



Interacting coexistence mechanisms in annual plant communities: Frequency-dependent predation and the storage effect

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ARTICLE INFO

Article history:

Received 25 August 2009

Available online 27 November 2009

Keywords:

Frequency-dependent predation
Switching
Foraging constraints
Foraging behavior
Apparent competition
Resource competition
Species coexistence
Storage effect
Annual plant community
Seed predator

ABSTRACT

We study frequency-dependent seed predation (FDP) in a model of competing annual plant species in a variable environment. The combination of a variable environment and competition leads to the storage-effect coexistence mechanism (SE), which is a leading hypothesis for coexistence of desert annual plants. However, seed predation in such systems demands attention to coexistence mechanisms associated with predation. FDP is one such mechanism, which promotes coexistence by shifting predation to more abundant plant species, facilitating the recovery of species perturbed to low density. When present together, FDP and SE interact, undermining each other's effects. Predation weakens competition, and therefore weakens mechanisms associated with competition: here SE. However, the direct effect of FDP in promoting coexistence can compensate or more than compensate for this weakening of SE. On the other hand, the environmental variation necessary for SE weakens FDP. With high survival of dormant seeds, SE can be strong enough to compensate, or overcompensate, for the decline in FDP, provided predation is not too strong. Although FDP and SE may simultaneously contribute to coexistence, their combined effect is less than the sum of their separate effects, and is often less than the effect of the stronger mechanism when present alone.

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1. Introduction

The complexity of ecological systems suggests that few ecological phenomena have a single cause. Species coexistence is no exception. Although most theoretical studies tend to focus on a single cause, species coexistence is likely caused by multiple mechanisms in nature. Moreover, these mechanisms are quite unlikely to be additive when present in combination. To understand non-additive (i.e. interactive) situations, multiple mechanisms must be studied in combination. We consider here interacting effects of coexistence mechanisms associated with predation, competition, and environmental fluctuations.

Recent work has drawn attention to similarities in the way predation and competition affect species coexistence (Chesson and Kuang, 2008; Krivan, 2003; Kuang and Chesson, 2008, 2009; Leibold, 1996) bolstering earlier work (Holt, 1984; Kotler and Holt, 1989). These developments led to a perspective where coexistence and exclusion mechanisms can both be classified as competition based or predation based. Following long-standing ideas in ecology (MacArthur and Levins, 1967), a competition-based coexistence mechanism works by intensifying intraspecific competition relative to interspecific competition,

promoting coexistence (Chesson and Kuang, 2008). Resource partitioning provides the classic example of a competition-based mechanism. In a similar way, predator partitioning, where predators are relatively specialized to prey on different prey species, leads to a predation-based coexistence mechanism, because it intensifies intraspecific apparent competition relative to interspecific apparent competition between prey individuals, again promoting species coexistence (Chesson and Kuang, 2008).

Along with this mechanism classification comes a new understanding of how competition-based and predation-based mechanisms can interact with each other (Chesson and Kuang, 2008). The strength of a competition-based coexistence mechanism, in terms of how strongly it promotes species coexistence, is proportional to the overall strength of competition, as discussed in Chesson and Kuang (2008). Thus, if the addition of predation weakens competition, it will undermine competition-based mechanisms. Likewise, the strength of a predation-based mechanism is proportional to the strength of apparent competition, which can be weakened with the addition of competition.

Chesson and Kuang (2008) studied mechanism classification and mechanism interactions in generic Lotka–Volterra models of resource partitioning and predator partitioning. Lotka–Volterra models are useful for establishing general tendencies, but their linear per capita growth rates restrict application in nature. Nonlinear models, and models with environmental variation, may introduce new phenomena modifying the predictions of

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Lotka–Volterra models. Thus, for understanding these issues, it is essential to study a variety of models applying to various important situations in nature. One system that has been much studied empirically and theoretically is the desert annual plant system (Chesson et al., 2004). For that system, we address here interactions between predation-based and competition-based mechanisms in a model that deviates in several ways from the Lotka–Volterra model of Chesson and Kuang (2008). First, in this model, environmental variation drives the competition-based mechanism, the storage effect. Second, here there is just a single predator, and so predator partitioning by prey is not possible. Instead, the predator has frequency-dependent behavior, which introduces major nonlinearities in the model. These nonlinearities introduce the potential for a single predator to act in a manner that is similar to the action of several predators that focus on different prey species, as discussed below.

This model has application to arid environments where high diversities of annual plant species often occur in areas of sparse perennial plant cover. Seed predation is an important phenomenon in desert annual communities (Davidson et al., 1985). However, the storage effect has been a favored hypothesis for desert annual plants (Chesson et al., 2004), as discussed below. In these systems, predation-based and competition-based mechanisms have been investigated separately as species coexistence mechanisms (Chesson et al., 2004; Davidson et al., 1985). In a recent publication, we showed how the addition of predation to a model of competing annual plant species undermines coexistence by the storage effect (Kuang and Chesson, 2009). However, in that study, there was a predator, but no predation-based coexistence mechanism. By reducing the strength of competition, predation reduced the strength of competition-based mechanisms, but there was no opportunity for competition-based coexistence to be replaced by predation-based coexistence. Thus, we could not address the interaction between competition-based and predation-based coexistence mechanisms in annual plant communities. We do that here by considering predators with frequency-dependent behavior.

Frequency-dependent predation (FDP), or “switching” (Murdoch et al., 1975), is a powerful coexistence mechanism. FDP promotes coexistence by shifting predation to the more abundant species, facilitating recovery of other species from low density. In effect intraspecific apparent competition is strengthened relative to interspecific apparent competition by frequency-dependent behavior, which automatically gives a species at low density an advantage. A similar outcome is promoted with multiple predators by predator partitioning in the Lotka–Volterra models of Chesson and Kuang (2008).

FDP can occur for many reasons. We divide them into two classes, which have different effects on prey populations: constraints on behavior, and optimal behavior. Constraints on behavior include the difficulties of learning about infrequently encountered prey, leading to poor search image development, poor foraging technique, and poor knowledge of prey location (Hughes and Croy, 1993; Murdoch et al., 1975; Persson, 1985; Warburton and Thomson, 2006). All these factors potentially result in reduced predation on any prey species if its relative abundance declines. With optimal diet selection (Charnov, 1976; MacArthur and Pianka, 1966), the predator seeks the most nutritious prey per unit of predation effort, only seeking less nutritious prey when the most nutritious prey are hard to find. Optimal diet selection leads to an asymmetrical form of FDP because less nutritious prey are never favored over more nutritious prey, regardless of their frequency. Optimal patch selection, where the predator remains longer in denser patches (Garb et al., 2000), combined with spatial segregation of prey species, also leads to FDP (Bonsall and Hassell, 1999; Marini and Weale, 1997; Murdoch, 1977; Murdoch et al.,

1975), but in this case there is no necessary asymmetry between species. In this paper, for simplicity, we focus on symmetric FDP that would result from foraging constraints.

We consider the competition-based coexistence mechanism, the storage effect (SE), because it has been a prominent hypothesis for the coexistence of desert annual plants (Chesson et al., 2004; Chesson and Huntly, 1989; Pake and Venable, 1995). With SE, temporal environmental fluctuations promote coexistence when different species have different responses to those fluctuating conditions, leading to a form of temporal resource partitioning (Chesson et al., 2004). Specifically, when a species drops to low density its increase is not opposed by intraspecific competition, and because it may experience a favorable physical environment when its competitors do not, it may increase at such times unopposed by interspecific competition also. A seed bank, or other persistent stages in the life cycle, prevent strong negative growth at other times, leading overall to recovery from low density, which promotes species coexistence. This is the storage effect.

Before SE became a popular explanation of coexistence in annual communities, predation was a favored hypothesis (Davidson et al., 1985). However, the recent understanding of competition–predation interactions, discussed above, suggests that it is time to revisit this hypothesis and how it interacts with the storage effect. This work provides the theoretical underpinnings of these questions. Below we present our model of annual plant dynamics incorporating competition, predation and environmental fluctuations. We analyze our model using techniques that provide quantitative measures of the strengths of the coexistence mechanisms (Chesson, 1994). We use these measures to study changes in mechanism strength as system properties change. By this means, we explain mechanism interactions, and the sizes and shapes of coexistence regions in parameter space. We then consider the implications of these results for further theoretical and empirical work on the coexistence of desert annual plants.

2. Model and assumptions

We modify the model in Kuang and Chesson (2009) so that predation is frequency dependent. The parameters defining the model are given in Table 1. Briefly, the model is as follows: desert annual plants compete, but also interact through common seed predators (Brown and Venable, 1991). For an individual species, at the beginning of each season, some fraction, G , of the seed, N , in the seed bank germinates. Without competition, a seedling would produce on average Y seeds by the end of the season. We assume that competition can be quantified by a number C linearly dependent on the densities of the seedlings of all competing species. The actual number of seeds produced with competition is given as Ye^{-C} per seedling, i.e., competition is of the Ricker form (Ricker, 1954). We assume that germination rates, G , vary stochastically over time, implicitly driven by a stochastically varying physical environment. The correlations between species are assumed to be less than 1 so that each species has a unique pattern of germination fluctuation over time in accordance with empirical studies of germination in annual plant communities (Adonakis and Venable, 2004; Facelli et al., 2005). For simplicity, we introduce stochastic variation into the model through the germination fraction alone. Thus, fluctuations in dormant seed survival and seed yield are not considered. This restriction is justified because variation in germination fraction is the clearest means by which coexistence arises via the storage effect in annual plant systems (Chesson et al., 2004).

In Kuang and Chesson (2008, 2009) we modeled seed predation using the Nicholson–Bailey formulation (Hassell, 2000) where the fraction of seed surviving predation is e^{-aP} , with P being predator density and a the attack rate. This assumption yields e^{-aP} as

Table 1
General notation.

