

Coexistence of annual plants: Generalist seed predation weakens the storage effect

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Abstract. We investigate the effect of seed predation on the coexistence of competing annual plants. We demonstrate a role for predation that is opposite to the conventional wisdom that predation promotes coexistence by reducing the intensity of competition. In the common situation where competitive coexistence involves intraspecific competition exceeding interspecific competition, predation can undermine coexistence by reducing the overall magnitude of competition, replacing competition with “apparent competition” in a way that does not lead to differential intraspecific and interspecific effects. We demonstrate this outcome in the case where coexistence occurs by “the storage effect” in a variable environment. The storage effect arises when the environment interacts with competition to create opportunities for species to increase from low density. Critical to the storage effect is positive covariance between the response of population growth to the environment and its response to competition, when a species is at high density. This outcome prevents species at high density from taking advantage of favorable environmental conditions. A species at low density has lower covariance and can take advantage of favorable environmental conditions, giving it an advantage over a high-density species, fostering its recovery from low density. Hence, species coexistence is promoted. Here we find that density-dependent predation lowers population densities, and so weakens competition, replacing competition with apparent competition, which does not covary with the environment. As a consequence, covariance between environment and competition is weakened, reducing the advantage to a species at low density. The species still strongly interact through the combination of competition and apparent competition, but the reduced low-density advantage reduces their ability to coexist. Although this result is demonstrated specifically for the storage effect with a focus on annual plant communities, the principles involved are general ones.

Key words: annual plant community; apparent competition; competition; seed predation; species coexistence; storage effect; temporal environmental variation.

INTRODUCTION

It has often been assumed that predation will promote coexistence of competing species by reducing the intensity of competition, and so prevent competitive exclusion (see review by Chase et al. 2002). Here we investigate circumstances leading to the opposite conclusion: when competing species coexist, adding predation, although reducing competition, undermines coexistence. In previous theoretical models, predation has promoted coexistence by enhancing distinctions between prey species through selective predation on competitively or numerically dominant species (Holt et al. 1994, Grover and Holt 1998, Krivan and Eisner 2003), or by creating fluctuations in time or space, which activate other mechanisms such as competition–colonization trade-offs (Caswell 1978) or relative nonlinearity (Kuang and Chesson 2008). However, no theoretical

model has ever supported the common perception that reduction or even elimination of competition is sufficient for coexistence (Chesson and Huntly 1997, Chase et al. 2002). The reason is that the reduction in competition is accompanied by the introduction of “apparent competition,” which is a form of density dependence, both within and between species, arising from feedback loops through predators (Holt 1977, 1984). Like competition, apparent competition can lead to exclusion (Chase et al. 2002). We go further by demonstrating a result that is quite the opposite of the conventional wisdom, with general implications for predation–competition interactions.

Stable coexistence mediated by predation has strong similarities to stable coexistence of competitors in the absence of predation. In the absence of predation, stable coexistence requires intraspecific competition to exceed interspecific competition. That leads to a tendency for species to recover from low density whenever perturbed there, which is the definition of stable coexistence that we use here (Chesson 2000). More generally, we can

Manuscript received 30 January 2008; revised 15 May 2008; accepted 19 May 2008. Corresponding Editor: J. M. Levine.

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think of stable coexistence as occurring when intraspecific density dependence (from all causes) is stronger than interspecific density dependence (Chesson 2000). Density-dependent predation (e.g., due to a numerical response of the predator to prey density) is the source of interspecific and intraspecific density dependence known as apparent competition (Holt 1977). Although addition of a predator has the potential to reduce competition, it may compensate for this reduction by the introduction of apparent competition. When predation introduces or enhances distinctions between species, it may intensify intraspecific density dependence relative to interspecific density dependence, and in this way can promote stable coexistence (see, for example, Holt et al. 1994, Grover and Holt 1998, Abrams 1999, Kuang and Chesson 2008).

When predation does not introduce or enhance species distinctions, it may undermine coexistence (Chase et al. 2002). One way that this might happen is if predation weakens the competition that maintains an intraspecific–interspecific distinction, replacing it by apparent competition without this distinction. Thus, predation would lessen the overall difference between intraspecific and interspecific density dependence, undermining coexistence. With so much focus on ways in which predation may promote coexistence, this potential has not been investigated to any significant degree.

We investigate this potential in a model of seed predation and competing desert annual plants where the competition-based coexistence mechanism is “the storage effect” (Chesson et al. 2004), and thus involves an interaction between fluctuating competition and species responses to the fluctuating physical environment. Desert annual plants provide one example in nature where both predation and variable environments have been studied empirically (although separately) as coexistence mechanisms (Davidson et al. 1984, Pake and Venable 1996). For annual plants, the storage effect works mostly through fluctuations in germination fraction, although correlation between yield and germination fraction (predictive germination) has the potential to enhance this effect (Pake and Venable 1996, Levine and Rees 2004). Importantly, germination rates are known to be highly environmentally dependent in nature, and to differ between species in their patterns of fluctuation over time, because different species have different germination responses to their common environment (Adonakis and Venable 2004, Chesson et al. 2004, Facelli et al. 2005).

In this paper, we focus on frequency-independent predation (i.e., predation in which the predator does not alter preferences for the various species as their relative abundances change). This choice prevents predation from generating differences between intraspecific density dependence and interspecific density dependence so that our key hypothesis can be investigated. In a subsequent paper (J. J. Kuang and P. Chesson, *unpublished manuscript*), we consider the interaction between the

storage effect and frequency-dependent predation as a coexistence mechanism.

MODEL AND METHODS

In this study, we add environmental variation to the seed predation model of Kuang and Chesson (2008). Briefly, the model is as follows: seeds germinate, the growing plants compete, flower, set seed, and have some of their seed consumed by a seed predator. The unconsumed seed is incorporated in the soil seed bank where it is assumed no longer susceptible to seed predation. For species j , N_j is the density of seed in the seed bank, and has germination fraction G_j . Without competition, a plant would produce, on average, Y_j seeds at the end of the season. However, competition reduces the actual yield below the maximum value of Y_j . We assume that competition can be quantified by a number C linearly dependent on the densities of the seedlings of each of the competing species. With competition of the Ricker form (Ricker 1954), the actual average number of seeds produced with competition is $Y_j e^{-C}$. Because C defines the total effect of competition on the reproductive fitness of an individual, it is “the response to competition” or “competitive response” of Goldberg (1990).

We use the Nicholson-Bailey formulation for predation (Hassell 2000). Thus, the fraction of seed surviving predation, and hence incorporated into the soil seed bank, is $e^{-a_j P}$, where P is predator density and a_j is the attack rate. The average number of seeds per plant finally incorporated into the soil bank is then $Y_j e^{-C-a_j P}$. The ungerminating or dormant fraction ($1 - G_j$) of the seed bank is subject to mortality, and is assumed to have a survival rate s_j to the beginning of the next germination season.

The above description gives the following equation for the dynamics of a given annual plant species j :

$$N_j(t+1) = N_j(t)[s_j(1 - G_j) + G_j Y_j e^{-C(t) - a_j P(t)}]. \quad (1)$$

Competition is given by the formula

$$C(t) = \sum_{j=1}^n G_j N_j(t) \quad (2)$$

which is simply the sum of the seedling densities of all n species. Predator reproduction is assumed to be proportional to the total number of seeds removed by the predator:

$$\sum_{j=1}^n G_j Y_j N_j e^{-C(t)} [1 - e^{-a_j P(t)}]. \quad (3)$$

The predator dynamics include also a density-independent survival term, $s_p P(t)$. The idea is that without harvesting new seed, the predator has positive survival from one year to the next, based either on stored seed or other resources, but this is not enough to allow population buildup. The complete equation for the

TABLE 1. General notation.

Symbol	Description
a	attack rate or instantaneous per capita predation rate
b	conversion rate between prey and predator
C	magnitude of competition, or "competitive response"
E	$= \ln(G)$, the environmental response
G	germination fraction
F	$= C + aP$, combined density-dependent limiting factor
i	index for invader
$\{-i\}$	superscript indicating a measurement with species i as invader
j	index for arbitrary species j
n	number of annual plant species
N	density of an annual plant species
P	predator density
r	population growth rate (when not a subscript) or index for a resident species (when a subscript)
s	seed survival in the seed bank
s_p	survival of the predator between years
Y	annual plant seed yield each season
β	$= 1 - s(1 - G)$, the fraction of seed lost from the seed bank over one year
ΔE	average fitness difference between a species and its competitors; more generally, the mean difference in standardized environmental responses (Chesson 1994)
ΔI	storage effect
η	$= \ln\{\bar{G}Y/[1 - s(1 - \bar{G})]\}$, the seed production per unit seed loss (log scale)
λ	finite rate of increase, $N(t+1)/N(t)$
ρ	correlation between environmental responses of different species

predator is thus

$$P(t+1) = \sum_{j=1}^n G_j Y_j N_j e^{-C(t)} [1 - e^{-a_j P(t)}] + s_p P(t). \quad (4)$$

A more general form of these equations that allows different plant species to have different competitive effects, and provide different levels of nutrition to the predator, is given in Appendix B, and is shown to reduce to Eqs. 1–4 (given above) using the technique of nondimensionalization. Table 1 and Appendix A summarize notation.

For simplicity, the equations above make the specific assumption that at any given time competition equally affects all growing plant individuals, regardless of species. This assumption means that stable coexistence is impossible in a constant environment without predation. Environmental fluctuations permit coexistence by favoring germination of different species in different years, which means that individual seedlings more commonly encounter conspecifics than heterospecifics, and create a distinction between intraspecific and interspecific competition at the population level when integrated over time. Our interest is in how predation modifies this outcome.

