$, $s_1 > s_2$), nonselective predation, and selective predation ($a_1 > a_2$, $s_1 > s_2$). The unhatched region bounded by dashed lines denotes coexistence without predation. See table A1 for definitions of symbols.

with seasonal recruitment, for which endogenous fluctuations potentially contribute to species coexistence. Endogenous fluctuations have been considered previously in discussions of the role of predation in species coexistence (Abrams 1999) but only concerning the possibility that endogenous fluctuations reduce the effectiveness of fluctuation-independent mechanisms. Our key example has been desert annual plants, but as discussed below, the findings are general to systems with seasonal recruitment.

We have restricted attention to the case of constant environmental conditions, and thus no exogenous fluctuations, not because we expect that case to be a reasonable approximation of nature but in order to examine coexistence mechanisms that do not require environmental fluctuations. It is reasonable to expect multiple coexistence mechanisms in any system, some relying on environmental fluctuations and others not. It is important to emphasize that different mechanisms can work in concert to yield an overall coexistence-promoting effect (Chesson 2000). Thus, the mechanisms discussed here may still be expected to be present when others relying on environmental fluctuations are present as well, even though environmental fluctuations might well modify their action.

In the absence of both environmental and endogenous fluctuations, we found support for the idea that coexistence results from a trade-off between competition and predation (Holt et al. 1994; Grover and Holt 1998; Abrams 1999). Our formulation gives particularly clear results in terms of simple inequalities that must be satisfied by competition and predation for coexistence to occur.

Endogenous fluctuations lead to the fluctuation-dependent mechanism termed “relative nonlinearity,” as defined in the introduction to this article. In most discussions of relative nonlinearity, the requisite nonlinearities arise from nonlinear functional responses of consumers to their resources (e.g., Armstrong and McGehee 1980; Abrams 2004). Here, the nonlinearities arise from the presence of the seed bank, which is protected from predation and competition, while these density-dependent processes affect the annual production of seed. Because the nonlinearities arise from life-history traits, life-history differences, which may result from standard life-history trade-offs between persistence and reproductive traits (Roff 2002), lead to relatively nonlinear population growth rates. The nonlinearities present here are convex (i.e., concave up; fig. 3). Higher persistence in the seed bank leads to greater convexity, which has two important effects for species coexistence. First, a species with a more convex growth rate gains greater long-term benefit from fluctuations. Second, when a species is in high abundance, greater convexity tends to dampen fluctuations in the system as a whole. A second species with lower convexity gains a relative advantage from these low levels of fluctuations, but if that

second species is more productive, it tends to generate large fluctuations when it is abundant, favoring the first species. The net outcome is that two species with opposite patterns of productivity and persistence in the seed bank each tend to promote conditions that favor the recovery of the other species from low density, promoting coexistence.

Coexistence between annual plants is possible by this mechanism in the absence of predation, but predation usually modifies the outcome. Fluctuating competition in the absence of predation depends on our use of the Ricker model of competition, which can cause fluctuations due to overcompensating density dependence. This is not the most realistic situation for plant species, although some overcompensation is found in some plant populations (MacDonald and Watkinson 1981). In some cases, we found that predation is necessary for population fluctuations to be present, and fluctuations arising in this way can also permit coexistence by means of relative nonlinearity. More commonly, predation decreased the size of the coexistence region. This reduction in the coexistence region occurred because the contrast in the magnitude of the population fluctuations for different species tended to be reduced with predation, even though the overall magnitude of fluctuations was often higher, thus undermining the mechanism, usually pivoting the coexistence region, and increasing the productivity required of the more productive species.

Although our development has focused on annual plant species, as noted in appendix F, equations of the same form also apply to perennial species. The key quantities—productivity, η , and persistence, $1 - \beta$ —are defined in analogous ways, with direct translation of the results from annual plants to the perennial context. Our results depend on the idea that competition and predation are of most importance in the recruitment of new individuals, whether they are seeds in the seed bank or new individuals joining the adult population. Similar features appear in models of freshwater zooplankton with persistent egg banks (Caceres 1997). Similar effects on community dynamics can arise from subdivision of a population in space into refuge and nonrefuge areas and, more generally, whenever the finite rate of increase of a population can be divided into contributions from processes that differ in their sensitivities to predation and competition (see discussion of covariance of sensitivity in Chesson 1990).