Symbol	Definition
*	Designates the equilibrium value of a variable
a	The maximum value of the attack rate (instantaneous per capita predation rate)
A	Magnitude of apparent competition
Ψ	The combined magnitude of the coexistence mechanisms
C	Magnitude of competition
E	The environmental response: $\ln(G)$
F	Limiting factor, combining resource and apparent competition
G	Germination fraction
i	Index for an invader
$\{-i\}$	Used as a superscript to indicate a measurement with species i as the invader
j	Index for an arbitrary species j
N	Density of an annual plant species (prey)
P	Density of the predator
r	Index for the resident when used as a subscript; population growth rate when not a subscript
s	Fraction of dormant seed surviving one year (the seed “survival rate”)
s_p	Predator persistence on alternative resources
w	Proportion of predation that is frequency dependent
Y_j	Per capita seed yield of species j before accounting for competition and predation
β	$= 1 - s(1 - \bar{G})$, the mean fraction of seed lost from the seed bank per year
ΔP	Magnitude of the coexistence promoting effect of frequency-dependent predation (FDP)
ΔN	Magnitude of nonlinear competitive variance (NCV)
ΔI	Magnitude of the storage effect due to competition (SE)
η	$= \ln(\bar{G}Y / [1 - s(1 - \bar{G})])$, \ln mean seed production per unit seed loss
ρ	Correlation between the environmental responses, E_j 's, of different species.
σ^2	The common variance, $\text{Var}(E)$, of the environmental responses.

the fraction of seed production surviving predation. To model frequency-dependent predation (FDP), we replace the constant a by a function of the relative abundance of the species. We derive this model as a special case (Appendix A) of McNair's 1980 model of foraging under learning constraints.

The seed production by species j is $G_j Y_j N_j e^{-C}$ seeds per unit area, which means that $G_j Y_j N_j / \sum_k G_k Y_k N_k$ is the fraction of new seed production contributed by species j . A parameter, w , between 0 and 1, determines the degree of frequency dependence. Then, aP in the previous formulation becomes the new predation rate

$$A_j = a \left((1 - w) + w G_j Y_j N_j / \sum_k G_k Y_k N_k \right) P, \quad (1)$$

where the symbol A_j stands for “apparent competition”. For species j , the proportion of seed surviving predation is thus

$$e^{-A_j}. \quad (2)$$

With $w = 1$, all predation is frequency dependent, and for $w = 0$, the frequency-independent Nicholson–Bailey model is recovered.

We assume that seed predation applies only to the newly produced seed. Nongerminating seeds are assumed not subject to seed predation, as they are dispersed in surface layers of the soil. However, they are subject to mortality. Their survival rate, s , is the fraction of these nongerminating seeds that survive to the beginning of the next germination season. Assembling these components, we obtain the following system of difference equations specifying the dynamics of n annual plant species and a seed predator, nondimensionalized for parameter reduction (Appendix B):

$$N_j(t+1) = N_j(t) (s_j(1 - G_j) + G_j Y_j e^{-C(t) - A_j(t)}); \quad (3)$$

$$j = 1, \dots, n$$

$$P(t+1) = \sum_{k=1}^n G_k Y_k N_k e^{-C(t)} (1 - e^{-A_k(t)}) + s_p P(t)$$

where

$$C(t) = \sum_{k=1}^n G_k N_k(t).$$

Here, the subscripts j indicate species-specific parameters and the term $s_p P(t)$ represents growth of the predator population not accounted for by predation on this annual plant community. We assume here that s_p is less than 1, and is in essence a rate of survival on resources that are poorer than those provided by annual plant seeds. These resources might be other plant products and insects that are available between seed harvests from annual plants (Brown et al., 1994). In the model, these resources are unable to support positive growth, but do enhance predator persistence.

These equations make the specific assumption that competition equally affects the growing seedlings of all species at any given time, which precludes stable coexistence in equilibrium settings without predation (e.g. Levin, 1970). The form of FDP here is symmetric in the sense that species with the same abundance experience the same predation rate. The effects of resource competition and apparent competition on seed production combine additively in these equations, so the seed production is a function of $F_j = C + A_j$. As discussed above, we assume that the environment fluctuates randomly over time, affecting the germination fraction. For simplicity, we assume that the germination fractions for different species have the same probability distribution. These germination fractions may be correlated between species, but are independent over time. For simplicity also, in our calculations survival in the seed bank, s , is assumed the same for all species. However, species can differ in their maximum seed yields, Y , and these differences lead to mean fitness differences between species. Although the model is defined for any number of annual plant species, for simplicity, we focus on the two-species case. The general conclusions in this work remain true for the n -species case, although more phenomena, including additional coexistence mechanisms, are possible with multiple annual plant species (Kuang and Chesson, unpublished manuscript).

3. Quantifying coexistence mechanisms

Throughout this paper, we focus on stable coexistence of competitors as defined by the invasibility criterion (Chesson and Ellner, 1989; Ellner, 1989; Turelli, 1978), which is discussed in detail for the present context in Appendix B. Briefly, we ask whether each species can increase following perturbation to low density in the presence of its competitors. In this analysis for the case of two competitors, one competitor is perturbed to low (effectively zero) density and is called the *invader*, and the other species is unperturbed, and is termed the *resident*. Coexistence conditions derived from an invasion analysis identify the state of a species as invader or resident. In the full analysis, each species is considered in both its invader and resident states. In general, we use the subscript i to identify a species in its invasion state, and use r to identify a species in the resident state. A quantity measured for species i in its invasion state takes the superscript $\{-i\}$. For example, apparent competition for a resident species r is denoted as $A_r^{\{-i\}}$ when i is invader.

On the basis of invasion analysis, we identify several mechanisms of coexistence, and provide formulae for their strengths (Table 2). These formulae provide key tools for identifying mechanisms, and for studying their interactions. These formulae are derived by partitioning long-term population growth rates into components corresponding to different coexistence mechanisms,

Table 2
Mechanism quantification.

Mechanism	Notation	Magnitude from quadratic approximation
Frequency-dependent predation (FDP)	ΔP	$aw\bar{p}^{(-i)}$
Nonlinear competitive variance (NCV)	ΔN	$\frac{(1-\beta)}{2} \left(\text{Var} \left(F_r^{(-i)} \right) - \text{Var} \left(F_i^{(-i)} \right) \right)$
Storage effect (SE)	ΔI	$s \left[\text{cov} \left(E_r, C^{(-i)} \right) - \text{cov} \left(E_i, C^{(-i)} \right) \right]$ $\approx s\sigma^2(1-\rho)\bar{G}N_r$

Notation: Resident species are indicated by the subscript r ; the superscript $\{-i\}$ indicates a measurement with species i as invader, following the convention of (Chesson, 2003). $\bar{p}^{(-i)}$ is the average predator density with species i as invader, and is equal to $P^{*(-i)}$ if the system is at equilibrium. C is the magnitude of competition, and A is the magnitude of apparent competition. F is the joint combined effect of resource and apparent competition, and equals $C + A$. $\beta = 1 - s(1 - \bar{G})$: the rate at which seeds are lost from the seed bank. The quantity σ^2 is the variance of $E = \ln G$, and ρ is the correlation between E 's of different species. See Table 1 for other symbols.

and comparing these components between invader and resident. In the case of just two plant species considered here, residents experience only intraspecific density dependence (intraspecific competition and intraspecific apparent competition), while invaders experience only interspecific density dependence (interspecific competition and interspecific apparent competition). Thus, these formulae measure how much each mechanism elevates intraspecific density dependence over interspecific density dependence. It is important to emphasize that these differences are long-term outcomes. For example, with the storage effect, there is no necessity for any difference between intraspecific and interspecific density dependence at any given time (Chesson, 2000). The difference between the two emerges as a long-term outcome. Note that a long-term excess of intraspecific density dependence over interspecific density dependence, as assessed by invader–resident comparisons, is the essential requirement for stable coexistence (Chesson, 2000), and this requirement is partitioned quantitatively between mechanisms by our techniques.

The formulae for mechanism strength are derived from quadratic approximations to the population growth rates (Appendix C), and are only expected to be accurate when temporal fluctuations are small (Chesson, 1994). Coexistence regions (Figs. 1 and 3) are calculated from invasion analyses using accurate simulations, by passing any concerns about the accuracy of the approximations. Plots of the magnitudes of the individual mechanisms in Fig. 2 necessarily use the approximate formulae in Table 2. Simulations show that they give accurate predictions for the cases studied here, which include large fluctuations Fig. C.1. Thus, we can use these approximations with confidence.

We first analyze frequency-dependent predation (FDP) in a constant environment, and then consider its interaction with the storage effect (SE) in a variable environment. Two quantities are key to these analyses: the rate of loss from the seed bank, β , and the maximum productivity, η . The loss rate, β , defines a natural timescale for a species, and is equal to $1 - s(1 - \bar{G})$. It is the average fraction of seed lost in one unit of time from germination or death. The productivity, η , is the seed yield per unit seed loss from the seed bank, on a log scale, $\ln(\bar{G}Y/\beta)$. This quantity equals the log of average lifetime production of new seed from a given seed in the absence of competition and predation.