The germination fraction, G , is a critical temporally fluctuating population parameter for desert annual plants because fluctuations in this parameter differ between species and cause fluctuations in competition (Chesson et al. 2004), which are key requirements for coexistence by the storage effect. Thus, we assume that the germination fractions, G_j , fluctuate over time as a function of the environment, as described in the *Coexistence conditions* section below.

Throughout this paper, we focus on stable coexistence of competitors as defined by the invasibility criterion (Turelli 1978, Chesson and Ellner 1989, Ellner 1989). To evaluate the invasibility criterion, one species ("the invader") is removed from the system and reintroduced at low density after the densities of the $n - 1$ other species ("the residents") have adjusted to the absence of the invader (i.e., have converged to a joint stationary probability distribution). The success of invasion is measured by the invader's long-term growth rate (\bar{r}_i), the "invasion rate" for short, as defined in Appendix C. If the invasion rate is positive, the invader's population increases in the long run, and the invasion is successful. If all species are able to invade the system with the rest of the species as residents, we say the species coexist (see Appendix C for more details). The conditions for invasion that we derive here all depend on comparisons between resident and invader performance. Residents always have zero long-term growth rates (Appendix C), and so the critical issue is how invaders gain advantages over residents that allow positive invasion rates.

COEXISTENCE CONDITIONS

To analyze the model we use the framework for competition in a variable environment of Chesson (1994), which extends also to apparent competition (Appendix D). The germination fraction, $G_j(t)$, fluctuates over time, t , but we express the results of the model in terms of the natural log, $E_j(t) = \ln G_j(t)$, which we call the "environmental response." For simplicity, we assume that the $E_j(t)$ s for different species have the same probability distribution describing their fluctuations over time. We assume also that the $E_j(t)$ s are uncorrelated between years (a strictly random environ-

TABLE 2. Components of the invasion rate.

Component	Two annual plant species	Multiple annual plant species
ΔE_i	$\eta_i - \eta_r$	$\eta_i - \bar{\eta}$
ΔI_i	$s[\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})]$ $\approx s(1 - \rho)\bar{G}\text{var}(E)\bar{N}_r$	$s\sum_{r \neq i} [\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})]/n - 1$ $\approx s(1 - \rho)\bar{G}\text{var}(E) \Sigma \bar{N}_i/(n - 1)$

Notes: ΔE_i is the average fitness difference between a species and its competitors; ΔI_i is the storage effect, expressed on a per-generation scale. Other notation is defined in the *Coexistence conditions* section and summarized in Table 1.

ment), but have correlation ρ between species. In general, we expect ρ to be <1 so that different species do indeed have different responses to their common fluctuating environment (“species-specific responses to the environment,” Chesson et al. 2004), in accordance with the empirical findings. We assume that the predator is nonselective, and that seed survival rates and mean seed germination fractions are the same for every species. Although, selective predation is more realistic, it does not affect our key conclusions (Appendix F).

Under the assumptions specified here, the invasion rate, \bar{r}_i , can be calculated approximately (Appendix D), and used to define the conditions for coexistence whose accuracy is illustrated in Appendix E. Several important quantities are involved. First is a measure of the magnitude of the storage effect, which is denoted ΔI_i , and is given here by the formulae in Table 2. The storage effect is the only coexistence mechanism that appears in the absence of selective predation. Another important quantity is the average rate of seed loss from the seed bank, $\beta = 1 - s(1 - \bar{G})$, where \bar{G} is the average germination fraction, which under the present assumptions is the same for each species. A critical issue for the fitness of a species is the extent to which losses from the seed bank are replaced by new production. This leads to a definition of productivity as production per unit loss from the seed bank, viz $\bar{G}Y_i/\beta$, which we express on the log scale as $\eta_i = \ln \bar{G}Y_i/\beta$. In our development, productivities differ between species because they have different Y values. The quantity $1/\beta$ is the expected longevity of a seed in the seed bank, and provides a natural time unit for the model. As a consequence, the invasion rate is most simply expressed as the ratio \bar{r}_i/β , which is the invasion rate on a per generation timescale.

With these definitions, the invasion rate is given by the formula

$$\bar{r}_i/\beta = \eta_i - \bar{\eta} + \Delta I_i \quad (5)$$

(Appendix D), where $\bar{\eta}$ is the average η for the competitors of species i . The quantity ΔI_i (the storage effect, Table 2) is positive in general, and increases the invasion rates of all species. In contrast, unless all species have the same productivity, $\eta_i - \bar{\eta}$ is only positive for species with higher than average productivity: it is a measure of the average fitness of species i relative to its competitors in this system, and therefore is negative for species with lower than average productivity. In the absence of environmental fluctuations ΔI_i is

zero, and then the invasion rate in Expression 5 becomes simply $\eta_i - \bar{\eta}$. In these circumstances, only the species with highest productivity persists: all others are excluded (Appendix D). The storage effect counteracts these tendencies for exclusion, and if large enough can lead to positive invasion rates for all species, and hence coexistence. This outcome occurs when the storage effect for each species i , ΔI_i , is greater than its fitness disadvantage, $\bar{\eta} - \eta_i$.

The question now is what determines the value of ΔI_i ? Critical to ΔI_i is the concept of covariance between environment and competition. The environmental response (here \ln [germination fraction]), $E_j(t)$, for any species j , varies over time as a function of the physical environment. Competition, $C(t)$, varies over time too, and the joint pattern of variation between $E_j(t)$ and $C(t)$ (their covariance, Fig. 1) determines how population

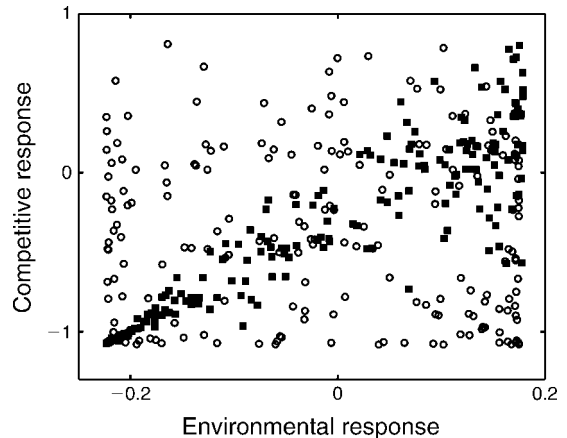


FIG. 1. Scatter plots of competitive response against the environmental response for an invader (open circles) and resident (solid squares) generated from a single simulation run (200 years). The resident displays positive covariance, while the invader has zero covariance. For the resident, low competition and a favorable environment can only occur after a run of bad years (lowering resident population size, and hence competition); but for the invader, this occurs whenever the environment is poor for the resident (which lowers competition at any population size) but good for the invader. For clarity of the figure, the responses are plotted transformed to a standard form, denoted \mathcal{E} and \mathcal{C} (Appendix D), centered on 0. The units are change in \ln (population size) per unit time. (All competitive response values greater than the minimum represent the presence of competition.) Parameters (Table 1) are: $s_r = 0.8$, $G_j \sim \beta(0.5, 0.5)$, independent between species, and $Y_r = 5$.

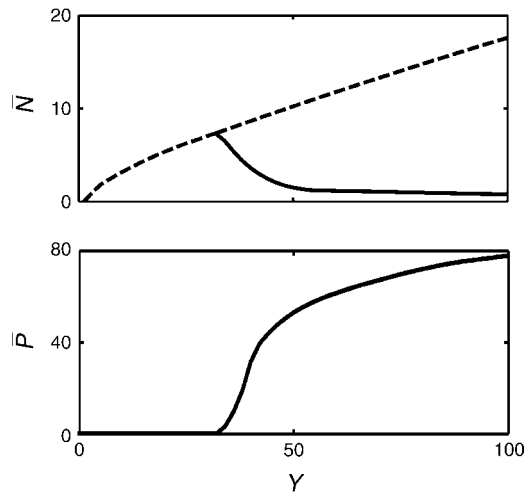


FIG. 2. Changes in average prey (\bar{N}) and predator (\bar{P}) densities as a function of seed yield, Y . The solid line shows densities with the predator; the dashed line shows average prey densities without the predator for seed yields where the predator would have nonzero average density. Parameters (Table 1) are: $s_1 = s_2 = 0.8$, $a_1 = a_2 = 0.05$, $s_p = 0.8$, G_1 and G_2 are independent β random variables with parameters (0.5, 0.5), which means that the germination rate is likely to be either high or low, with mean 0.5.

growth rates vary. Under positive covariance, a species is limited in its ability to take advantage of favorable environmental conditions because these favorable conditions are opposed by higher competition. Such positive covariance occurs in the present model for resident species because competition reflects total germination of residents, and therefore reflects their environmental responses (Fig. 1). With negative covariance, favorable environmental conditions are generally made more favorable by coinciding with lower competition, while with zero covariance, favorable environmental conditions occur independently of competition. Critically, the pattern of covariance depends on the state of a species as resident or invader. An individual seedling experiences the same magnitude of competition, $C(t)$, in year t regardless of species, but species contribute differentially to the magnitude of competition. Because competition does not reflect the environmental responses of invaders, covariance between environment and competition is lower for invaders, and can be zero or negative depending on the circumstances. This means that invaders are generally less limited than residents in their abilities to increase under favorable environmental conditions. In Fig. 1, the invader has an independent response to the environment compared with the resident, and it has times when it is strongly favored by the physical environment but at the same time experiences low competition (lower right in Fig. 1). Such times are extremely rare for the resident.