One caveat is that the equations of the text assume a particular order of action of competition and predation, with competition occurring earlier in the season and predation being of importance later. This fits well with observations of annual plant species where seed predators attack the seeds after they have been produced. However, for perennial species, where our focus is on recruitment

not to the seed bank but to the adult population, there is no expectation that competition will precede predation. However, preliminary studies of the model with the opposite ordering of predation and competition (app. F) reproduce the phenomena reported here. Understandably, coexistence regions change quantitatively, but no major qualitative effects have been seen.

As in most other coexistence mechanisms, trade-offs of one form or another are required for the coexistence mechanisms discussed here (Chase and Leibold 2001), but we find some new insights into the way trade-offs can work. We found cases where a major disadvantage in one attribute can be compensated for by a slight advantage in another attribute. In the fluctuation-independent case, we found that a less-preferred prey might be unable to support the predator by itself. As a consequence, any productivity advantage at all (even a very small one) was sufficient to allow invasion (fig. 2). When this more productive species was more strongly preferred by the predator and able to support the predator, coexistence was possible. Coexistence resulted because the predator kept this species in check. Thus, the trade-off necessary for coexistence here could be satisfied by only slight productivity differences, even though predation differences might have been large. Similar phenomena were found in the fluctuation-dependent case. For example, one prey might have been unable to generate fluctuations due to low productivity. Then a species with a slight fitness advantage might have been able to invade the system despite the fact that it had much lower tolerance to newly arising fluctuations generated by its presence and preventing it from excluding the other species (fig. 4).

In all forms of our models here, the coexistence mechanisms depend on the fact that predation is density dependent and specifically that the predator has a numerical response to the prey. With predation-competition trade-offs, this numerical response allows one species to have strong density-dependent limitation by predation while the other has strong density-dependent limitation by competition, enabling their coexistence. In the fluctuation-dependent case, the numerical response is a strong generator of endogenous fluctuations, which can greatly modify the outcome with competition alone. In contrast, adding density-independent

predation to a model is equivalent to altering the mortality rates and therefore introduces no new dynamical features, whether the system comes to an equilibrium (Slobodkin 1961; Abrams 1977) or maintains fluctuations (Chesson and Huntly 1997), although with nonlinear competition, modifying density-independent mortality rates can have surprising effects (Holt 1985).

Previous work on coexistence of annual plants has emphasized the effects of temporal environmental fluctuations, and the fundamental concept extends to many seasonally recruiting species (Comins and Noble 1985; Caceres 1997; Chesson 1997; Chesson et al. 2004). Coexistence may also be promoted by spatiotemporal variation arising when natural enemies act as disturbance agents (Caswell 1978) or create spatiotemporally varying patterns of predation risk (Pacala and Crawley 1992). Previous work, however, has not explored the potential for predator-mediated coexistence involving endogenous temporal fluctuations with no spatial or exogenous component. Our findings, however, suggest coexistence of no more than three species in such circumstances (app. G), while in nature, rich communities are often found. However, as discussed above, multiple coexistence mechanisms acting in concert are likely to be found in most systems in nature. In species with seasonal recruitment, in addition to the mechanisms discussed here, we can well expect to find mechanisms associated with environmental fluctuations, frequency-dependent predation (Roughgarden and Feldman 1975; Krivan 2003), and multiple predators with different prey preferences (Grover 1994). Such mechanisms applied to species with seasonal recruitment are the subjects of future manuscripts.