The invasibility criterion is that each species i as invader should have a positive invasion rate, designated as \bar{r}_i . For our model, this invasion rate takes the form

$$\bar{r}_i \approx \eta_i - \eta_r + \Psi_i, \tag{4}$$

where $\eta_i - \eta_r$ is the invader–resident productivity difference (Appendix C), and Ψ_i defines the combined magnitudes of the coexistence mechanisms in units of growth of natural log (\ln)

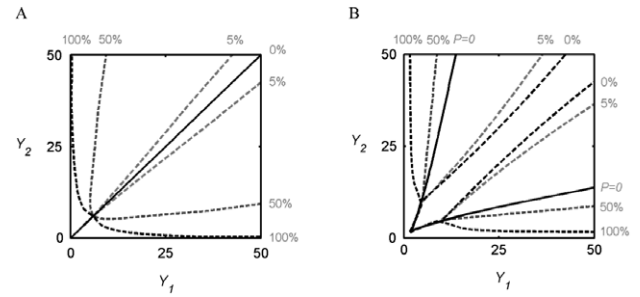


Fig. 1. Coexistence regions for two species with different strengths of FDP, with and without environmental variation. Y is the seed yield, which reflects the productivity, η (Table 1). The species are labeled 1 and 2. A coexistence region for a given situation is the region between two lines with the same terminal label defining the %FDP (100w%) for that region. These regions are thus the nested wedge-shaped regions, symmetrical about 45° , bounded by the lines in the Y_1 – Y_2 plane. (A) Constant environment. The interior 45° line is the neutral coexistence boundary with no predation or with frequency-independent predation (0% FDP). Moving out from the 45° line are the boundaries for 5% FDP, 50% FDP and 100% FDP. (B) Variable environment. From the interior are the coexistence boundaries for frequency-independent predation (0% FDP), 5% FDP, no predation ($P = 0$), 50% FDP, and 100% FDP. The parameter values are $s = 0.8$; $a = 0.1$; $s_p = 0.8$; with $G = 0.5$ in (A) and G having the beta distribution with parameters (0.5, 0.5), independent for each species in (B).

population size per unit time. The unit of time in the quantities \bar{r}_i and Ψ_i is the mean longevity, $1/\beta$, of seed in the seed bank, which simplifies these formulae (Appendix C). Multiplication by β converts back to a time unit of one year. Formula (4) means that for species i to invade, the following condition must be satisfied:

$$\eta_i > \eta_r - \Psi_i. \tag{5}$$

Thus, the minimum value of η_i allowing species i to invade is equal to the resident productivity less Ψ_i . In general Ψ_i is positive, and this fact means that a species with productivity less than that of the resident can invade. Indeed, Ψ_i defines exactly how much less the productivity of the invader must be before the invader is excluded from the system. Positive values of Ψ_i thus allow species with different productivities to coexist with one another.

Here Ψ_i has contributions from up to three different mechanisms, which combine additively to determine the value of Ψ_i :

$$\Psi_i = \Delta P - \Delta N + \Delta I. \tag{6}$$

These mechanisms are defined in Table 2, and discussed further below. Briefly, ΔP is the excess average predation on resident species due to FDP. The term ΔN , “nonlinear competitive variance (NCV)” (Snyder and Chesson, 2004), measures the effect of variance in competition (resource and apparent combined); and ΔI is the storage effect. In all of these quantities, the symbol Δ signifies that the quantity comes from an invader–resident comparison with respect to some particular aspect of ecology. The terms ΔP , ΔN and ΔI thus reflect differences between interspecific and intraspecific density dependence.

The form (5) of the coexistence condition is a standardized way of viewing coexistence regions (Chesson, 2003), which allows mechanisms to be studied in combination, and also allows an analysis of stabilizing and equalizing components of coexistence mechanisms (Chesson, 2000; Snyder et al., 2005). Differences between η 's define average fitness differences in the sense that, in the absence of a coexistence mechanism (i.e. $\Psi_i = 0$), the species with the larger value of η excludes the other species. Nonzero values of Ψ_i modify this result, and in particular, positive values allow coexistence, as mentioned above.

3.1. Effects of frequency-dependent predation ($\Delta P - \Delta N$)

If there are no environmental fluctuations, and resident density converges on equilibrium, the sole coexistence mechanism is frequency-dependent predation (FDP), i.e. $\Psi_i = \Delta P$. In a resident–invader scenario with two annual plant species, the single resident

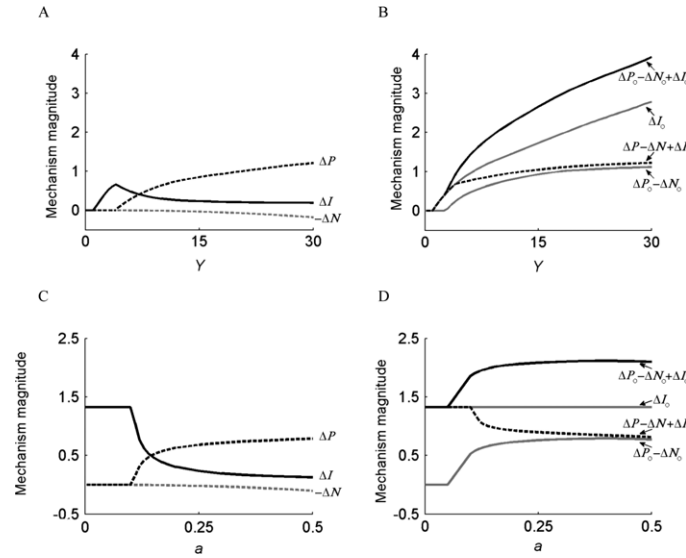


Fig. 2. Mechanism magnitudes. Y is the seed yield, and a is the attack rate. In the left column (panels A&C) the magnitudes of the individual mechanisms, present together, are plotted: ΔP (frequency-dependent predation), ΔI (the storage effect), and $-\Delta N$ (the negative of nonlinear competitive variance). The right column (panels B&D) plots competition-based (ΔI_0) and predation-based ($\Delta P_0 - \Delta N_0$) mechanisms, measured separately. Thus, ΔI_0 , the storage effect, is measured without the predator ($P = 0$), and the combined predation-based mechanisms ($\Delta P_0 - \Delta N_0$) are measured in a constant environment so that the storage effect cannot occur. Thus, $\Delta P_0 - \Delta N_0 + \Delta I_0$ is the sum of the separate effects, while $\Delta P - \Delta N + \Delta I$ is the combined effect of the mechanisms when present together, and is equal to the sum of the curves in the left panel. Parameters: Panels A&B, $a = 0.2$; Panels C&D, $Y = 10$; all panels, $s = 0.8$, $s_p = 0.8$, $w = 0.4$; G has a beta distribution with parameters (0.5, 0.5), independent between species.

species is necessarily at 100% relative abundance, and experiences the maximum effects of predation. Thus, the predation rate on the resident given by Eq. (1) is $aP^{*(-i)}$ where $P^{*(-i)}$ is the predator density at equilibrium with the resident, i.e. in the absence of the invader species i . The invader is effectively at zero relative abundance, and experiences only the frequency-independent component of predation, which is $1 - w$ of the total predation intensity experienced by the resident. Thus, the predation rate experienced by the resident exceeds that experienced by the invader by the amount $awP^{*(-i)}$. Appendix C shows that this difference is in fact ΔP , i.e.

$$\Psi_i = \Delta P = awP^{*(-i)}. \quad (7)$$

This means that an invader with lower productivity, η , than the resident can enter the system provided its productivity disadvantage is less than $awP^{*(-i)}$. A species with higher productivity than the resident can always invade, and so the mutual invasibility criterion implies that two species with the same or different productivity can always coexist provided their productivity difference is not too large: not larger than $awP^{*(-i)}$. Numerical results show that ΔP increases with w and a , even though $P^{*(-i)}$ may decrease. Thus, the coexistence region, defined in terms of allowable productivity differences (equivalently seed yield differences), enlarges as w increases (Fig. 1A), and also enlarges as a increases, but only subtly (not shown).

These effects of FDP are modified slightly when resident populations fluctuate over time. These fluctuations can be due to a fluctuating environment, or can be endogenous for certain parameter values (Kuang and Chesson, 2008). In both cases, the magnitude of FDP, ΔP , becomes $aw\bar{P}^{(-i)}$ (Table 2), where $\bar{P}^{(-i)}$ is the time average predator density in the absence of species i . Simulations show that $\bar{P}^{(-i)}$ is lower than $P^{*(-i)}$ when population fluctuations are present. In addition, population fluctuations in the presence of FDP cause nonlinear competitive variance (measured by ΔN ; Table 2) to be present and so the total effect of FDP on Ψ_i is equal to

$$\Delta P - \Delta N. \quad (8)$$

Simulations show also that ΔN is positive, and therefore has a negative contribution to Ψ_i , reducing, but not eliminating, the coexis-

tence promoting effect of FDP (Fig. 2). The ΔN term arises because the growth rate is a concave up function of F (competition plus apparent competition), and so fluctuations in F make a positive contribution to the long-term growth rate, by Jensen's inequality (Kuang and Chesson, 2008). However, this contribution is greater for residents than invaders because resident F is more variable than invader F , giving a positive value of ΔN , and hence a negative effect on coexistence (Appendix C). In particular, the coexistence regions in Fig. 1 would be slightly larger without the contributions of ΔN .

3.2. The storage effect (ΔI)

With a temporally varying environment the storage effect arises. A critical concept in storage-effect theory is covariance between the environment and competition (covEC) (Chesson, 1994; Chesson et al., 2004; Kuang and Chesson, 2009), which is the covariance over time between the response of a species to the physical environment and its response to competition. Here, the response to the physical environment is the germination fraction, G_j , which for the purpose of covariance calculation is measured on the log scale as $E_j = \ln G_j$. The response to competition is measured as $C^{(-i)}$: the magnitude of competition as defined by Eq. (3) with species i as invader and the other species, labeled r , as resident. Resident and invader values of covEC are the standard statistical covariances, $\text{cov}(E_r, C^{(-i)})$ and $\text{cov}(E_i, C^{(-i)})$.

In storage-effect theory, persistence in the seed bank, as measured here by the survival rate, s , makes low covariances more advantageous to long-term population growth than high covariances (Kuang and Chesson, 2009). Thus, an invader can gain an advantage over a resident, depending on the value of s , by having a lower covariance. Indeed, the resident–invader covariance difference, multiplied by s , gives the magnitude of the storage effect (Appendix C):

$$\Delta I = s [\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})]. \quad (9)$$

This covariance difference is positive because $C^{(-i)}$ is here equal to resident seedling density, and so increases as a function of E_r ,

creating a positive value of $\text{cov}(E_r, C^{(-i)})$. The invader experiences competition, but does not contribute to its magnitude because its density is effectively zero. Thus, $C^{(-i)}$ does not depend on invader seedling density, and so it is not a function of E_i . In particular, when the germination fractions of the two species fluctuate independently over time, $\text{cov}(E_i, C^{(-i)})$ is zero, and the magnitude of the storage effect is simply proportional to the resident covariance. However, in general we assume that E_i and E_r have correlated fluctuations over time with correlation coefficient ρ . Provided ρ is less than 1, the invader covariance is less than the resident covariance, leading again to a positive magnitude, ΔI . Indeed, ΔI is approximately proportional to $\sigma^2(1-\rho)$, where σ^2 is the variance of the \ln germination fraction (variance of E) (Table 2). Thus, ΔI is nonzero whenever ρ is less than 1, and is larger in magnitude when ρ is smaller or σ^2 is larger.