Covariance between environment and competition for any species j is measured by the standard statistical covariance over time, $\text{cov}(E_j, C)$, between the environ-

mental response $E_j(t)$ and competition, $C(t)$. The storage effect, ΔI_i , depends specifically on the difference in $\text{cov}(E_j, C)$ between resident and invader species; i.e., on $\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})$, where i is the subscript for the invader, r is the subscript for any of the $n - 1$ resident species, and the superscript $\{-i\}$ on C indicates that it is measured for species i as invader. This covariance difference measures specifically the advantage that invaders have over residents in their abilities to take advantage of favorable environmental conditions. In the two-species case, ΔI_i is just this covariance difference times the dormant seed survival rate, s (Table 2). Survival in the seed bank provides buffered population growth, which means that jointly unfavorable environmental and competitive conditions (low germination and high competition, upper left in Fig. 1) matter much less than jointly favorable conditions (lower right in Fig. 1). This fact makes covariance between environment and competition important to long-term population growth, allowing an invader to gain advantage over a resident through the covariance difference (Chesson et al. 2004). The multispecies case is a straightforward extension of the two-species case (Table 2). The multispecies case has multiple resident species, r , and then ΔI_i is proportional to the average covariance difference between resident and invader.

To understand the storage effect, it is necessary to understand why the resident–invader covariance difference is normally positive. The invader does not contribute to $C^{(-i)}$. So there is no direct causative relationship between E_i ($\ln[\text{invader germination}]$) and $C^{(-i)}$, but there still can be a correlation through a third factor, specifically the possibility that E_i is correlated with E_r because they both depend on the common environment of species i and species r . Without a correlation between E_i and E_r , $\text{cov}(E_i, C^{(-i)})$ is zero. With a correlation between E_i and E_r , $\text{cov}(E_i, C^{(-i)})$ is not zero because $C^{(-i)}$ depends on E_r , which is correlated with E_i . However, unless the correlation between E_i and E_r is perfect, $\text{cov}(E_i, C^{(-i)})$ should be less than $\text{cov}(E_r, C^{(-i)})$. In the particular cases where E_i and E_r are negatively correlated, or have zero correlation, $\text{cov}(E_i, C^{(-i)})$ will be negative or zero, in contrast to the positive value of $\text{cov}(E_r, C^{(-i)})$, as illustrated in Fig. 1.

MAGNITUDE OF THE STORAGE EFFECT, WITH AND WITHOUT PREDATION

The positive covariance difference explains the positive value of the storage effect. This explanation applies with or without predation. To understand the magnitude of the storage effect, and how predation affects this magnitude, we need to understand the magnitude of the covariance difference. First of all, note that $C^{(-i)}$ is a linear function of resident densities. Therefore, when resident densities are larger, the environment–competition covariances are larger. Indeed, in the approximate covariance formulae (Table 2) the storage effect, ΔI_i , is proportional to $\sum_r \bar{N}_r / (n - 1)$, which is the average over

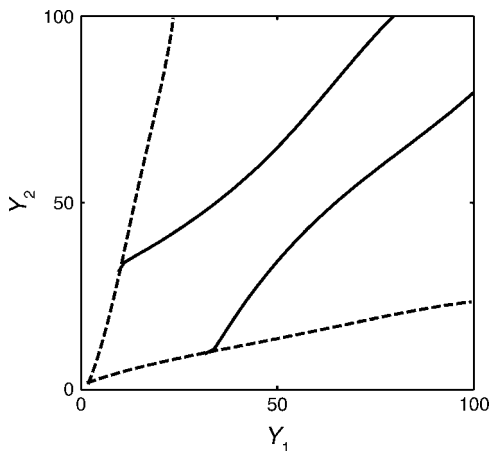


FIG. 3. Coexistence region for two annual plants with and without predation. The axis labels Y_1 and Y_2 are, respectively, seed yield per germinated seed for each of species 1 and 2. The region between the two dashed lines is the prey coexistence region without predation. The region between the two solid lines is the coexistence region with predation. Parameters (Table 1) are: $s_1 = s_2 = 0.8$, $a_1 = a_2 = 0.05$, and $s_p = 0.8$; G_1 and G_2 are independent β random variables with parameters (0.5, 0.5). Note that Y is proportional to $\exp(\eta)$.

resident species of their mean densities over time. This average mean resident density depends on several factors, including the presence of predation. Without predation, resident densities increase with productivity, and so ΔI_i increases with productivity. However, in the presence of predation, the usual expectation from the theory of trophic cascades (Oksanen and Oksanen 2000) is that increasing productivity increases not plant species density but the density of the seed predators. Fig. 2 shows the outcome for this model in the case of a single-species resident; the multispecies case (discussed later in this section) is similar but more complex.

In Fig. 2, a strong increase in mean resident density occurs with resident productivity while predation is absent. With the introduction of a predator, resident density decreases to low levels as productivity increases beyond the threshold level needed to maintain the predator. The predator is the beneficiary of productivity increases. Thus, in the presence of predation, we expect ΔI_i to decrease with increasing productivity, undermining coexistence. This prediction from the approximate invasion conditions is borne out in Fig. 3, where simulation results give the boundaries of the coexistence region in the two species case. There, we compare regions of coexistence with and without predation in terms of Y_1 and Y_2 values, which determine productivities. At low Y values (below $Y = 32$), the predator cannot be maintained in the system, but as Y increases from this value, predator density increases and is soon high enough to sharply narrow the coexistence region. Accompanying such changes is a sharp decline in resident covariance between environment and competition (Fig. 4A) as expected when the mechanism is the

storage effect. A similar change can be seen when the attack rate, a , increases past the value needed to sustain the predator (Fig. 4B).

Fig. 5 illustrates the effect of predation in a multispecies simulation. With the chosen parameter values, five species coexist in the absence of predation. Introducing a predator drives the long-term growth rates of three of these species to negative values at all densities, and these species drop out of the system. The remaining two prey species have much lower density, meaning that competition is much lower. According to the coexistence theory from the *Coexistence conditions* section, the only coexistence mechanism present is the storage effect relying on covariance between environment and competition, which is therefore weakened by this density reduction. The persisting species have

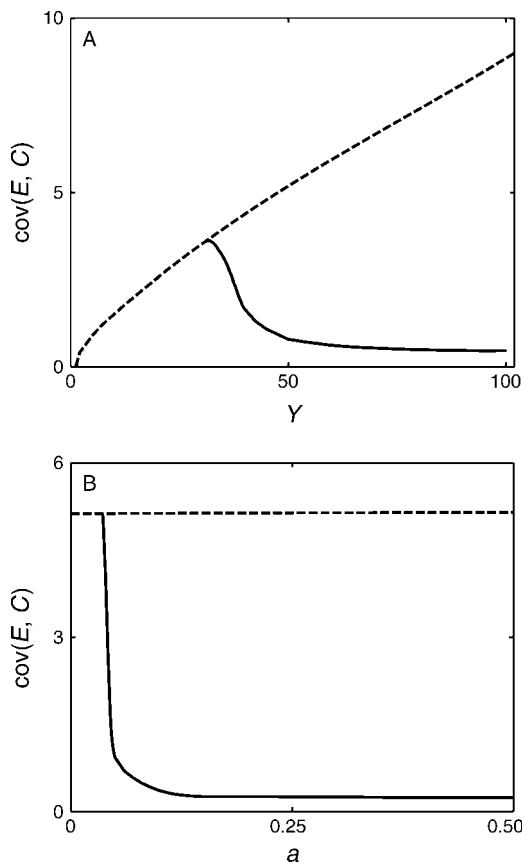


FIG. 4. Behavior of resident covariance between environment and competition, $\text{cov}(E, C)$, as predation intensity increases. Solid lines are with the predator present. Dashed lines are with the predator absent. (A) Productivity (in terms of seed yield per germinated seed, Y) increases predator density (see Fig. 1), and decreases $\text{cov}(E, C)$, in contrast to increasing $\text{cov}(E, C)$ without predation. Parameters are: $s = 0.8$, $a = 0.05$, and $s_p = 0.8$; $G \sim \beta(0.5, 0.5)$. (B) The predation intensity aP increases as the attack rate, a , increases, decreasing $\text{cov}(E, C)$ when the predator is present. Parameters are: $s = 0.8$, $Y = 50$, and $s_p = 0.8$; $G \sim \beta(0.5, 0.5)$. In both panels, the predator is not sustained where the solid line is absent.

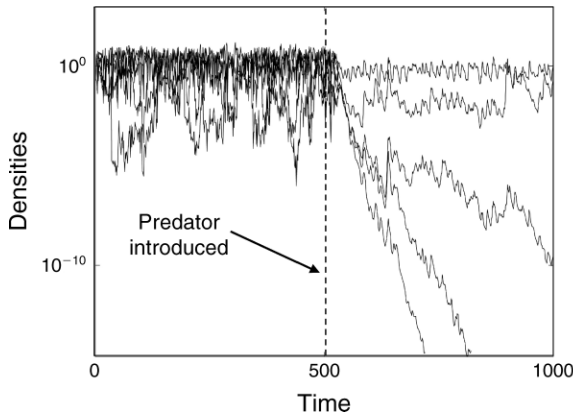


FIG. 5. Dynamics of five prey species with and without predation. Five species coexist before predator introduction. With the predator, the three species with the lowest productivities (η values) are driven extinct. Parameters are: $s_j = 0.8$, $a_j = 0.05$, G_j independent $\beta(0.5, 0.5)$, for $j = 1-5$, and $Y_1 = 28$, $Y_2 = 29.5$, $Y_3 = 31$, $Y_4 = 32.5$, $Y_5 = 34$, $s_p = 0.8$.

relatively small productivity differences, permitting their coexistence from this weakened storage effect.