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APPENDIX A

General Notation

Table A1: General notation

Symbol	Definition
*	Equilibrium
a	Per capita predation rate on a prey species
b	Conversion coefficient from prey to predator

Table A1 (Continued)

Symbol	Definition
β	Equal to $1 - s(1 - G)$, the loss rate from the seed bank
C	Magnitude of competition
d	Competition coefficient
F	Combination of competition and predation
G	Germination fraction
i	Index for the invader
j	Index for an arbitrary species j
n	Number of competitors (annual plant species)
N	Density of prey (annual plant)
$O(x)$	A quantity that remains the same order of magnitude as x , as x becomes small
P	Density of predator
r	Population growth rate; when subscript, index for the resident
R_j	Per capita recruitment in the absence of predation and competition (perennial model)
s	Seed dormancy rate
s_A	Adult survival rate in the perennial model
s_p	Survival of the predator
Y	Annual plant seed yield
η	Equal to $\ln \{GY/[1 - s(1 - G)]\}$, the seed production per unit seed loss, log scale
λ	Equal to $N(t + 1)/N(t)$, the finite rate of increase

APPENDIX B

Nondimensionalization of the Dynamical Equations

To nondimensionalize equations (1), first, the separate parameters b_j and d_j are replaced by the ratio b_j/d_j . Assuming that this ratio is the same for each species (as discussed in the text), we can replace N_j with $d_j N_p$, P with $(d/b)P$, and a_j with $(b/d)a_j$. The above system then reduces to the following set of equations:

$$\begin{cases} N_j(t + 1) = N_j(t)[s_j(1 - G_j) + G_j Y_j e^{-C(t) - a_j P(t)}] \\ P(t + 1) = \sum_{j=1}^n G_j Y_j N_j e^{-C(t)} [1 - e^{-a_j P(t)}] + s_p P(t) \end{cases} ; j = 1, \dots, n, \quad (B1)$$

where $C(t) = \sum_{j=1}^n G_j N_j(t)$. It is worthwhile to note that in these nondimensionalized equations, seed density is measured in units of competitive effect per unit area because d_j is the competitive effect of a seedling, which may be proportional to biomass.

APPENDIX C

Invasibility Criteria

As stated in the text, we use the invasibility criterion to define stable coexistence. Although originally developed for stochastic models (Turelli 1978; Chesson and Ellner 1989; Ellner 1989), it also applies to deterministic models (Armstrong and McGehee 1980). It is necessary but not

sufficient for coexistence in the sense of permanence (Hutson and Schmitt 1992); that is, population densities are eventually bounded away from zero and infinity. Invasion fails to be equivalent to permanence when increasing population fluctuations are possible or when crashes to arbitrarily low density from intermediate densities are possible (Hofbauer and Sigmund 1989). The competition present in our model means that all populations are bounded above and ever-increasing cycles are not possible. Although we have not rigorously proved that permanence is equivalent to invasibility here, it appears to be the case, as backed up by simulations.

In an invasion analysis, one species (the “invader”) is removed from the system and reintroduced at low density with the $n - 1$ other species (the “residents”) whose densities have converged to a joint equilibrium or steady fluctuations (e.g., as defined in a deterministic model by a limit cycle or ergodic chaos; Matsumoto 1996). The success of invasion is measured by the invader’s long-term growth rate (\bar{r}), as defined below. If the long-term growth rate of the invader is positive, we conclude that its population increases in long run, and the invasion is successful. If the long-term growth rate of each species as invader is positive, we say the species coexist.

We define the growth rate of any species for the time interval t to $t + 1$ as the change in \ln population size; in other words,

$$r(t) = \ln N(t + 1) - \ln N(t). \quad (C1)$$

This quantity is the same as $\ln \lambda(t)$, where

$$\lambda(t) = \frac{N(t+1)}{N(t)} \quad (\text{C2})$$

is the finite rate of increase. In our models, the finite rate of increase of a prey species is

$$\lambda(t) = s(1 - G) + GYe^{-C(t) - aP(t)}, \quad (\text{C3})$$

and so $r(t)$ is given as

$$r(t) = \ln[s(1 - G) + GYe^{-C(t) - aP(t)}]. \quad (\text{C4})$$

The long-term population growth rate is defined as

$$\begin{aligned} \bar{r} &= \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} r(t)}{T} = \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} \ln N(t+1) - \ln N(t)}{T} \\ &= \lim_{T \rightarrow \infty} \frac{\ln N(T) - \ln N(0)}{T}. \end{aligned} \quad (\text{C5})$$