With the storage effect and predation, the combined magnitude of the various mechanisms is again given by expression (6),

$$\psi_i = \Delta P - \Delta N + \Delta I.$$

Once more, a species with inferior productivity can invade a resident community, but the maximum degree of inferiority for invasion, defined by ψ_i , reflects three different mechanisms. Fig. 1B shows the contribution of the storage effect to coexistence. In the absence of predation, the storage effect gives a broad coexistence region, which contracts sharply when frequency-independent predation ($w = 0$, $\Delta P = 0$) is added, as demonstrated previously (Kuang and Chesson, 2009). This occurs because strong predation reduces ΔI by reducing the overall magnitude of competition. Although FDP also reduces the strength of competition, and hence the strength of the storage effect, the direct coexistence promoting effects of FDP give it the capacity to compensate or overcompensate for the reduction in the storage effect that results from the introduction of predation. Hence as w increases, i.e. the degree of frequency dependence increases, the coexistence region in Fig. 1B broadens, ultimately fanning out to a region much larger than that given by the storage effect alone.

4. Interactions between coexistence mechanisms

The formula (6) for ψ_i , which is the combined magnitude of the coexistence mechanisms, is the sum of the separate measures for these mechanisms. A standard definition of an interaction is that the combined effects cannot be written as the sum of the separate effects. Hence, at first sight, the mechanisms appear not to interact. However, in this definition, the separate effects of the mechanisms need to be determined in the absence of the other mechanisms, while in formula (6) each mechanism magnitude is the additional effect of that mechanism in the presence of the others. In fact the mechanisms interact in the sense that factors that enhance one mechanism modify the magnitude of the other mechanisms (Figs. 2 and 3). In examining such interactions, we divide these factors into trophic effects (productivity and foraging rate), and behavior and life-history.

4.1. Trophic factors in mechanism interactions

Trophic factors have a critical role in the magnitudes of coexistence mechanisms and the interactions between them. At low productivity ($Y < 4$), the predator is not supported, and hence predation-based mechanisms (ΔP and ΔN) are absent (Fig. 2A). As productivity is increased, resident density increases until it is high enough to support the predator. At that point the predator begins to control the prey, shunting further productivity increases to its own density, reducing prey density, as shown in previous work (Kuang and Chesson, 2009). With increasing productivity, the magnitude, ΔI , of the storage effect at first increases. When

the predator enters, ΔI shows a decline coincident with the rise of FDP as a mechanism. Finally, ΔI levels off because the predator controls prey density at a relatively constant value, independent of seed yield, and FDP (ΔP) becomes stronger than the storage effect. Nonlinear competitive variance (ΔN), although relatively small in magnitude, increases in magnitude as Y increases. This mechanism has a small negative effect on coexistence by reducing the impact of predation through FDP.

The predator attack rate, a , reflecting the efficiency of the forager, also has a strong effect on the relative importances of the different mechanisms, as illustrated in Fig. 2C. When a is small ($a < 0.1$), the predator's foraging is insufficient to sustain it. As a is increased past the threshold of predator maintenance, prey densities drop and the storage effect is sharply reduced. After an initial sharp increase, FDP (ΔP) subsequently increases only slowly, and appears to plateau (Fig. 2C). Like productivity, a large attack rate makes predation more important, but leads to a reduction in the storage effect. The magnitude of the storage effect (ΔI) is directly proportional to mean resident prey density (Table 2), and so we can see that the decline of the storage effect is due directly to suppression of prey by the predator. With both high productivity and high attack rates, suppression of prey reduces the magnitude of competition, and hence the magnitude of covariance between environment and competition. Fundamentally, in both cases, the competition-based mechanism, the storage effect, declines as the magnitude of competition declines.

To view these results in terms of traditional interaction ideas, we now separately remove predation-based and competition-based mechanisms, and append the subscript O to the mechanism magnitudes to indicate that they are measured alone. Thus, ΔI_0 is the storage effect in the absence of predation-based mechanisms, which we achieve by setting, predator density, P , to zero. Correspondingly, $\Delta P_0 - \Delta N_0$ is the combined predation-based mechanisms measured without the storage effect, which we achieve by setting environmental fluctuations to zero. For simplicity of language we refer to $\Delta P_0 - \Delta N_0$ as FDP. In any case, ΔP_0 and ΔN_0 cannot be measured in the absence of each other. Thus, we have two interacting mechanisms, FDP and the storage effect. The sum of the mechanisms measured alone, $(\Delta P_0 - \Delta N_0) + \Delta I_0$, can now be compared against the combined mechanisms, $(\Delta P - \Delta N) + \Delta I$, measured in the presence of each other (Fig. 2 B&D). Note that the sum of the separate mechanisms is always substantially greater than the combined mechanisms. Moreover, in Fig. 2, the combined mechanisms never exceed the strength of the stronger separate mechanism, which is the storage effect in this case due to the particular parameter values used. From Fig. 1 it is clear that FDP can easily be the stronger mechanism. For 100% FDP, Fig. 1 again shows that the combined mechanism is weaker than the stronger separate mechanism, in this case FDP, as assessed by the change in the size of the coexistence region between Fig. 1A and B. However, at 50% FDP, careful comparison of Fig. 1A and B shows that the coexistence region is slightly larger for the combined mechanism than either mechanism alone. Although these figures are just particular slices through parameter space, broad exploration upholds the conclusion that the combined mechanism is frequently, although not exclusively, weaker than the stronger separate mechanism.

4.2. Life-history and behavior in mechanism interactions

Changes in life-history and behavioral traits also reveal mechanism interactions. To evaluate these we consider changes in the coexistence region as factors affecting each mechanism are changed (Fig. 3). For the storage effect, key life-history parameters are the survival rate, s , and sensitivity of annual plant

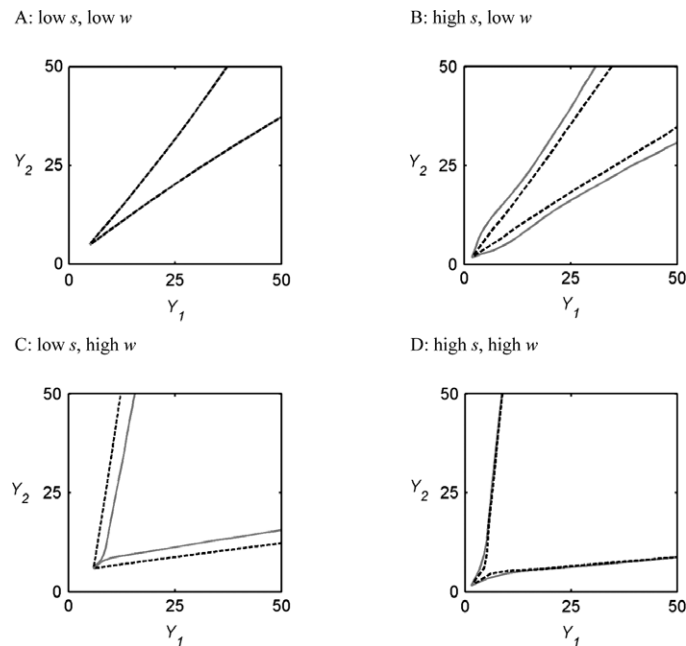


Fig. 3. Interactions between predation-based and competition-based coexistence mechanisms. Each panel compares coexistence regions for low environmental sensitivity (the entire wedge-shaped region enclosed by the two dashed lines), and high environmental sensitivity (the entire wedge-shaped region enclosed by the two solid lines), with dormant seed survival, s , and the degree of frequency dependence, w , varying between panels. (A) $w = 0.1$, $s = 0.05$ (the coexistence regions coincide); (B) $w = 0.1$, $s = 0.8$; (C) $w = 0.5$, $s = 0.05$; (D) $w = 0.5$, $s = 0.8$. Parameters common to all panels: $s_p = 0.8$, $a = 0.2$, G is beta (0.5, 0.5) for high environmental sensitivity, and beta (2, 2) for low environmental sensitivity, independent between species in both cases.

germination to environmental fluctuations. Because in this section we wish to think about life-history attributes, we think of the underlying environmental fluctuations as having fixed variance, and the parameter σ^2 (the variance of the \ln germination fraction) as reflecting the sensitivity of the species to those underlying environmental fluctuations. The behavioral trait is w , the degree of frequency dependence of predation. Environment sensitivity negatively affects FDP ($\Delta P - \Delta N$), but positively affects the storage effect, ΔI . In Fig. 3, we ask when the net effect of environmental sensitivity is to enlarge the coexistence region. The different panels of Fig. 3 vary the expected relative importance of the storage effect and FDP by varying s and w . When s is large but w is small, the coexistence region understandably enlarges with an increase in environmental sensitivity (Fig. 3B). Correspondingly, with small s and large w , an increase in environmental sensitivity leads to contraction of the coexistence region (Fig. 3C). With s and w both small (Fig. 3A) or both large (Fig. 3D), it is possible for environmental sensitivity to be neutral in effect due to countervailing effects on FDP and the storage effect.

5. Discussion

We have studied a competition-based coexistence mechanism, the storage effect (SE), a predation-based coexistence mechanism, frequency-dependent predation (FDP), and the interactions between the two in a model of desert annual plant species. Like our previous work (Kuang and Chesson, 2008, 2009), the key findings extend to seasonally reproducing species in a variable environment. Both the competition-based and the predation-based mechanisms promote stable coexistence, and both do so when there is but a single resource or a single predator. In contrast, previous work showing similar roles for predation and competition in diversity maintenance involved multiple resources and multiple predator species (Chesson and Kuang, 2008). However, a single resource can be partitioned over time, and a single frequency-dependent predator can have a similar diversity promoting effect to that of several specialist predators, as we discuss in detail below.