In the multispecies case, the coexistence region is most easily represented in terms of the minimum η required for invasion. The approximation (Eq. 5) to the invasion rate implies that for invasion

$$\eta_i > \bar{\eta} - \Delta_i \quad (6)$$

so that the right-hand side indeed gives an approximation to the minimum value of η_i that allows a species to invade (i.e., the minimum condition for species i to persist in the presence of its competitors). This condition naturally increases with resident average productivity and decreases as the storage effect increases. If resident productivities are fixed, changes in the minimum invasion condition are direct reflections of changes in the storage effect. We determined the minimum invasion condition by simulation to see how the storage effect changes with the number of resident species (Fig. 6A, B). As explained previously, the multispecies storage effect (Table 2) is proportional to the average resident-invaser covariance difference, which is, in turn, proportional to the average over resident species of their mean densities, $\Sigma \bar{N}_r / (n - 1)$. Competition tends to fix the total mean density of resident species, $\Sigma \bar{N}_r$, as species richness changes (Appendix D), which means that the average mean density, $\Sigma \bar{N}_r / (n - 1)$, is approximately inversely proportional to the number of resident species, $n - 1$. Thus, the minimum invasion requirement must increase with the number of resident species, at least in the presence of competition alone.

The minimum invasion requirement is generally much greater in the presence of predation (Fig. 6A, B), but does not change with the number of residents in quite so simple a manner. The storage effect remains proportional to the average mean resident density (Table 2), and, like the two-species case, the lowering of this

average mean density by predation explains the effects of the predator. However, with few resident species, the average mean resident density, and hence the storage effect, are no longer inversely proportional to the number of resident species, because as the number of residents increases, the total mean density of prey, $\Sigma \bar{N}_r$, falls, and so the decline in the storage effect is more than proportional to the change in $1/(n - 1)$ alone. This effect is most striking as the number of residents increases from one to two (Fig. 6C, D), where the minimum η for invasion increases sharply, reflecting sharp decline in the storage effect corresponding to sharp decline in total mean prey density. The reason for this seems to be that with few resident species, fluctuations in total annual seed production lead to low mean predator density, and therefore low impact of the predator on the prey, giving a high total mean prey density. At higher numbers of prey species, their total mean density is less and approximately constant (i.e., fixed by the joint effects of competition and predation). Thus, the minimum invasion requirement becomes again approximately inversely proportional to $n - 1$, the number of resident species.

DISCUSSION

We find that predation can undermine the storage effect. In other words, contrary to conventional wisdom (Chase et al. 2002), we find that a generalist predator, by reducing the intensity of competition, undermines coexistence. Our focus is on annual plant communities, but the implications are much broader, as outlined in the *General implications and prospectus* section. Annual plant communities, especially those in arid environments, are of special interest because annual plants show striking dependence of seed germination on the physical environment (Adonakis and Venable 2004, Chesson et al. 2004, Facelli et al. 2005). In models, these features promote coexistence by the storage effect (Chesson 2000). These same natural systems are noted also for their abundance of seed predators (Davidson et al. 1985, Guo et al. 1995, Baez et al. 2006), which are principally rodents, ants, and birds. Seed predation potentially takes many different forms; for example, it can be selective where some prey species are preferred over others (Chesson 1983), nonselective where no such differences occur, or frequency dependent where preferences change with relative abundances (Roughgarden and Feldman 1975, Murdoch and Bence 1987, Celis-Diez et al. 2004). Although predation appears selective on annual plant species (Davidson et al. 1985, Brown and Heske 1990, Guo et al. 1995), to our knowledge there have been no studies of frequency-dependent predation in annual plant communities. Here we assume no frequency dependence, and no selective predation. Our key conclusions, however, are robust to selective predation as discussed in the *General implications and prospectus* section. Under these assumptions, our key finding is that predation undermines the storage effect,

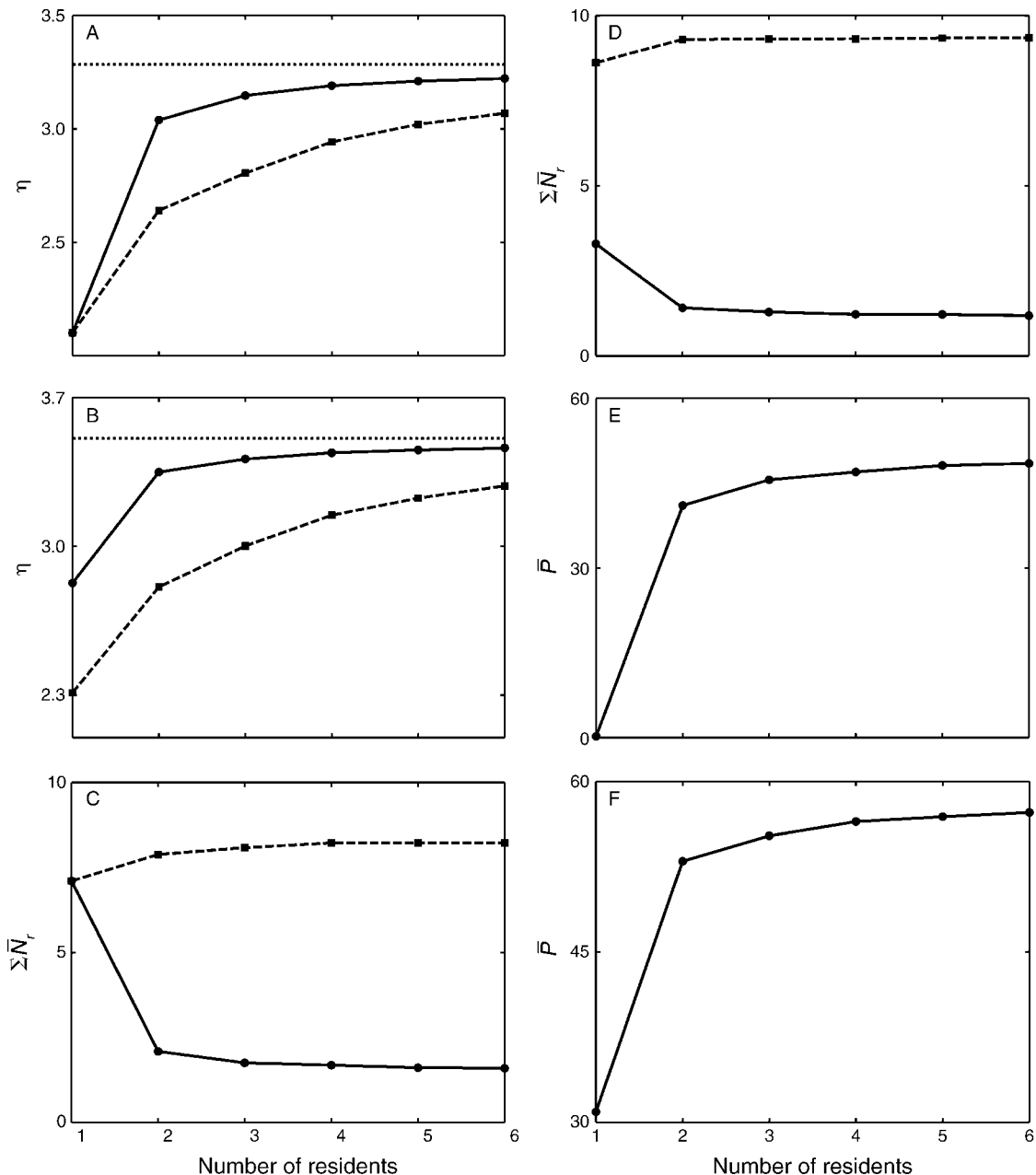


FIG. 6. Quantitative effects of predation in multispecies systems as a function of the number of prey species. (A, B) Minimum value of η , $\ln(\text{seed production})$ per unit seed loss, for invasion with predation (solid line), and without predation (dashed line). The horizontal dotted line represents the resident value of η . In (A), resident seed yield is close to the minimum necessary to sustain the predator in a single-prey system; in (B), resident seed yield is well above the minimum necessary to sustain the predator in a single-prey system. (C, D) Total mean resident seed density ($\Sigma \bar{N}_r$) as a function of the number of prey species, with (solid line) and without (dashed line) predation; parameters are as for (A) and (B), respectively. (E, F) Mean predator density as a function of the number of prey species; parameters are as for (A) and (B), respectively. In all cases, resident seed yields are equal ($Y=32$ in A and C, $Y=40$ in B and D), $s_j=0.8$, $a_j=0.05$, G_j independent $\beta(0.5, 0.5)$, for $j=1-6$.

and promotes exclusion, in essence because it reduces the intensity of competition. This finding is at odds with the conventional wisdom that diversity is limited by competition, and the addition of predation promotes diversity, although theoretical models have presented more complex views (Chase et al. 2002).

How predation undermines coexistence

As discussed previously (see *Introduction*), stable coexistence requires intraspecific density dependence to be stronger than interspecific density dependence. Although we assume that in any year competition between seedlings entails no distinction between intra-

specific and interspecific competition, the storage effect creates this distinction at the population level integrated over time. The addition of a predator reduces prey densities, and thereby reduces competition. Of most importance, it reduces the total magnitudes of interspecific and intraspecific density dependence attributable to competition. This outcome by itself would not undermine coexistence, because it need not change the relative magnitudes of interspecific and intraspecific density dependence. Indeed, the introduction of predation with constant mortality rates on prey species can reduce competition without necessarily altering the outcome of competition (Abrams 1977, Holt 1985, Chesson and Huntly 1997, Chase et al. 2002). However, predators often have a numerical response to their prey, as assumed here, and thus increase in abundance as prey densities increase (Baez et al. 2006). This outcome means that mortality rates on prey will increase also, creating interspecific and intraspecific density dependence between prey individuals, termed apparent competition by Holt (1977). When the predator has constant prey preferences, no distinction between intraspecific and interspecific density dependence is created, and so the predator reduces the intra–inter distinction provided by the storage effect, undermining coexistence.