For the residents, population densities are bounded provided that they converge on a bounded attractor. As a consequence, the right-hand side of (C5) converges to zero; in other words, the long-term population growth rates of residents are zero. For an invader species i , $r_i(t)$ in (C5) is evaluated for $N_i(0) = 0$, using equation (C4). This quantity, \bar{r}_i , can be regarded as the limit as $N_i(0) \rightarrow 0$ of the quantity on the right in (C5) (taking the limit as $N_i(0) \rightarrow 0$ first) or simply as the time average of $r_i(t)$, as defined above with $N_i(0) = 0$. The long-term growth rate \bar{r}_i can be regarded as the long-term growth trend while the invader remains at low density. Invader growth rates can be positive, negative, or zero. As mentioned above, for coexistence we seek conditions that lead to positive invader growth rates ($\bar{r}_i > 0$).

APPENDIX D

Fluctuation-Independent Coexistence

In this case, long-term low-density growth rates are just the particular growth rates that invaders have with the resident species at equilibrium. Thus, coexistence by the invasibility criterion is the same as each species having a low-density finite rate of increase greater than 1, that is, $\lambda_i > 1$, where we use the subscript i as the index for an invader. We begin with the two-species case, which means there is one resident species, designated by the index r . Then, using the formula in (C3) for λ , we need to find conditions such that

$$\lambda_i = [s_i(1 - G_i) + G_i Y_i e^{-C_r^* - a_i P_r^*}] > 1, \quad (\text{D1})$$

where C_r^* and P_r^* refer to competition and predation supported by the resident species r at equilibrium. Since the resident is present alone, $C_r^* = G_r N_r^*$.

Equations for C_r^* and P_r^* do not yield explicit solutions. However, we can eliminate C_r^* from expression (D1) using the fact that resident finite rates of increases (values of λ_r) are equal to 1. Thus,

$$\lambda_r = [s_r(1 - G_r) + G_r Y_r e^{-C_r^* - a_r P_r^*}] = 1,$$

implying

$$C_r^* + a_r P_r^* = \eta_r, \quad (\text{D2})$$

where $\eta_r = \ln \{G_r Y_r / [1 - s_r(1 - G_r)]\}$, that is, productivity per unit seed lost.

Substituting expression (D2) in inequality (D1), we obtain

$$\begin{aligned} \lambda_i &= [s_i(1 - G_i) + G_i Y_i e^{-C_r^* - a_i P_r^*}] \\ &= [s_i(1 - G_i) + G_i Y_i e^{-\eta_r + (a_r - a_i) P_r^*}]. \end{aligned} \quad (\text{D3})$$

When this is evaluated for both $i = 1$ and $i = 2$, we can see that the two species coexist if

$$\begin{cases} \lambda_1 = [s_1(1 - G_1) + G_1 Y_1 e^{-\eta_2 + (a_2 - a_1) P_2^*}] > 1 \\ \lambda_2 = [s_2(1 - G_2) + G_2 Y_2 e^{-\eta_1 + (a_1 - a_2) P_1^*}] > 1 \end{cases}. \quad (\text{D4})$$

If $a_2 = a_1$, conditions (D4) lead to the contradiction that $\eta_2 > \eta_1$ and $\eta_2 < \eta_1$. Thus, stable coexistence cannot result if the species are equally affected by competition and predation. Hence, without loss of generality, we assume that $a_2 > a_1$. Then, expressions (D4) rearrange to the following condition:

$$P_1^* < \frac{\eta_2 - \eta_1}{a_2 - a_1} < P_2^*. \quad (\text{D5})$$

If the species do coexist and come to a joint equilibrium, the values of C and P (C_{12}^* and P_{12}^*) at this joint equilibrium are given by the expression

$$\begin{bmatrix} C_{12}^* \\ P_{12}^* \end{bmatrix} = \frac{1}{a_2 - a_1} \begin{bmatrix} a_2 \eta_1 - a_1 \eta_2 \\ \eta_2 - \eta_1 \end{bmatrix}, \quad (\text{D6})$$

according to (D2).