5.1. Density-dependent feedback loops: Within versus between species

Competing species (here annual plants) interact within and between species through density-dependent feedback loops, which may be mediated by a resource or by a predator. As emphasized in Chesson and Kuang (2008), the strength of a coexistence mechanism depends on how much the mechanism increases the strengths of within-species feedback loops relative to between-species feedback loops. This idea is the basis of our technique of quantifying coexistence mechanisms. In Chesson and Kuang (2008), feedback loops through predators involve the numerical response by which predator density increases or decreases according to the abundance of prey. Although the numerical response is involved here too, critical to coexistence, the feedback loops here involve also changes in the behavioral state of the predator as prey relative abundances change, altering per capita rates of foraging on all prey. In particular, with frequency-dependent predation (FDP), buildup of a particular prey species causes the predator to focus more on that prey species, decreasing rates of foraging on other prey species.

In contrast, with predator partitioning (Chesson and Kuang, 2008), as any given prey species increases in abundance, predators that prefer that prey species increase also, increasing the rate of predation on that prey species more than those on other prey species. With both FDP and predator partitioning, prey intraspecific feedback loops are intensified relative to interspecific feedback loops. In other words, intraspecific density dependence is strengthened relative to interspecific density dependence, promoting coexistence. The role of the numerical response is quite different in the present model compared with that of Chesson and Kuang (2008). Because here there is just a single predator, which attacks all species, in the absence of FDP, predator buildup intensifies prey species intraspecific and interspecific feedback loops equally and does not favor coexistence. However, with FDP present, higher predator density increases the importance of FDP as a coexistence mechanism, which is revealed by our quantitative

measures of mechanism strength. At the same time, high predator density weakens competition-based mechanisms, as discussed below.

5.2. Short-term versus long-term density dependence

Predation-based coexistence mechanisms can work on behavioral and population dynamic timescales. Behavior can respond rapidly to density changes, while predator buildup occurs over generations (multiple years in the model analyzed here). These differences lead to the distinction between short-term and long-term apparent competition (Holt and Kotler, 1987; Murdoch and Bence, 1987). Short-term apparent competition includes foraging behavior and foraging constraints, and thus involves density dependence on a behavioral timescale. The form of multi-species density dependence that emerges from the specific foraging model that we use is strict frequency dependence where foraging rates (capture rates per unit prey density) depend on relative but not absolute abundances. Long-term apparent competition has most commonly been assumed to involve the numerical response, i.e. the buildup or decline of the predator population in response to prey density (Holt and Kotler, 1987).

Like predator behavior, competition works on a within-year timescale. Because competition at any given time has the same intensity for all species, our model corresponds to the existence of just one limiting resource (for example, water for desert annuals), or several limiting resources used at the same relative rates by all species. Thus, there is no resource partitioning within any year. However, by having different responses to the physical environment through their germination rates, the species are most actively using resources in different years. Most important, seed persists in the seed bank, and so the benefits of seed production during favorable times are not lost when unfavorable periods occur. Thus, as a dual outcome of species-specific germination responses and seed bank storage, feedback loops through resources are separated by time. The magnitude of the storage effect is a direct measure of the separation of intraspecific and interspecific feedback loops by time (Kuang and Chesson, 2009). It involves both the rate of survival of dormant seed in the seed bank, and how much environmental fluctuations are associated with fluctuations in intraspecific competition compared with interspecific competition. These associations between environmental fluctuations and competition fluctuations are measured by the quantity that we define formally as covariance between environment and competition. This quantity is proportional to the mean magnitude of competition, and so any factor weakening competition overall weakens the storage effect.

The storage effect can also occur as a consequence of predation, but not in the circumstances that we have modeled here because covariance between environment and predation (apparent competition) does not occur. The assumption of independence of the environmental fluctuations over time, and the long timescale of predator build up, mean that covariance between predator density and environment does not occur. Also, with the two-species case that we consider, there is no covariance between foraging rates and the environment despite the fact that foraging rates can change on a short timescale. The reason is the strict frequency dependence in our foraging model. In a resident–invader analysis with two species, there is a single-species resident at 100% relative abundance. Relative abundances thus do not vary, and so foraging rates, which depend on relative abundance alone, cannot respond to changes in the environment. Relaxation of either of these assumptions, however, does lead to a storage effect due to predation (Kuang and Chesson, unpublished manuscript). Instead, with the assumptions of the present model, predation has the effect of weakening the storage effect because it reduces

the magnitude of competition. In this way, predation weakens all competition-based mechanisms, as found previously for the storage effect in annual plant models (Kuang and Chesson, 2009), and for resource partitioning in Lotka–Volterra models (Chesson and Kuang, 2008).

5.3. Interactions between density-dependent feedback loops through resources and predators

When predation is present, but there is no predation-based coexistence mechanism, an overall weakening of coexistence necessarily occurs, although the storage effect is never eliminated even with strong predation. If predation is frequency dependent, then the reduction in the storage effect (the competition-based mechanism) can be compensated for by the predation-based mechanism, FDP. With strong predation, the presence of frequency dependence determines whether the coexistence region will be broad or narrow. In the present model, the strength of predation is determined by the attack rate of the predator, and the seed yields of the prey. The predator cannot be sustained when the attack rate is low or seed yields are low. Increasing either parameter past the point where the predator can persist can seriously lower prey density, sharply reducing the competition-based mechanism, the storage effect. These effects quickly become strong as seed yield or attack rates are increased. The fact that the predator is limited primarily by the focal prey species appears responsible for these quickly acting effects compared with more gradual effects seen previously in Lotka–Volterra models where predators have limitation outside the focal prey species (Chesson and Kuang, 2008).

When predation and competition are both significant forces, the potential exists for interactions between predation-based and competition-based mechanisms. Mechanism interactions occur here in the sense that factors strengthening one mechanism diminish the strength of another. Thus, increases in seed yield or attack rates strengthen predation-based mechanisms while simultaneously weakening competition-based mechanisms. In contrast, we found that increasing environmental fluctuations (or sensitivity to environmental fluctuations) weakens predation, and hence predation-based mechanisms, while enhancing the storage effect. Consistent with these observations, we found that the combination of the storage effect and frequency-dependent predation promotes coexistence less strongly than predicted by the sum of the separate mechanisms when present alone. Moreover, in many cases, the combined mechanisms have a weaker effect than the stronger mechanism present alone. This outcome is understandable from the observation above that factors enhancing one of these mechanisms tend to diminish the other.

5.4. Other studies of FDP and prospectus

The model of FDP used in this paper is derived mechanistically from foraging constraints expected to apply to predators (Appendix A). Optimal diet selection is the most common explanation for FDP in theoretical studies (Abrams and Matsuda, 2004; Krivan, 1996; Ma et al., 2003), while foraging constraints are considered much less commonly (Krebs and Inman, 1992; McNair, 1980) despite much emphasis on constraints by some evolutionary theorists (Gould and Lewontin, 1979). When optimal diet selection considers only energy maximization and not nutrient balance, it leads to wholesale inclusion and exclusion of items from the diet depending on their profitability, with lower ranked items being included only when the absolute abundance of higher ranked items falls (Krivan, 1996). Krivan (2003) showed that with two prey items, this form of optimal diet selection can promote coexistence in the face of apparent competition. On the other hand,

Table 3
Empirical studies of frequency-dependent predation.

Study	Predator	Prey	Setting	Conclusion about FDP ^a	Max w^b
Lawton et al. (1974)	Aquatic insects	Aquatic insects	Laboratory	+	0.8
Murdoch et al. (1975)	Fish	Invertebrates	Laboratory	+	0.7
Goss-Custard (1977)	Birds	Invertebrates	Field	+ or 0	NA
Bond (1983)	Birds	Seeds	Laboratory	+	0.8
Hughes and Croy (1993)	Fish	Zooplankters	Laboratory	+	0.6
Marini and Weale (1997)	Egg predators	Bird eggs	Field	+	NA
Warburton et al. (1998)	Fish	Zooplankters	Mesocosm	+	NA
Hulme and Hunt (1999)	Rodents	Seeds	Field	0	NA
Kunin (1994)	Ants	Seeds	Field	+ or 0	NA
Bond and Kamil (2002)	Birds	Invertebrates	Laboratory	+	NA
Elliott (2004)	Aquatic insects	Aquatic insects	Laboratory	+	0.6
Celis-Diez and Bustamante (2005)	Rodents	Seeds	Field	– or 0	NA
Almany et al. (2007)	Fish	Fishes	Field	–	NA

We used the Science Citation Index to find foraging studies that cite the first three works in the table. Foraging studies were included in this table if they drew explicit conditions about frequency-dependent predation. The second to last column gives the qualitative conclusion on frequency dependence. Where suitable data were provided we fitted expression (1) of the text.

^a + means higher predation on more common species, – means higher predation on rarer species, 0 means no frequency dependence detected.

^b The degree of frequency dependence, w , was fitted to data on relative frequencies of prey consumed as functions of relative frequencies of prey available. Where a studied provided multiple data sets, the maximum value of w is reported. NA means that the data appeared unsuitable for fitting the model.

nutrient balance (Abrams and Shen, 1989; Simpson et al., 2004) considerations lead to inverse frequency dependence and promotion of exclusion, as do constraints that occur when different predator individuals have different fixed prey preferences (Chesson, 1984).

To our knowledge this is first study to examine the interaction between FDP and the storage effect. However, other studies have considered interactions between FDP and other mechanisms; for example (Roughgarden and Feldman, 1975) show that FDP can greatly strengthen species coexistence in the presence of resource partitioning, a competition-based mechanism. Specifically, they show that the presence of FDP allows coexistence with much greater overlap in resource use. As Roughgarden and Feldman (1975) assumed 100% FDP (i.e. $w = 1$), FDP more than made up for weakening of the competition-based mechanism, although this fact was not noted directly in their study. Predation is often uncritically perceived as contributing positively to coexistence, but as pointed out by Chase et al. (2002), predation can have many different effects depending on the circumstances. Our results show that mechanisms in combination can have far from additive results. Although the coexistence conditions derived here can be expressed in terms of the sums of the effects of the separate mechanisms, the magnitudes of the individual terms in these sums are dependent on one another. Such major interactive effects are impossible to uncover from studying mechanisms in isolation. Moreover, our technique of expressing mechanism strength quantitatively in terms of contributions from different mechanisms has been an essential tool in understanding these effects.