In the storage effect, a distinction between intraspecific and interspecific density dependence arises from an interaction between environmental fluctuations and competition. Why does no similar interaction arise with apparent competition? With the storage effect, variation in the physical environment determines when a species is most actively growing and placing demands on resources (i.e., causing and experiencing competition). In the present model, germination is the population parameter that determines growth activity in the sense that only if an individual germinates can it grow and use resources. By having different germination responses to the physical environment, different species have different times when they are most actively growing and using resources. This fact leads to weaker effects of interspecific competition than intraspecific competition at the population level when integrated over time.

Such differences do not arise with apparent competition because of different assumptions about the time taken for predators to build up, compared with the time for resources to be drawn down. Higher germination is assumed to lead to higher competition between growing seedlings later in the same year. Higher germination might also lead to a higher seed crop for predators, allowing their abundance to increase, but due to developmental delays, that increase in abundance would not increase the predation rate until the following year when germination rates might well be different. Thus, high seed production by one set of species may lead to higher predation on a different set of species the next year. For example, a given species with high germination might cause the predator build up, but then have low germination the next year, and so only minimally

experience the effects of that predator buildup because the next year most of its seeds remained dormant in the seed bank.

These effects are most obvious in the simplest situation of two annual plant species with opposite germination responses to the physical environment. For the sake of illustration, assume also that the physical environment varies randomly over time favoring germination of each species equally frequently, but in different years. If one species germinates, the other does not, and so an individual species experiences only intraspecific competition, never interspecific competition. This extreme case thus leads to complete separation between species of the feedback loops associated with competition. Thus, intraspecific density dependence occurs without interspecific density dependence. However, even in this extreme circumstance, the feedback loops associated with predation are not separated. A species germinating well in a given year leads to high survival and reproduction in the predator population, and hence a higher predator population to attack the next year's seed crop. The critical issue is that next year's seed crop is just as likely to have been produced by the other plant species. Thus, 50% of the time high seed production by a plant species leads to higher predation on itself the next year (if its germination is favored also the next year), and 50% of the time this higher predation falls on the other species. When integrated over time, a given species has the same effects on itself as it has on the other species. In other words, equally strong intraspecific and interspecific density dependence effects arise from predation.

If predation is dominant over competition (i.e., if prey densities are maintained at low levels by the predator, allowing little competition), the overall strengths of intraspecific and interspecific density dependence will be similar, because they result predominantly from apparent competition. In this circumstance, a species with high average productivity compared with the other species, will maintain predator densities at a level that the other species cannot tolerate, and lead to exclusion. On the other hand, if predation is weak or absent, the separation of feedback loops through competition leads to much stronger intraspecific density dependence than interspecific density dependence, and the species may coexist in spite of large differences in average productivity.

The role of covariance between environment and competition

The undermining of the storage effect by predation is understood comprehensively by consideration of the concept of covariance between environment and competition, which has also been proposed as the route for rigorous field testing of the storage effect (Sears and Chesson 2007, Chesson 2008). As described in the *Coexistence conditions* and the *Magnitude of the storage effect, with and without predation* sections above, the

storage effect is proportional to the difference between invader and resident covariance. This difference also is responsible for the difference between intraspecific and interspecific density dependence. Fundamentally, the effects we see here come from weakening of covariance between environment and competition by predation, because predation weakens competition. Because predation is not itself correlated with the environment, covariance between environment and apparent competition, which might promote coexistence, does not occur. More generally, we can think of this absence of covariance between environment and apparent competition as occurring because the time taken for predator buildup can decouple predator abundance from the current physical environment (Ernest et al. 2000, Brown and Ernest 2002). The assumption of independence of the environment from one time to the next is an approximation to the high unpredictability of environmental fluctuations observed in nature (e.g., Pake and Venable 1995, Davidowitz 2002). However, high correlation from year to year might lead to a storage effect associated with apparent competition, potentially compensating for the decline in the storage effect associated with competition studied here (J. J. Kuang and P. Chesson, *unpublished manuscript*).

Predation naturally comes in different strengths. According to our model it is strongest when plant productivities are highest and attack rates are greatest. Correspondingly, covariance between environment and competition, and hence the storage effect, varies inversely with the strength of predation, being strongest with weak or no predation (Fig. 4). Although manipulating predation on appropriate temporal and spatial scales provides challenges in the field, nevertheless measuring covariance between environment and competition in the field (e.g., Sears and Chesson 2007, Chesson 2008), with and without predation, could test the ideas presented in this paper.

Multispecies coexistence

The storage effect is also affected by the number of species, weakening as the number of species is increased. In traditional terms, this outcome can be understood as the filling of temporal niche space as the number of species increases. In the terms discussed here, it represents a lowering of the difference in magnitude between intraspecific and interspecific effects due to the fact that average species densities are lower when there are more species. In effect, the total density of annual plants does not change greatly as the number of species is increased, and so the density achieved by any individual species is approximately inversely proportional to the number of species. In the formulae for the storage effect, this outcome is realized as lower magnitudes of covariance between environment and competition. A similar outcome is found in the presence of predation. Except when there are few prey species, the predator maintains an approximately constant total

prey density, and so again the average density of an individual species is approximately inversely proportional to the number of species. As a consequence the storage effect is approximately inversely proportional to the number of species both with and without predation, even though it is weaker with predation.

The situation occurring with few species deserves special mention. Because the species have different germination behavior, the phenomenon of complementarity, discussed in the ecosystem functioning literature (Yachi and Loreau 1999, Chesson 2001), is found. Complementarity means that ecosystem-level outcomes, such as total biomass, increase with the number of species due to the complementary nature of their niches. The ecosystem-level outcome expressed here is the total density of seeds in the seed bank. In the absence of predation, this quantity only weakly increases with the number of species, with the strongest increase between one and two species (Fig. 6). This outcome reflects the role of covariance between environment and competition, which reduces the difference in seed production between favorable and unfavorable periods, and hence reduces complementarity. Because apparent competition does not generate covariance, it gives full rein to complementarity. This outcome is seen in Fig. 6 as a major increase in predator density, and a major decrease in prey density, as the number of resident prey species increases from one to two. This effect is likely enhanced also by a nonlinear response of predator density to prey productivity.

General implications and prospectus

Throughout this work, we have assumed that the predator is nonselective. Selective predation can promote coexistence if predation is focused on the strongest competitor, a situation often referred to as a competition–predation tradeoff (Grover and Holt 1998, Abrams 1999, Kuang and Chesson 2008). However, selective predation still undermines the storage effect, and reduces the size of the coexistence region provided the predator has a numerical response to the prey, similar to the demonstrations here for nonselective predation (Appendix F). We have also assumed that the predator does not change seed preference over time as prey densities change. In particular, we have assumed that predation is not frequency dependent. Frequency-dependent predation can lead to a distinction between intraspecific and interspecific density dependence, promoting coexistence (Comins and Hassell 1976, Hutson 1984, Krivan 2003, Krivan and Eisner 2003). Although, this outcome would not alter the fact that predation can undermine the storage effect, it might not undermine coexistence if predation is sufficiently strongly frequency dependent. Examination of this issue is the subject of other work (J. J. Kuang and P. Chesson, *unpublished manuscript*). It is critical, however, that predation is density dependent through the numerical response of the predator to prey density, for this is the source of density

dependence that alters the ratio of interspecific to intraspecific density dependence so important to our results.

Although the work here is framed in terms of annual plants, temporally fluctuating germination fractions, and seed predation, the basic model is easily translated into other contexts, such as perennial species (Kuang and Chesson 2008), or annuals with temporal fluctuations and predation on other life history stages. For perennials, the storage effect works on recruitment of new individuals or biomass, with environmental fluctuations having their strongest effect on reproduction or juvenile survival (Chesson 2003). Predation or herbivory might occur at several stages in the life cycle, including the stage at which competition occurs. While buildup of predators or herbivores works with a time delay, the results given here extend easily to show that predation also undermines coexistence by the storage effect in the manner that we have seen for annual plant species, seed predation, and temporally fluctuating germination fractions. In a similar manner, the results of the annual model extend to having environmental fluctuations in early seedling mortality rather than in the germination fraction. The model is then mathematically equivalent to the perennial model, as is evident from Kuang and Chesson (2008: Appendix F). As in the perennial model, predation can be on other life history stages without affecting our conclusions. Moreover, the model used here can be applied also to freshwater zooplankton with an egg bank (Caceres 1997) and fish predators.

Although the most common perception of the role of predation is to make species coexistence easier (Chase et al. 2002), the work here highlights the previous theoretical finding that the circumstances are highly important in achieving this outcome. In Lotka-Volterra models, with predators having no numerical response to the prey (density-independent predation), it has long been known that predation can change the outcome of the interaction between species, but has no overall effect in promoting or demoting coexistence (see review in Holt 1985). This is not so, however, with nonlinear models (Holt 1985) where lowered prey density can sometimes change the ratio of intraspecific to interspecific competition. In a spatial context, predators have also been noted to promote coexistence when they act as disturbance agents, but with competition-colonization trade-offs being the coexistence mechanism, as first noted by Caswell (1978).

Multiple predators, specializing on different prey species have a strong coexistence promoting effect (Holt 1984), perhaps most prominently considered in the Janzen-Connell hypothesis (Adler and Muller-Landau 2005). Similar results are found when predation is frequency dependent. In all of these cases, predation leads to stronger intraspecific density dependence than interspecific density dependence. Although the potential for predation to undermine coexistence has long been known (Holt 1977, 1984, Chase et al. 2002), it has

received little emphasis in the literature. The powerful effect that we find here of predation undermining the storage effect indicates to us that much more attention should be given to this negative role of predation in species coexistence.