Simulations have shown that invasion need not lead to

convergence onto the C - P equilibrium given by (D6). Instead, the system may converge on a limit cycle. Nevertheless, the values in (D6) remain equilibria regardless of whether the system converges on them. Using (D6), we see that (D5) can be written as

$$P_1^* < P_{12}^* < P_2^*,$$

which is equation (3) in the main text. So for coexistence, P_{12}^* must lie between the equilibrium predator densities supported by each prey species separately. These predator equilibrium relationships imply equilibrium relationships for competition too because at equilibrium, competition intensity and predator density must balance productivity, and so they are linearly related as follows:

$$\begin{cases} C_1^* + a_1 P_1^* = \ln \eta_1 = C_{12}^* + a_1 P_{12}^* \\ C_2^* + a_2 P_2^* = \ln \eta_2 = C_{12}^* + a_2 P_{12}^* \end{cases} \quad (D7)$$

Using these relationships, we see that condition (3) becomes

$$C_2^* < C_{12}^* < C_1^*,$$

and positivity of expression (D6) is a direct consequence of the above competition-predation trade-off. Recalling that C is just the density of growing plants, the above condition means that among two coexisting species, the species with lower productivity has higher seedling density at its equilibrium as a single-species resident. This surprising result is a consequence of predation. In the presence of predation, the joint competitive factor, $C_{12}^* = (a_2 \eta_1 - a_1 \eta_2) / (a_2 - a_1)$, must be positive. Thus, it is necessary for the following inequality to be true:

$$\frac{\eta_2}{a_2} < \frac{\eta_1}{a_1}.$$

APPENDIX E

Quadratic Expansion of Prey Population Growth Rate and Coexistence Conditions for the Nonequilibrium Case

We consider here the special case of equal predation ($a_j = a_k$ for each species j and k), which, as we know from above, does not yield coexistence in equilibrium settings. Recall that the prey population growth rate is

$$r_j(C, P) = \ln [s_j(1 - G_j) + G_j Y_j e^{-C - aP}].$$

We let $F = C + aP$, and then we perform quadratic ex-

pansion on $r_j(F)$ around the equilibrium of F , which is denoted F_j^* , as follows:

$$\begin{aligned} r_j &= r_j|_* + \left. \frac{dr_j}{dF} \right|_* (F - F_j^*) \\ &+ \left. \frac{1}{2} \frac{d^2 r_j}{dF^2} \right|_* (F - F_j^*)^2 + O(\sigma^3). \end{aligned} \quad (E1)$$

Evaluating the derivatives in (E1) and averaging over time yields the mean growth rate of species j , expressed as

$$\bar{r}_j = -\beta_j(\bar{F} - F_j^*) + \frac{1}{2} \beta_j(1 - \beta_j) \overline{(F - F_j^*)^2} + O(\sigma^3), \quad (E2)$$

where the overbars indicate the time average and $\beta = 1 - s(1 - G)$ is the loss rate of the seed bank.

If the magnitude of the fluctuations is small, so that $F - \bar{F} = O(\sigma)$, and $F_j^* - \bar{F} = O(\sigma^2)$, then $\overline{(F - F_j^*)^2} = \text{Var}(F_j) + O(\sigma^3)$. Thus the long-term growth rate scaled by β_j is

$$\frac{\bar{r}_j}{\beta_j} \approx -(\bar{F} - F_j^*) + \frac{1}{2}(1 - \beta_j)\text{Var}(F). \quad (E3)$$

(A more detailed derivation of [E3] can be found in Chesson 1994.) On the left-hand side of this equation, \bar{r}_j/β_j is the rescaled long-term population growth rate. In invasion analysis, we are interested only in the sign of the long-term low-density population growth rate, and since β_j is always positive, rescaling \bar{r}_j does not change the results of the invasion analysis. It does, however, simplify the calculations and aid the biological interpretation of the results.