This work shows major potential for frequency-dependent predation to contribute to coexistence in desert annual communities. Unfortunately, the study of frequency-dependent predation in nature has been quite limited. All of the studies that we could find are listed in Table 3. Laboratory studies have found frequency dependence in a variety of systems, and frequency dependence can be quite strong, with w values for our foraging model as high as 0.8 (Table 3), but not necessarily under realistic conditions. Field studies have been mixed with positive, negative and no FDP claimed in various settings (Table 3).

Although much other work has been done on foraging by desert rodents on annual plant seed, the focus has been on optimal patch use and caching behavior (see the review by Longland et al., 2001), or on changes in foraging ranges and behavior when the seed predators themselves are exposed to predation (Brown et al., 1994) with little information on how seed predators change their preferences for annual plant species as the relative abundances of annual plants change. Studies by Davidson et al. (1985) and Garb

et al. (2000) did find higher preference for the most abundant seed type, which were from species with the largest seed size. However, as preference was not measured for different relative abundances, it is not known whether the stronger preference for the more abundant species is a fixed preference or a reflection of frequency-dependent predation. Other studies of optimal patch use involving seed trays set out in the field by Veech (2001) indicated a preference for larger seeds with smaller seeds taken only as larger seeds were depleted. This outcome appears to be a form of optimal diet selection, as discussed above.

The results of our model suggest that even moderately frequency-dependent predation can have a powerful coexistence promoting effect. The dearth of the relevant field studies, however, leaves uncertain the importance of this mechanism in nature. Numerous studies of foraging by rodents and ants in the field focusing on caching behavior, and optimal patch use (Ben-Natan et al., 2004; Brown, 1989; Hobbs, 1985; Schmidt and Brown, 1996) suggest that the relevant studies of frequency-dependent behavior should not be difficult, and would greatly contribute to the understanding of diversity maintenance in nature.

Acknowledgments

We are grateful for comments on drafts of the manuscript by P. Abrams, B. Kotler, J. Levine, M. McPeck, M. Turelli, L. Venable, an anonymous reviewer, and the Chesson Lab discussion group. We thank Larry Bai-lian Li for his generous provision of office space for JJK at University of California (UC), Riverside, and Yun Tao for computational support for Appendix A. This work was supported by a UC Davis dissertation-year fellowship, and National Science Foundation grants DEB-0542991 and DEB-0717222.

Appendix A. Models of frequency-dependent predation

Here we justify the frequency-dependent attack rates of the predator used in the text. McNair (1980) develops a stochastic model of foraging on multiple prey species with learning. An individual predator is modeled repeatedly searching for, encountering, capturing and handling prey. The idea of learning is incorporated by assuming that the predator has higher success capturing the prey species most recently consumed. A simplifying assumption, making the mathematics tractable, is that this success rate depends only on the last prey consumed, not any previous experience. As prey are not depleted, the stochastic capture process approaches a stationary stochastic process, with

asymptotic capture rate, $\Omega^{(k)}$, of prey species k . In our notation $\Omega^{(k)}$ corresponds to $A_k N_k / P$. We express this formula using McNair's notation where P_{ij} is not predator density, but is instead the probability that species j is the first species encountered after consuming species i , π is the vector of stationary probabilities for the Markov chain with transition matrix \mathbf{P} ($= [P_{ij}]$), γ_{ij} is the probability of success in capturing species j on an encounter after consuming species i , and μ_{ij} is the average sum of search and handling times in capturing and consuming species j after consuming i . With this notation, the asymptotic capture rate, $\Omega^{(k)}$, given by McNair (1980) is

$$\Omega^{(k)} = \frac{\sum_i \pi_i P_{ik} \gamma_{ik}}{\sum_i \pi_i \sum_j P_{ij} \mu_{ij}}. \quad (\text{A.1})$$

In applying the result (A.1), we assume that the predator encounters a prey species j in proportion to its abundance, with proportionality constant, a_j , independent of the most recently captured species. Thus,

$$P_{ij} = a_j N_j / \sum_l a_l N_l. \quad (\text{A.2})$$

Assuming that handling time is negligible, the mean time between successive encounters is

$$\mu_{ij} = 1 / \sum_l a_l N_l. \quad (\text{A.3})$$

By rescaling the parameters if necessary, we can assume that the predator has 100% success capturing the species last consumed when encountered next. The probability of success for a different species is $\alpha < 1$, i.e. less than 100%. Thus, the most recently consumed species is more likely to be caught on encounter, incorporating the idea of training. Hence

$$\gamma_{ik} = \begin{cases} 1, & k = i \\ \alpha, & k \neq i. \end{cases} \quad (\text{A.4})$$

As noted by McNair (1980), $\pi_i = a_i N_i / \sum_l a_l N_l$. Substituting this result, and expressions (A.2) and (A.3), in expression (A.1), the asymptotic capture rate of species j becomes

$$\Omega^{(k)} = \frac{\sum_i \frac{a_i N_i}{\sum_l a_l N_l} \frac{a_k N_k}{\sum_l a_l N_l} \gamma_{ik}}{\sum_i \frac{a_i N_i}{\sum_l a_l N_l} \sum_j \frac{a_j N_j}{\sum_l a_l N_l} \frac{1}{\sum_l a_l N_l}}. \quad (\text{A.5})$$

On substituting (A.4), this result simplifies to

$$\Omega^{(k)} = [\alpha + (1 - \alpha) a_k N_k / \sum_l a_l N_l] a_k N_k. \quad (\text{A.6})$$

We can now define $w = 1 - \alpha$, so that w measures the failure rate when the predator encounters an unfamiliar prey. Assuming that the encounter rates, a_i , do not differ between species, expression (A.6) divided by N_k becomes the attack rate formula (1) used in this study. Thus, we identify the failure rate, $1 - \alpha$, for unfamiliar prey with the degree of frequency dependence, w . It is worth noting that when the a_i 's are different, predation is selective as well as frequency dependent, and the ratio $a_k N_k / \sum_l a_l N_l$ increases more rapidly with frequency for the preferred species, indicating that frequency dependence is stronger for the preferred species.

The asymptotic capture rate in expressions (A.1) and (A.5) is for a continuous time model, but we use it in discrete time with the assumption that predation preference does not change within a given season when annual plant seed is available. Specifically we assume that preferences are fixed by the relative abundances of annual plant seeds early in the season, and do not change even though relative abundances may change as more preferred species are depleted. This assumption is made for analytical convenience. However, the mechanistic partitioning of the invasion rate in

Table 2 is unaffected by relaxation of this assumption to allow continuous change in preference with prey depletion because this merely changes the functional form of the prey mortality term, not the presence of frequency dependence. Hence, the developments of Appendix C, in which the partitioning of mechanisms is derived, are unaffected. Moreover, simulations show that the qualitative results reported here are unaffected.

Although derived on the basis of foraging behavior, in the two-species case very similar models have been proposed on intuitive grounds by others (Bonsall and Hassell, 1999; Comins and Hassell, 1976; Tansky, 1978).

Appendix B. Nondimensionalization and coexistence criteria

B.1. Nondimensionalization

A more general form of the seed bank model of Eqs. (3) in the text was discussed in Kuang and Chesson (2008). Incorporating FDP, i.e., Eq. (A.6) above, the general model in the text is given by the equations

$$N_j(t + 1) = N_j(t) (s_j(1 - G_j(t)) + G_j(t) Y_j e^{-C(t) - A_j(t)});$$

$$j = 1, \dots, n$$

$$P(t + 1) = \sum_{k=1}^n b_k G_k(t) Y_k N_k(t) e^{-C(t)} (1 - e^{-A_k(t)}) + s_p P(t)$$

where

$$C(t) = \sum_{k=1}^n d_k G_k(t) N_k(t), \quad (\text{B.1})$$

$$A_j(t) = a_j P(t) \left[(1 - w) + w \frac{G_j(t) Y_j a_j N_j(t)}{\sum_k G_k(t) Y_k a_k N_k(t)} \right].$$

In these more general equations, two new parameters are introduced: d_k , a competition coefficient, and b_k , the rate of conversion 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 have limited ability to give different dynamics, because with some reasonable assumptions, they reduce to expressions (3) of the text by nondimensionalization. We assume that the ratios $d_k : b_k : a_k$ are the same for all species. This means that a plant species with a higher competitive effect has a higher nutritional value, and is encountered more frequently relative to its abundance. This would occur, for example, if all these rates were proportional to seed size. With these assumptions, we replace $d_k N_k$ by N_k , $(d_k / b_k) P$ by P , and $(b_k / d_k) a_k$ by a_k . Noting that d_k / b_k and a_k / d_k do not depend on k , Eqs. (B.1) become

$$N_j(t + 1) = N_j(t) (s_j(1 - G_j(t)) + G_j(t) Y_j e^{-C(t) - A_j(t)});$$

$$j = 1, \dots, n$$

$$P(t + 1) = \sum_{j=1}^n G_j(t) Y_j N_j(t) e^{-C(t)} (1 - e^{-A_j(t)}) + s_p P(t)$$

where

$$C(t) = \sum_{k=1}^n G_k(t) N_k(t), \quad (\text{B.2})$$

$$A_j(t) = a_j P(t) \left[(1 - w) + w \frac{G_j(t) Y_j N_j}{\sum_k G_k(t) Y_k N_k} \right].$$

Finally assuming that predation is nonselective, Eq. (B.2) becomes (3) in the text.

These nondimensionalized equations may look odd in that they appear to assume that each annual plant individual has a competitive effect of 1, as C is the simple sum of seedling densities.

However, the nondimensionalization has simply changed the units so that seedling density is measured in competitive effect units. More surprising is the fact that consumption of one seed appears to be enough to make one new predator individual. However, the nondimensionalization changes the units of predator density so that they are plant-competitive effect equivalents, and there is in fact nothing odd or unrealistic about these relationships. They do mean, however, that the units on the axes of graphs of predator and prey densities may sometimes appear to give larger densities of predators than prey, when in nature the density of annual plant seeds is in fact orders of magnitude larger than densities of seed predators, taken literally as numbers per unit area.