This work suggests a multitrophic-level perspective on species coexistence. We find coexistence to be the outcome of an interaction between resources, prey, and predators. Critical to our findings is the ability of predator species to respond numerically in the long run to changes in prey density. The addition of further trophic levels will modify the ability of a species to respond to such changes, so that trophic cascades (Knight et al. 2005, 2006), most often thought of in terms of their effects on the total biomass of all species at a given trophic level (Oksanen and Oksanen 2000), are likely also to have effects on diversity maintenance at a given trophic level.

ACKNOWLEDGMENTS

We are grateful for comments on the manuscript by Michael Turelli, Larry Venable, the Chesson lab discussion group, and four anonymous reviewers. We thank Larry Bai-lian Li for providing space in the University of California, Riverside, for J. J. Kuang. This work was supported by the GGAM block grant (UC Davis), a UC Davis dissertation-year fellowship, and NSF grants DEB-0542991 and DEB-0717222.

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APPENDIX A

General notation (*Ecological Archives* E090-010-A1).

APPENDIX B

A more general form of the model (*Ecological Archives* E090-010-A2).

APPENDIX C

Invasibility criteria (*Ecological Archives* E090-010-A3).

APPENDIX D

Derivation of the invasion rate (*Ecological Archives* E090-010-A4).

APPENDIX E

Comparison of true and approximate coexistence regions (*Ecological Archives* E090-010-A5).

APPENDIX F

Selective predation (*Ecological Archives* E090-010-A6).

Ecological Archives E090-010-A1

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix A. General notation

*	The equilibrium value of the variable
a	The attack rate or instantaneous per capita predation rate. In appendix D this symbol is used also as sensitivity of competition to the environment following (Chesson 1994).
b	Conversion rate between prey and predator
C	The magnitude of competition, or “competitive response”
\mathcal{C}	Standardized competitive response
d	Competitive coefficient
E	$= \ln(G)$, the environmental response
\mathcal{E}	Standardized environmental response
G	Germination fraction
F	$= C + aP$, combined density-dependent limiting factor
i	Index for invader
$\{-i\}$	Used as a superscript to indicate a measurement with species i as the invader
j	Index for an arbitrary species j
n	Number of annual plant species
N	Density of an annual plant species
$O(x)$	Standard mathematical notation meaning any quantity that remains of comparable magnitude to a variable x as x becomes small
P	Predator density
r	Population growth rate, when not a subscript. When a subscript, it is an index for a resident species.

- s Seed survival in the seed bank
- s_p Survival of the predator between years
- Y Annual plant seed yield each season
- $\beta = 1 - s(1 - \bar{G})$, the mean fraction of seed lost from the seed bank over one year
- ΔE Average fitness difference between a species and its competitors, or more generally, the mean difference in standardized environmental responses (Chesson 1994)
- ΔI The storage effect
- $\eta = \ln \left\{ \bar{G}Y / [1 - s(1 - \bar{G})] \right\}$, seed production per unit seed loss (log scale)
- λ Finite rate of increase, $N(t+1)/N(t)$.
- ρ Correlation between the environmental responses of different species
- σ^2 the common variance, $\text{Var}(E)$, of the environmental responses

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Ecological Archives E090-010-A2

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix B. A more general form of the model

As discussed in Kuang and Chesson (2008), a more general form of the model in the text is given by the equations

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

where

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

In these more general equations, two new parameters are introduced: d_j , a competition coefficient, and b_j , the conversion rate between prey consumption and predator birth. These two parameters give each prey species a unique competitive effect and a unique nutritional value to the predator. However, these more general equations do not give different dynamics because they reduce to expressions (1-4) of the text by nondimensionalization. For this nondimensionalize, the separate parameters b_j and d_j are replaced by their ratios b/d_j . Assuming that these ratios are the same for each species under the reasonable assumption that nutritional value and competitive effect are proportional to each other (Kuang and Chesson 2008), we can replace N by dN , P by $(d/b)P$, and a by $(b/d)a$. Equations (B.1) then become (1-4). It is worthwhile noting that in these nondimensionalized equations, seed density is measured in units of competitive effect per unit area because d is the competitive effect of a seedling, which may be proportional biomass.

Literature Cited

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Ecological Archives E090-010-A3

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix C. Invasibility criteria

Throughout this paper, we focus on stable coexistence of competitors defined by the invasibility (Turelli 1978, Chesson and Ellner 1989, Ellner 1989). In an invasion analysis, one species ('the invader') is removed from the system and reintroduced at low density (effectively zero) when the densities of $n - 1$ other species ('the residents') have converged to a joint stationary distribution. The success of invasion is measured by the invader's long-term growth rate (\bar{r}_i), 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, i.e.

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

which is the same as $\ln \lambda(t)$ where

$$(C.2) \quad \lambda(t) = N(t+1)/N(t)$$

is the finite rate of increase. Note that the finite rate of increase is defined even when $N(t) = 0$, although the right hand side of (C.2) would not apply. It is average individual fitness more generally, and this concept has a well-defined value in models. In our models, the finite rate of increase of a prey species is

$$(C.3) \quad \lambda(t) = s(1 - G(t)) + G(t)Ye^{-C(t)-aP(t)},$$

which remains meaningful when $N(t) = 0$. The growth rate is

$$(C.4) \quad r(t) = \ln \left(s(1 - G) + GYe^{-C(t)-aP(t)} \right).$$

The long-term population growth rate for residents is defined as

$$(C.5) \quad \bar{r} = \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} r(t)}{T} = \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} \ln N(t+1) - \ln N(t)}{T} = \lim_{T \rightarrow \infty} \frac{\ln N(T) - \ln N(0)}{T} .$$

For the residents, population densities will normally converge on a stationary stochastic process (Chesson and Ellner 1989, Ellner 1989) . Residents persist when the stationary probability distribution for the population density of each species is on the positive real numbers. For this stationary distribution, the expected value of $r(t)$ is zero because $E[\ln N(t+1)]$ must equal $E[\ln N(t)]$. The law of large numbers for stationary processes (Breiman 1968) now guarantees that $\bar{r} = 0$. For an invader species i , $r_i(t)$ is evaluated for $N_i(0) = 0$ using equation (C.4). This quantity, \bar{r}_i , can be regarded as the limit as $N_i(0) \rightarrow 0$ of the quantity on the right in (C.5) (taking this limit before letting $T \rightarrow \infty$), 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 ($\bar{r}_i > 0$) .

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Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix D. Derivation of the invasion rate

Coexistence of annual plant species in presence of environmental fluctuations is studied in detail in Chesson (1994). The basic idea is to evaluate the invasion rate, and partition it into terms representing the different coexistence mechanisms and the fitness comparison discussed in the text. Although Chesson (1994) did not consider predation explicitly, its general results apply here by substituting the combination of competition and predation, $F = C + aP$, for competition, C , in Chesson (1994). These general results require certain technical assumptions, which are satisfied whenever temporal fluctuations are small and the parameter differences between species are comparable to the variances of the environmental responses. Although these assumptions are restrictive, we shall find that they point the way to the larger patterns. We specialize the results of Chesson (1994) to the present context where we assume that the log germination fractions, the $E_j(t)$'s, have the same probability distribution for all species as well as at different times.

Thus, $\bar{E}_j = \bar{E}_k$ (where \bar{E}_j means the expected value, $E[E_j(t)]$, of the random variable $E_j(t)$).

Also, $\text{var}(E_j) = \text{var}(E_k)$, and we denote the common value of this variance by σ^2 . For the approximations below, we need to assume that this variance is small. However, appendix E shows that the results are qualitatively correct even with large σ^2 .

Like Chesson (1994), we assume independence over time, but the $E_j(t)$'s are correlated between species with common correlation ρ . For simplicity, we assume also that the seed dormancy rate, and predator attack rate, are same for each species, i.e. $s_j = s_k$, $a_j = a_k$, for each j and k . Thus, it follows that the seed loss rate, β , is same for each species, i.e., $\beta_j = \beta_k$. Chesson (1994) uses a slightly different definition of β_j , replacing \bar{G} by $\exp(E_j^*)$, where E_j^* is defined below. However, the difference is $O(\sigma^2)$, which changes the results below by $O(\sigma^4)$. This difference is less than the accuracy of the approximations below as explained in Chesson (1994),

and so is of no significance. To achieve this outcome, however, we must assume that the Y 's for different species differ only by $O(\sigma^2)$. The final assumption that we make is that the variance in F over time is also $O(\sigma^2)$. This is to be expected when the underlying models would have stable equilibria in the absence of environmental fluctuations (e.g. Ripa and Ives 2003). That will be the case in some regions of parameter space, but not in others. Nevertheless, the formulae we obtain do give qualitatively correct results, at least for two species (appendix E).

To begin the analysis, we note that from equation (C.4) that we can write the growth rate of species j in the form

$$(D.1) \quad r_j(t) = \ln \left(s(1 - e^{E_j}) + Y_j e^{E_j - F} \right),$$

where t is suppressed on the right in E_j and F for notational convenience; and Y , but not s , is assumed to depend on j . This formula is just a special case of the general form used in Chesson (1994), where

$$(D.2) \quad r_j(t) = g_j(E_j, C_j),$$

g_j is an arbitrary continuously twice differentiable function, E_j is an environmental response satisfying the assumptions above, and C_j is the competitive response of species j , which is here simply F , the combination of competition and predation. Thus, here $r_j(t) = g_j(E_j, F)$.