Recall that the long-term growth rate of the resident, \bar{r}_r , is zero. Thus, the long-term growth rate of the invader can be written $\bar{r}_i/\beta_i = \bar{r}_i/\beta_i - \bar{r}_r/\beta_r$, or approximately

$$\frac{\bar{r}_i}{\beta_i} \approx (F_i^* - F_r^*) - \frac{1}{2}(\beta_i - \beta_r)\text{Var}(F_r), \quad (E4)$$

where $\text{Var}(F_r)$ means the variance of F with the particular resident r .

According to equation (D2), the total competition at equilibrium for any species j is equal to the productivity of species j ; that is, $F_j^* = \eta_j$. Thus, equation (E4) can be simplified to

$$\frac{\bar{r}_i}{\beta_i} \approx (\eta_i - \eta_n) - \frac{1}{2}(\beta_i - \beta_n)\text{Var}(F_i). \quad (\text{E5})$$

For coexistence, this invasion rate must be positive for each species as invader, which implies the coexistence condition

$$\frac{\text{Var}(F_1)}{2} < \frac{\eta_2 - \eta_1}{\beta_2 - \beta_1} < \frac{\text{Var}(F_2)}{2}.$$

APPENDIX F

A Perennial Model

Equations (1) in the text, defining the model for annual plants, can be modified for perennials. Both perennials and annuals have a stage in the life cycle that persists over time. For annuals it is the seed stage, and for perennials it is the adult individual. The state variable to be used in the model is the density of this persistent stage. Thus, while in the annual model $N_j(t)$ is the density in the seed bank, in the perennial it is the adult density. For perennials, we introduce the parameter R_j for the per capita yield of new adults in the absence of predation and competition. It includes seed production, germination, and density-independent survival before recruitment to the adult stage. The quantity R_j replaces $G_j Y_j$ of the annual model, and $d_j R_j$ replaces $d_j G_j$. (Although d_j disappears on nondimensionalization, it remains important to recognize that it has a different value in perennial and annual cases.) The quantity $s_j(1 - G_j)$ of the annual model (the fraction of seed surviving in the seed bank) is replaced by $s_{A,j}$ the adult survival rate, in the perennial model. If predation comes after competition, as in the annual model, the equations for the perennial are identical to those of the annual model, with these parameter substitutions. Thus, the dynamics of the system are described by the following set of equations, in nondimensional form:

$$\begin{cases} N_j(t+1) = N_j(t)[s_{A,j} + R_j e^{-a_j P(t) - C(t)}] \\ P(t+1) = \sum_{j=1}^n R_j N_j e^{-C(t)} [1 - e^{-a_j P(t)}] + s_p P(t) \end{cases} ; j = 1, \dots, n, \quad (\text{F1})$$

where $C(t) = \sum_{j=1}^n R_j N_j(t)$.

An alternative formulation that may be more realistic in some circumstances is to have predation occur before competition. Then competition is reduced in proportion to the number of juveniles that have been lost to predation. In this case, we obtain the following equations:

$$\begin{cases} N_j(t+1) = N_j(t)[s_{A,j} + R_j e^{-a_j P(t) - C(t)}] \\ P(t+1) = \sum_{j=1}^n R_j N_j [1 - e^{-a_j P(t)}] + s_p P(t) \end{cases} ; j = 1, \dots, n, \quad (\text{F2})$$

where $C(t) = \sum_{j=1}^n R_j e^{-a_j P(t)} N_j(t)$.

In reality, we can expect the periods of competition and predation to overlap with one another, even though their relative intensities may well vary during the season. By considering both extremes we can hope to bracket the possibilities.