B.2. Coexistence criteria

In this paper, the success of invasion is measured by the invader's long-term low density growth rate (\bar{r}_i), as defined and summarized below. If the long-term growth rate of the invader is positive, we conclude that its population increases in the 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, as justified below.

We define the growth rate, $r_j(t)$, of any species for the time interval t to $t + 1$ as the change in \ln population size, i.e.

$$r_j(t) = \ln N_j(t + 1) - \ln N_j(t). \quad (\text{B.3})$$

For our seed bank model, according to expression (3), expression (B.3) becomes

$$r_j(t) = \ln (s_j(1 - G_j(t)) + G_j(t)Y_j e^{-F_j(t)}) \quad (\text{B.4})$$

where F_j is the combination of resource and apparent competition, $C + A_j$. The predation rate A_j is given as

$$A_j = a \left((1 - w) + wG_j(t)Y_jN_j / \sum_{k=1}^n G_k(t)Y_kN_k \right) P. \quad (\text{B.5})$$

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

$$\begin{aligned} \bar{r}_r &= \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} r_r(t)}{T} = \lim_{T \rightarrow \infty} \frac{\sum_{t=0}^{T-1} \ln N_r(t + 1) - \ln N_r(t)}{T} \\ &= \lim_{T \rightarrow \infty} \frac{\ln N_r(T) - \ln N_r(0)}{T}. \end{aligned} \quad (\text{B.6})$$

For the residents, population densities are expected to converge on a stationary distribution (Ellner, 1989). As a consequence, the right hand side in (B.6) converges to zero, i.e. the long-term population growth rates of residents are zero. For an invader species i , expression (B.4) for $r_i(t)$ is evaluated at $N_i(0) = 0$, i.e., as the limit of low density. The quantity \bar{r}_i is the time average of $r_i(t)$ and represents 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 ($\bar{r}_i > 0$).

In deterministic systems, invasibility is related to the concept of permanent coexistence, which implies the existence of a set of species densities, bounded away from zero, that the population trajectories must enter from all positive starting points. Invasibility is a necessary but not sufficient condition for permanence (Hofbauer et al., 1987). Permanence follows provided certain regularity conditions apply. Simulation results suggest that invasibility and permanence are the same thing for the models investigated here.

The idea corresponding to permanence in stochastic models is stochastic boundedness, which requires that low densities must have uniformly low probabilities of occurrence (Chesson, 1978). Under certain regularity conditions, invasibility is equivalent to stochastic boundedness in two-species models (Chesson and Ellner, 1989; Ellner, 1989).

Appendix C. Derivation of invasion conditions

C.1. Derivation of invasion conditions at equilibrium

Here we define $C^{*(-i)}$ and $P^{*(-i)}$ as the equilibrium of C and P , with species i being the invader. These quantities are thus determined by the resident species at equilibrium. Species i can invade if its growth rate is positive ($r_i > 0$). However, in the equilibrium case, it is easier to work with the finite rate of increase, $\lambda_i = e^{r_i}$, which is $N_i(t + 1)/N_i(t)$. Using Eq. (B.4) above, the finite rate of increase of species j is

$$s_j(1 - G_j) + G_jY_j e^{-C - A_j}.$$

The rate of predation on invader species i is always $A_i = a(1 - w)P^{(-i)}$, because the invader is at zero density, and experiences only the frequency-independent component of predation. The relative abundance of resident species r is equal to 1. Thus, it always experiences maximum predation and so $A_r = aP^{(-i)}$. To invade, the finite rate of increase of species i must be greater than 1 with the resident at equilibrium, i.e.

$$\begin{aligned} s_i(1 - G_i) + G_iY_i e^{-C^{*(-i)} - a(1-w)P^{*(-i)}} &> 1, \quad \text{or equivalently} \\ s_i(1 - G_i) + G_iY_i e^{-C^{*(-i)} - aP^{*(-i)}} e^{awP^{*(-i)}} &> 1. \end{aligned} \quad (\text{C.1})$$

Since the resident is at equilibrium, it has finite rate of increase 1, i.e.

$$\begin{aligned} s_r(1 - G_r) + G_rY_r e^{-C^{*(-i)} - aP^{*(-i)}} &= 1, \quad \text{or equivalently} \\ e^{-C^{*(-i)} - aP^{*(-i)}} &= \{1 - s_r(1 - G_r)\} / G_rY_r. \end{aligned} \quad (\text{C.2})$$

Substituting (C.2) in (C.1), we see that successful invasion requires

$$s_i(1 - G_i) + G_iY_i \{1 - s_r(1 - G_r)\} / G_rY_r e^{awP^{*(-i)}} > 1. \quad (\text{C.3})$$

Setting $\eta = \ln(GY/[1 - s(1 - G)])$, the \ln mean seed production per unit seed loss, (C.3), rearranges to

$$\eta_i > \eta_r - \Delta P, \quad (\text{C.4})$$

where $\Delta P = awP^{*(-i)}$ is the excess predation on the resident due to FDP.

C.2. Derivation of the invasion conditions with environmental fluctuations

Coexistence of annual plant species in the 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) does not consider predation explicitly, its general results apply here on substituting the combination of competition and predation, $F = C + A$, 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 magnitude of the variances of the environmental responses. Although these assumptions are restrictive, we shall find that they point the way to the larger patterns. Moreover, they can produce surprisingly accurate results even when these assumptions seem clearly violated (Appendix C.3). We specialize the results of Chesson (1994) to the present context where we assume that the \ln germination fractions, the $E_j(t) = \ln[G_j(t)]$'s, have the same probability distribution for all species, and that this probability distribution is independent of time. Thus, $\bar{E}_j = \bar{E}_k$ (where \bar{E}_j means the expected value, $E[E_j(t)]$, of the random variable $E_j(t)$), and $\text{var}(E_j) = \text{var}(E_k)$. 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 C.3 shows that the results are qualitatively correct even with large σ^2 . We use the standard mathematical notation $O(x)$ to indicate a quantity that remains of comparable magnitude to x as x becomes small (Hughes-Hallett, 2000). With these assumptions, we expect $\bar{r}_i = O(\sigma^2)$ (Chesson, 1994), and in approximating \bar{r}_i , we neglect terms equal to $O(\sigma^m)$ where m is 3 or more, as these cannot give important contributions to \bar{r}_i for small 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 survival rate, and predator attack rate, are the same for the two species, i.e. $s_j = s_k, a_j = a_k$, for each j and k . Thus, it follows that the seed loss rate, $\beta = 1 - s(1 - \bar{G})$, is the same for the two species, i.e., $\beta_j = \beta_k$. Relaxing the above assumption would lead to extra nonlinear competitive variance (NCV) terms (Snyder and Chesson, 2004).

To ensure $\bar{r}_i = O(\sigma^2)$, the η 's should not differ between species more than $O(\sigma^2)$, and w should be $O(\sigma^2)$, which means $\Delta P = O(\sigma^2)$. To constrain η differences, we must assume that the Y 's for different species differ by at most $O(\sigma^2)$. However, Appendix C.3 shows that the results are qualitatively correct even with large w and large differences in Y . 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 (e.g. small a and Y , and large s), but not in others. However, Appendix C.3 demonstrates excellent agreement between the coexistence regions derived from the formulae, and those derived from accurate simulations. Consistent predictions from the formulae are found generally, as a comparison between formulae and figures in the text attests.

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

$$r_j(t) = \ln \left\{ s \left(1 - e^{E_j(t)} \right) + Y_j e^{E_j(t) - F_j(t)} \right\}, \quad (C.5)$$

where t is suppressed on the right in E_j and F_j 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

$$r_j(t) = g_j(E_j(t), C_j(t)), \quad (C.6)$$

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 F_j , the combination of competition and predation. Thus, here

$$r_j(t) = g_j(E_j(t), F_j(t)). \quad (C.7)$$

The analysis in Chesson (1994) uses a quadratic-level two-variable Taylor expansion of r_j in E_j and F_j . 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_j , because it leads to the storage effect. It arises in the quadratic expansion from the product of E_j and F_j , which can be thought of as defining the interaction between E_j and F_j in determining r_j . This interaction, in biological terms, measures the effects of persistence in the seed bank, and is more generally referred to as buffered population growth (Chesson et al., 2004).

To perform a Taylor expansion, we must first choose fixed values, E_j^* and F_j^* , of E_j and F_j , about which to perform the

expansion. The standard choice (Chesson, 1994) is fixed values with the property

$$g_j(E_j^*, F_j^*) = 0 \left(\text{i.e. } \ln \left\{ s(1 - e^{E_j^*}) + Y_j e^{E_j^* - F_j^*} \right\} = 0 \right), \quad (C.8)$$

i.e. these are values at which the growth rate (expression (C.5)) would be zero. A natural choice for F_j^* is $\eta_j = \ln(GY_j/[1 - s(1 - \bar{G})])$, because it is the value of F_j that gives species j zero growth at equilibrium in a constant environment. Having chosen F_j^* , E_j^* is found from Eq. (C.8) to be $\ln \bar{G}$, and so is the same for the two species.

We wish to understand the effects that E_j and F_j , and their interaction, have on the growth rate r_j . One way to proceed is to expand r_j around E_j^* and F_j^* up to the quadratic order. However, a more informative and standard way is to rewrite r_j so that r_j is equal to the sum of environmental and competitive factors measured in the same units, and their interaction. We follow Appendix D of Kuang and Chesson (2009), modifying the development to include FDP. The first part of this process is to transform the variables E_j and F_j 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_j^* and E_j^* , as follows:

$$\mathcal{E}_j = g_j(E_j, F_j^*), \text{ i.e. } \mathcal{E}_j = \ln \left\{ s \left[1 - e^{E_j} \right] + Y_j e^{E_j - F_j^*} \right\}, \quad (C.9)$$

and

$$\mathcal{C}_j = -g_j(E_j^*, F_j), \text{ i.e. } \mathcal{C}_j = -\ln \left\{ s \left[1 - e^{E_j^*} \right] + Y_j e^{E_j^* - F_j} \right\}. \quad (C.10)$$

In these standard forms, \mathcal{E}_j and \mathcal{C}_j have the property that they are increasing functions of respectively E_j and F_j , but are in the same units as r_j , so it is easier to compare their effects. 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_j , and is used below to derive the fitness comparison measure, $\eta_i - \eta_r$, which then is a distinct element of the invasion rate. Similarly, averaging \mathcal{C}_j over time gives the average effect of the competition and predation on the growth of species j , at a fixed level of the density-independent factor E_j , and is used below to derive the frequency-dependent predation (FDP) measure, which then is also a distinct element of the invasion rate.