The analysis in Chesson (1994) uses a quadratic-level two-variable Taylor expansion of r_j in E_j and F . This expansion is then averaged over time to get the invasion rate. By expanding the growth rate to quadratic order, it is possible to see the effects of means (from the linear part the Taylor expansion), and variances and covariances (from the quadratic terms of the Taylor expansion) on the invasion rate. Of special note here is the covariance between E_j and F , because it leads to the storage effect. It arises in the quadratic expansion from the product of E_j and F , which can be thought of as defining the interaction between E_j and F in determining r_j .

This interaction, in biological terms, measures buffered population growth, as discussed in the text.

To perform a Taylor expansion, we must first choose fixed values, E_j^* and F^* , of E_j and F , about which to perform the expansion. The standard choice (Chesson 1994) is fixed values with the property

$$(D.3) \quad g_j(E_j^*, F^*) = 0 \quad (\text{i.e. } \ln(s(1 - e^{E_j^*}) + Y_j e^{E_j^* - F^*}) = 0),$$

i.e. these are values at which the growth rate (D.1) would be zero. A natural choice for F^* is the average over species of η because η_j is the value of F that gives species j zero growth in a constant environment. However, it does not matter exactly what F^* is so long as it is within $O(\sigma^2)$ of the constant-environment equilibrium F values of all species (Chesson 1994). Having chosen F^* , E_j^* is chosen as the solution to equation (D.3).

We wish to understand the effects that E_j and F , and their interaction, have on the growth rate r_j . The first part of this process is to transform the variables E_j and F into variables \mathcal{E}_j and \mathcal{C}_j representing their direct effects on r_j , with the other variable held fixed respectively at F^* and E_j^* , as follows:

$$(D.4) \quad \mathcal{E}_j = g_j(E_j, F^*), \text{ i.e. } \mathcal{E}_j = \ln \left\{ s \left[1 - e^{E_j} \right] + Y_j e^{E_j - F^*} \right\},$$

and

$$(D.5) \quad \mathcal{C}_j = -g_j(E_j^*, F), \text{ i.e. } \mathcal{C}_j = -\ln \left\{ s \left[1 - e^{E_j^*} \right] + Y_j e^{E_j^* - F} \right\}.$$

In these standard forms, \mathcal{E}_j and \mathcal{C}_j have the property that they are increasing functions respectively of E_j and F , but are in the same units as r_j . We can thus use these variables to partition out the direct effects of environment and competition on r_j , leaving behind their interaction. For example, averaging \mathcal{E}_j over time gives the average effect of the environment on the growth of species j , at a fixed level of the density dependent factor F , and is used below to

derive the fitness comparison measure $\eta_i - \bar{\eta}$, which then is a distinct element of the invasion rate, separate from the storage effect.

To proceed, Chesson (1994) uses these standard variables, rather than E_j and F directly, for the quadratic expansion of r_j . Averaging the resulting approximation over time then shows that the invasion rate can be expressed in terms of three generic components, \bar{r}_i' , ΔN , and ΔI , which correspond to different coexistence mechanisms, as follows:

$$(D.6) \quad \bar{r}_i = \bar{r}_i' - \Delta N + \Delta I,$$

(Chesson 1994, equation 52). The quantity \bar{r}_i' represents the effects of average fitness differences and coexistence mechanisms that do not rely on fluctuations over time. The term ΔN is the fluctuation-dependent mechanism called relative nonlinearity (see Chesson 1994), and ΔI is the storage effect. The relative nonlinearity term depends on differences between species in the shape of $g_j(E_j, F)$ as a function of F , and the variance of F . Here those shape differences depend on the differences between the Y_j , but as we assume these differences to be $O(\sigma^2)$, and $\text{var}(F)$ is also assumed to be $O(\sigma^2)$, those shape differences are too small to be important in the final result, and so ΔN can be ignored here.

Because there is only one limiting factor, $F = C + aP$, there is no fluctuation-independent coexistence mechanism, and so the term, \bar{r}_i' , consists only of average fitness differences. These fitness differences are written as ΔE in Chesson (1994). Thus, (D.1) reduces to the formula

$$(D.7) \quad \bar{r}_i = \Delta E + \Delta I.$$

Next we show that ΔE can be approximated as $\beta (\eta_i - \bar{\eta})$. The formal definition of ΔE is

$$(D.8) \quad \Delta E = E[\mathcal{E}_i] - \sum_{r \neq i}^n q_{ir} E[\mathcal{E}_r],$$

where q_{ir} is the partial derivative of \mathcal{E}_i with respect to \mathcal{E}_r . This particular quantity q_{ir} serves the purpose of adjusting the comparisons between species due to differences in their sensitivities to competition (here, read F). For example, a less sensitive species is not harmed so easily by a more sensitive species, leading to a low q_{ir} for that comparison. In more general models, q_{ir} also has the effect of partitioning out fluctuation-independent mechanisms. For this model, table II of Chesson (1994) gives $q_{ir} = \beta_i / \beta_r (n - 1)$. Because the β 's are the same here, as explained above, $q_{ir} = 1 / (n - 1)$. Hence

$$(D.9) \quad \Delta E = E[\mathcal{E}_i] - \frac{1}{n-1} \sum_{r \neq i}^n E[\mathcal{E}_r],$$

which is a comparison of mean invader and resident environmental responses. This quantity can be evaluated to sufficient accuracy following the techniques of Chesson (1994). First \mathcal{E}_j is expanded as a second order Taylor approximation about the value E_j^* to give

$$(D.10) \quad \mathcal{E}_j \approx (1-s)(E_j - E_j^*) + \frac{1}{2}s(1-s)(E_j - E_j^*)^2,$$

where “ \approx ” means with an $O(\sigma^4)$ error. Taking expected values gives

$$(D.11) \quad E[\mathcal{E}_j] \approx (1-s)(E[E_j] - E_j^*) + \frac{1}{2}s(1-s)\sigma^2,$$

using the fact (Chesson 1994) that $E[(E_j - E_j^*)^2] = \sigma^2 + O(\sigma^4)$. Because $E[E_j]$ is the same for all species, we see that

$$(D.12) \quad \Delta E \approx -(1-s)(E_i^* - \bar{E}^*),$$

where the bar on E^* means the average over resident species. The equilibrium relationship (D.3) allows Y_j and hence η_j to be written as a function of E_j^* . Differentiating this relationship shows that $d\eta_j/dE_j^* = -(1-s)/(1-s[1 - \exp(E_j^*)])$, which equals $-(1-s)/\beta + O(\sigma^2)$. By assumption, the E^* 's differ between species by $O(\sigma^2)$, and so linearly approximating the E^* difference (D.12) in terms of η differences gives

$$(D.13) \quad \Delta E \approx \beta(\eta_i - \bar{\eta}).$$

Table 2 of the text follows the convention of (Chesson 2008) and lists ΔE in natural units (per seed life time) as simply $\eta_i - \bar{\eta}$, i.e. (D.13) divided by β . Note that $\bar{\eta}$ is the average of the η 's of resident species, not the average η of all species, and thus differs slightly from the nominal F^* value suggested here. In the absence of environmental fluctuations, ΔE would be the only term in \bar{r}_i , and only species with higher than average η could invade. In fact, in that case, the growth rates of the species are ranked uniformly in magnitude according to the value of η , which directly reflects Y , and thus only the species with largest η value can persist in the long run. Its long-term growth rate must be zero as a resident. All other species have negative long-term growth rates and so are excluded.

The second term in the formula (D.7) for \bar{r}_i , is the storage effect, ΔI . To define it, we need a formal measure of the interaction between environment and competition (buffered population growth discussed in the text), which for species j is the quantity γ_j given as

$$(D.14) \quad \gamma_j = \frac{\partial^2}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \Bigg|_{\mathcal{E}_j = \mathcal{C}_j = 0}.$$

The storage effect is defined in Chesson (1994, equation 23) as

$$(D.15) \quad \Delta I = \gamma_i \text{cov}(\mathcal{E}_i, \mathcal{C}_i^{\{-i\}}) - \sum_{r \neq i}^n q_{ir} \gamma_r \text{cov}(\mathcal{E}_r, \mathcal{C}_r^{\{-i\}}),$$

where the superscript $\{-i\}$ specifies a calculation with species i in the invader state. Table II of Chesson (1994) gives the γ 's here as identical, and equal to $1 - (1-s)^{-1}$. Moreover, Chesson (1994) shows that \mathcal{E}_j can be linearly approximated as $(1-s)(E_j - E_j^*)$, and \mathcal{C}_j can be linearly approximated as $\beta(F - F^*)$. (All these results from Chesson (1994) can be easily verified directly from expressions (D.1), (D.4) and (D.5), above, with a little calculus and algebra.) It follows that

$$(D.16) \quad \text{cov}(\mathcal{E}, \mathcal{C}) = (1-s)\beta \text{cov}(E, F) + O(\sigma^4).$$

Recalling that $q_{ir} = \beta_i/\beta_r(n-1) = 1/(n-1)$, it follows that

$$(D.17) \quad \Delta I \approx s\beta \left\{ \frac{1}{n-1} \sum_{r \neq i} \left[\text{cov}(E_r, F^{\{i\}}) - \text{cov}(E_i, F^{\{i\}}) \right] \right\}.$$

Since $F = C + aP$, only C is directly a function of the E_j 's, and the E_j 's are not correlated over time, $P(t)$ has zero covariance with $E_j(t)$ — predator density does depend on past values of E_j , but does not depend on the current one. Thus, (D.13) reduces to

$$(D.18) \quad \Delta I \approx s\beta \left\{ \frac{1}{n-1} \sum_{r \neq i} \left[\text{cov}(E_r, C^{\{i\}}) - \text{cov}(E_i, C^{\{i\}}) \right] \right\},$$

which is reported in natural units in table 2 (i.e. divided by β following the convention of Chesson 2008).