In both cases, the equations for the prey species are derived simply by parameter substitution in the equations for annual plants. The critical quantities, η_j , β_j , C_{12}^* , and P_{12}^* , all come from the prey equations and therefore can be obtained from the corresponding quantities for the annual plant by making these parameter substitutions. In particular, η_j and β_j are given, respectively, as $\ln [R_j / (1 - s_{A,j})]$ and $(1 - s_{A,j})$. The fluctuation-independent coexistence conditions and the quadratic approximation for the fluctuation-dependent case also all come from the prey equations, and so they also agree exactly with those of the annual model, given these parameter substitutions, regardless of the order of predation and competition. However, the quantities C_j^* and P_j^* do depend on the predator equation, and although the coexistence conditions in terms of C_j^* and P_j^* do not change with the order of predation and competition, they do change when expressed in terms of the underlying parameters. Similarly, for the fluctuation-dependent case, although the coexistence conditions in terms of $\text{Var}(F_j)$ are independent of the order of predation and competition, the values of $\text{Var}(F_j)$ do depend on this order. However, our preliminary exploration of equations (F2) has revealed no qualitative changes in the conclusions.

APPENDIX G

Three-Species Coexistence

The section ‘‘Coexistence Conditions’’ in the main text shows two-species coexistence through selective predation, in the equilibrium case, or through relative nonlinearity, when endogenous fluctuations are present. Because these mechanisms arise in very different ways, they appear to be independent of one another, which suggests that in combination, three or more species may potentially coexist. Thus, we need to study selective predation in the presence of endogenous fluctuations. Unfortunately, a satisfactory quadratic approximation is not yet available in this case. The quadratic expansion would have to be two-dimensional because with selective predation there is no common factor F that summarizes the combined intensity

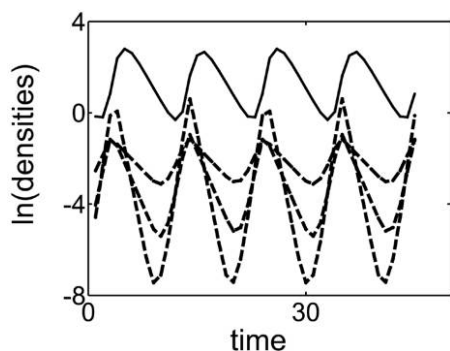


Figure G1: Coexistence of three prey species. Two different kinds of trade-offs are present: a productivity-seed persistence trade-off between species 1 and 2, and predation-competition (attack rate vs. productivity) trade-offs between species 1 and 3 and between species 2 and 3. $s_1 = s_2 = s_3 = 0.8$, $Y_1 = Y_2 = Y_3 = 30$, $a_1 = a_2 = 1$, $a_3 = 1.31$, $G_1 = 0.75$, $G_2 = 0.1$, $G_3 = 0.4$, and $s_p = 0.5$. See table A1 for definitions of symbols.

of predation and competition for both prey species. Although such a two-dimensional approximation might be developed according to the methods in Chesson (1994), the results below do not justify going beyond simulation.

Figure G1 shows the coexistence of three species with selective predation and endogenous fluctuations. There are two different kinds of trade-offs between these species: a productivity-seed persistence trade-off between species 1 and 2, and predation-competition (attack rate vs. productivity) trade-offs between species 1 and 3 and between species 2 and 3. Although productivity-seed persistence trade-offs are included between 1 and 3 and between 2 and 3, these were found insufficient for three-species coexistence without predation-competition trade-offs. These pairwise trade-offs, each of which allows two-species coexistence alone, combine to allow three-species coexistence. Notice that only parameters a and G differ between species. Thus, these trade-offs allowing three-species coexistence require only two-dimensional parameter variation as a consequence of the fact that G drives a trade-off between the two processes, persistence and productivity, as discussed above.

Simulations show that in three-species coexistence, the two-dimensional sections through the coexistence region are much smaller than the corresponding sections with two-species coexistence, as shown in figure 7. Also, invasion rates of one or more species may be very small, and it may take more than 20,000 time steps before this system has converged on its attractor, starting from low densities. Thus, conditions created by residents, which yield zero growth in the long run for residents, give only weak long-run invader growth, indicating that two residents in combination leave fewer or weaker ecological op-

portunities for an invader to exploit. Thus, we do not view this three-species coexistence system as ecologically meaningful, since its rate of convergence to the orbit is too slow to be robust in the face of environmental fluctuations, even those of small magnitude.

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