Further simplification of this formula is possible by using expression (80) of Chesson (1994), which shows that (D.18) can be written as

$$(D.19) \quad \Delta I \approx \beta \bar{a} (-\gamma) (1 - \rho) \alpha^2 \sigma^2,$$

where α is $1-s$ (Table II of Chesson 1994 — it is just the linear coefficient in the expansion (D.6) of \mathcal{E}_j in terms of E_j), and here \bar{a} is not the attack rate, but the average over resident species of the quantity

$$(D.20) \quad a_r = E \left[\partial C^{\{i\}} / \partial \mathcal{E}_r \right].$$

(The quantity a_r arises because it defines the slope in the linear approximation of $C^{\{i\}}$ in terms of \mathcal{E}_r , and thus allows the covariance to be approximated.). A little calculus shows that $a_r =$

$\bar{G}E[N_r]/(1-s)$, and so (D.19) becomes

$$(D.21) \quad \Delta I \approx \beta s (1 - \rho) \sigma^2 \bar{G} \sum E[N_r]/(n-1) .$$

In the absence of predation, Chesson (1994, appendix II) shows that $E[C]$ must be within $O(\sigma^2)$

of F^* . However, $E[C] = E[G] \cdot \sum_r E[N_r] = \bar{G} \sum_r \bar{N}_r$. Hence, as the number of species, n , increases, total resident density cannot change greatly.

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Ecological Archives E090-010-A5

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix E. Comparison of true and approximate coexistence regions.

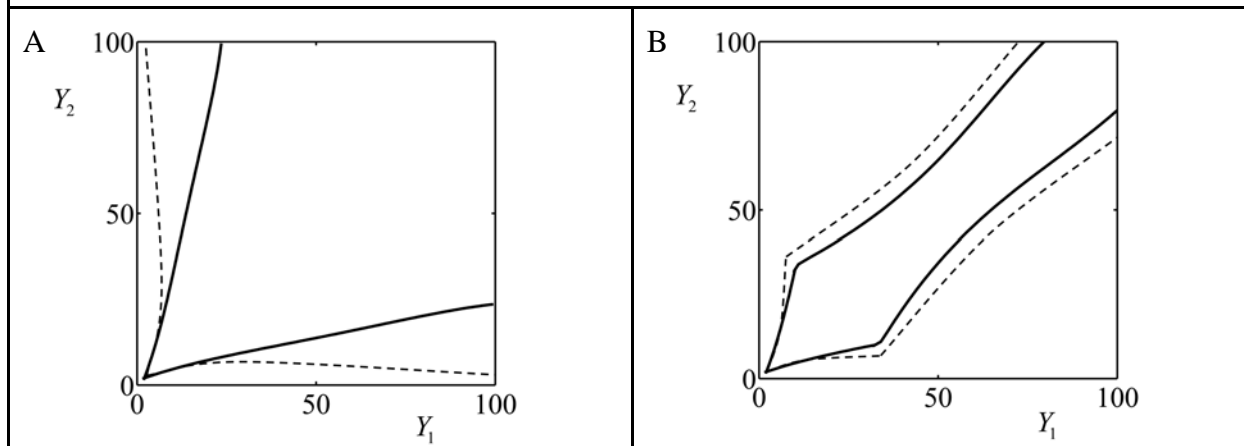
The figures in the text show coexistence regions defined by simulation. However, analytical approximations are used to obtain theoretical insight. Below, we compare the coexistence regions that are implied by the analytical approximations with those found by simulation. For the analytic regions, we use the two-species invasion rate combining (D.13) and (D.18) for $n = 2$, to obtain

$$\bar{r}_i / \beta = \eta_i - \eta_r + s \left[\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)}) \right].$$

Now $\text{cov}(E_j, C^{(-i)}) = \text{cov}(E_j, G_r) \bar{N}_r$, which in (D.21) is approximated by $\sigma^2 \bar{G} \bar{N}_r$ for $j = r$, and $\rho \sigma^2 \bar{G} \bar{N}_r$ for $j = i$, when σ^2 is small. Qualitatively, these two formulae are the same. As we have large σ^2 , in the graphs below, we use the formula $\text{cov}(E_j, C^{(-i)}) = \text{cov}(E_j, G_r) \bar{N}_r$. Note that the true and approximate coexistence regions give essentially the same message, although quantitative differences are present.

Figure E1: Comparison of true and approximate coexistence region.

On the left is the comparison between true (between the two solid lines) and approximate (between the two dashed lines) coexistence regions without predation. On the right is this comparison with predation. Parameters: $s_1 = s_2 = 0.8$, $a_1 = a_2 = 0.05$, $s_p = 0.8$, G is beta random variable with parameters (0.5,0.5).



Ecological Archives E090-010-A6

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

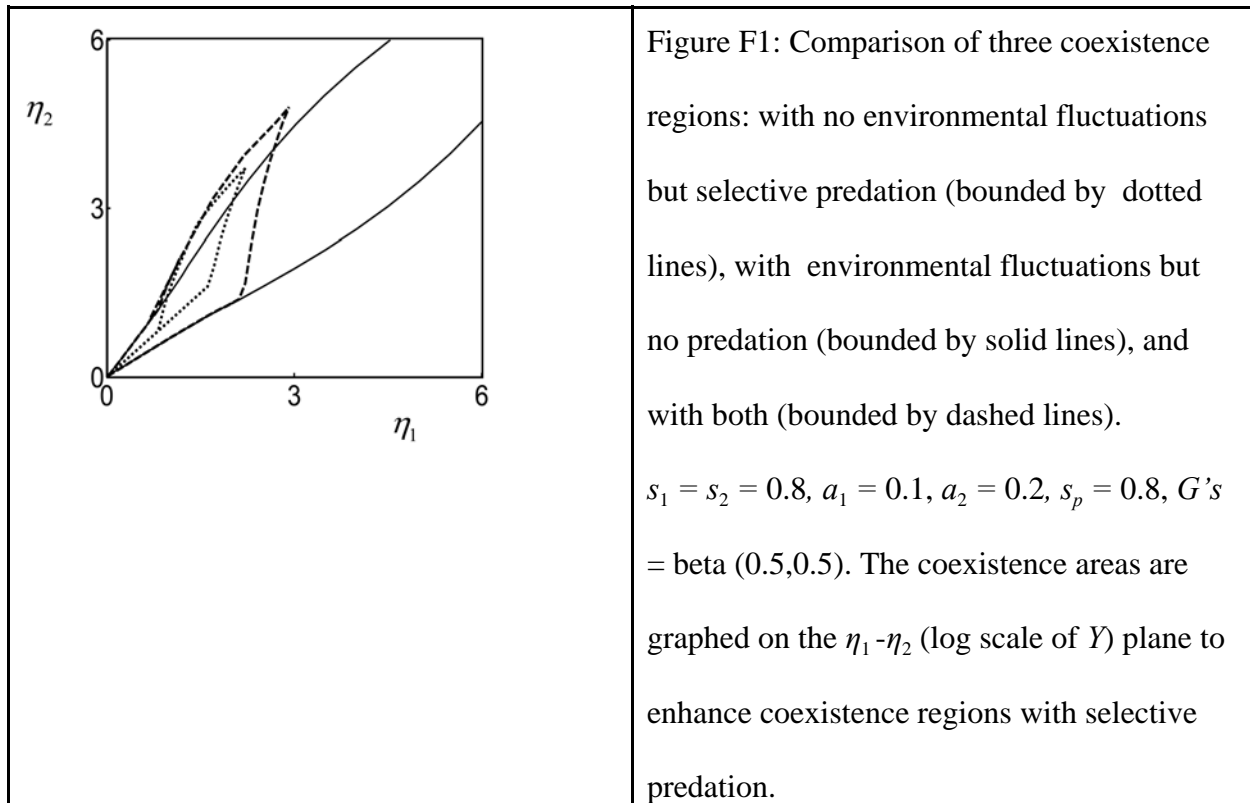
Appendix F. Selective predation

The text considers the effects of nonselective predation on species coexistence. Here we check the extent to which those findings hold up in the more realistic but more complex case of selective predation, i.e. when the attack rates, a , differ between species. However, attention is restricted to the case where the attack rates do not change with density, i.e. frequency dependence is not considered. It is well-known that selective predation can lead to coexistence when it is associated with a predation-competition tradeoff, as discussed in the text. That case is discussed for seed predation with the same model as we use here in Kuang and Chesson (2008). Although the existence of selective predation will allow coexistence in some situations where it would not be possible without it, selective predation might nevertheless continue to undermine the storage effect in a variable environment, with the potential of greatly reducing the coexistence region, as we have found here for the case of nonselective predation.

In the presence of selective predation and environmental fluctuations, the potential exists for three coexistence mechanisms: predation-competition tradeoffs, the storage effect, and another fluctuation-dependent mechanism termed *relative nonlinearity* (Chesson 1994) discussed for this model in a constant environment in Kuang and Chesson (2008). Our purpose here is not to disentangle the contributions from these different mechanisms, but instead simply to see how the coexistence region without predation changes when selective predation is added. In general we find that although selective predation does lead to some new opportunities for coexistence, it greatly reduces the coexistence region overall. We illustrate this outcome in Fig. F1.

Starting with selective predation, Fig. F1 shows that adding environment fluctuations increases the area of coexistence region: the region with the dotted boundary expands to the region with the dashed boundary. However, predation continues to undermine the effect of

environmental fluctuations: the area enclosed by the solid lines is replaced by the smaller region enclosed by the dashed lines. Thus, predation can contribute to coexistence through competition-predation tradeoffs, but the stronger mechanism, the storage effect, is undermined by predation, and overall predation has a strong negative effect on coexistence when the storage effect is present.



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