The interaction between environmental and limiting factors is expressed by the product of \mathcal{E}_j and \mathcal{C}_j . Straightforward calculus gives

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \quad (C.11)$$

where

$$\gamma_j = \frac{\partial^2}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \Big|_{\mathcal{E}_j = \mathcal{C}_j = 0} \quad (C.12)$$

(Chesson, 1994). Using these standard variables, rather than E_j and F_j directly, for the quadratic expansion of r_j , the calculations below are not dependent on the particular choice of population growth function. Indeed, (C.11) is a generic formula.

Long-term growth rates of species in this system are then found by averaging (C.11) over time:

$$\bar{r}_j \approx E[\mathcal{E}_j] - E[\mathcal{C}_j] + \gamma_j E[\mathcal{E}_j \mathcal{C}_j], \quad (C.13)$$

where on the right, we use standard expected value notation $E[\cdot]$ in place of a bar, for our more formal mathematical development that follows. Note that resident values of the long-term growth rate (expression (C.13)) are necessarily zero, but by comparing the components of the long-term growth rates between resident and invader, we can see how the interactions between species lead to

coexistence mechanisms. Thus, we write the invader growth rate as a comparison with the resident growth rate as follows (Chesson, 1994):

$$\bar{r}_i = \bar{r}_i - q_{ir}\bar{r}_r = \Delta E - \Delta C + \Delta I, \quad (\text{C.14})$$

where the q_{ir} are constants to be defined, \bar{r}_r is the zero long-term growth rate of a resident species, labeled r . The terms on the right are

$$\Delta E = E[\mathcal{E}_i] - q_{ir}E[\mathcal{E}_r], \quad (\text{C.15})$$

$$\Delta C = E[\mathcal{C}_i^{\{-i\}}] - q_{ir}E[\mathcal{C}_r^{\{-i\}}], \quad (\text{C.16})$$

where the superscript $\{-i\}$ denotes a measurement with species i in the invader state, and finally

$$\Delta I = \gamma_i E[\mathcal{E}_i \mathcal{C}_i^{\{-i\}}] - q_{ir} \gamma_r E[\mathcal{E}_r \mathcal{C}_r^{\{-i\}}]. \quad (\text{C.17})$$

We shall see below that $\Delta E = 0$, and

$$\Delta C = -\beta(\eta_i - \eta_r) - \Delta P + \Delta N, \quad (\text{C.18})$$

so the invader growth rate becomes

$$\bar{r}_i \approx \beta(\eta_i - \eta_r) + \Delta P - \Delta N + \Delta I. \quad (\text{C.19})$$

This equation expresses the invader growth rate as a fitness comparison between species (the productivity, η , difference), a frequency-dependent predation (FDP) comparison, nonlinear competitive variance (NCV), and the storage effect (SE).

Before calculating these quantities, we need to define q_{ir} . This quantity is intended to serve the purpose of adjusting the comparisons between species due to differences in their sensitivities to common density-dependent limiting factors, here measured as F less FDP. 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. It was originally defined as the partial derivative of \mathcal{C}_i with respect to \mathcal{C}_r (Chesson, 1994). Because of FDP here, it is not possible to express \mathcal{C}_i exactly as a function of \mathcal{C}_r in this model following the calculations in Chesson (1994) and Kuang and Chesson (2009). However, without FDP, this is possible, and so we ignore FDP in deriving q_{ir} . With the assumptions here, this procedure cannot lead to a final error more than $O(\sigma^4)$, and so can be ignored. In this case, q_{ir} is $(\partial r_i / \partial F) / (\partial r_r / \partial F)$ evaluated at $E_i = E_i^*$, $E_r = E_r^*$, $F_i = F_r = F_r^*$. This procedure gives $q_{ir} = \beta_i / \beta_r + O(\sigma^2)$, as in Kuang and Chesson (2009). Because the β 's are the same here, as explained above,

$$q_{ir} = 1. \quad (\text{C.20})$$

We now derive the approximations for each term in expression (C.14). First, of all

$$\Delta E = E[\mathcal{E}_i] - E[\mathcal{E}_r], \quad (\text{C.21})$$

which is a comparison of mean invader and resident environmental responses. Using definition (C.9) of \mathcal{E}_j , and noting that $F_j^* = \eta_j$, we see that

$$\mathcal{E}_j = \ln \{s + (1-s)G_j/\bar{G}\}. \quad (\text{C.22})$$

Since the G_j 's have the same distribution for all j , $E[\mathcal{E}_j]$ does not depend on j , and so

$$\Delta E = 0. \quad (\text{C.23})$$

We now establish Eq. (C.18), i.e. $\Delta C = -\beta(\eta_i - \eta_r) - \Delta P + \Delta N$, with

$$\Delta P \approx \beta a w \bar{P}^{\{-i\}}, \quad (\text{C.24})$$

and

$$\Delta N \approx \frac{\beta(1-\beta)}{2} \left(\text{Var}(F_r^{\{-i\}}) - \text{Var}(F_i^{\{-i\}}) \right). \quad (\text{C.25})$$

In Table 2 of the text, these quantities are all reported in natural units (i.e. divided by β following the convention of Chesson (2008)). To derive them, we expand \mathcal{C}_i and \mathcal{C}_r to quadratic order in F about their equilibrium values F_i^* and F_r^* . The first derivative of either \mathcal{C} in F at the equilibrium value is β , and the second derivative is $\beta(1-\beta)$, while the value of \mathcal{C} at $F = F^*$ is necessarily zero. These facts are derived in Chesson (1994) but are also easily checked. Thus, $\Delta C/\beta$ is approximately

$$E[F_i] - F_i^* - (E[F_r] - F_r^*) - \frac{1}{2}(1-\beta) \times \left(E[(F_i - F_i^*)^2] - E[(F_r - F_r^*)^2] \right). \quad (\text{C.26})$$

Because $E[F_j]$ is within $O(\sigma^2)$ of F_j^* (Chesson, 1994), the expected squares in (C.26) become the variances $\text{Var}(F_i)$ and $\text{Var}(F_r)$. Thus, the quadratic part of (C.26) becomes $\Delta N/\beta$ as given by (C.25) above. The quantity $(1-\beta)$ is a measure of the nonlinearity of the growth rate as a function of F . Because $1-\beta$ is positive, this means that the growth rate is a concave up function of F , and fluctuations in F make a positive contribution to the growth rate (Kuang and Chesson, 2008). However, this contribution is greater for residents than invaders because resident F is more variable than invader F .

The linear part of (C.26) rearranges to

$$-(F_i^* - F_r^*) + E[F_i - F_r]. \quad (\text{C.27})$$

The equilibrium comparison (first term) is simply $-(\eta_i - \eta_r)$, and the difference between the resident and average invader F values simplifies to $-aw\bar{P}^{\{-i\}}$. Thus, we have established (C.18), i.e. $\Delta C = -\beta(\eta_i - \eta_r) - \Delta P + \Delta N$, with ΔP and ΔN given by (C.24) and (C.25).

The last term in the formula (C.19) for \bar{r}_i is the storage effect, ΔI . Because we have $E[\mathcal{C}] = O(\sigma^2)$ (Chesson, 1994), the definition of the storage effect (C.17) is equivalent to

$$\Delta I = \gamma_i \text{cov}(\mathcal{E}_i, \mathcal{C}_i^{\{-i\}}) - q_{ir} \gamma_r \text{cov}(\mathcal{E}_r, \mathcal{C}_r^{\{-i\}}), \quad (\text{C.28})$$

which is in fact the more common definition of the storage effect. 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 $\beta(F_j - F_j^*)$. (All these results from Chesson (1994) can be easily verified directly from expressions (C.5), (C.9) and (C.10), above, with a little calculus and algebra.) It follows that

$$\text{cov}(\mathcal{E}, \mathcal{C}) = (1-s)\beta \text{cov}(E, F_j) + O(\sigma^4). \quad (\text{C.29})$$

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

$$\Delta I \approx \beta s \left[\text{cov}(E_r, F_r^{\{-i\}}) - \text{cov}(E_i, F_i^{\{-i\}}) \right]. \quad (\text{C.30})$$

Now $F_j = C + A_j$, with $A_r = aP$, and $A_i = aP(1-w)$. Since we assume there is no time correlation in $E(t)$, there is no correlation between $E(t)$ and $P(t)$ or $N(t)$. Hence expression (C.30) reduces to the storage effect due to competition,

$$\Delta I \approx \beta s \left[\text{cov}(E_r, C^{\{-i\}}) - \text{cov}(E_i, C^{\{-i\}}) \right], \quad (\text{C.31})$$

and is $\approx \beta s(1-\rho)\sigma^2\bar{G}\bar{N}_r$ (Kuang and Chesson, 2009). Like the other components of the invader growth rate, \bar{r}_i , ΔI is reported in natural units in Table 2 (i.e. divided by β following the convention of Chesson (2008)).

C.3. Comparison of true and approximate coexistence regions

The figures in the text show coexistence regions defined by simulations, which have been replicated many times to give highly accurate coexistence boundaries. However, analytical approximations are used to obtain theoretical insight. Some particular assumptions are made to obtain the analytical approximations, i.e., we assumed that the degree of frequency dependence, w , the difference between species seed yields, $Y_j - Y_k$, and the magnitudes of environmental fluctuations are all comparably small. Here, we investigate the robustness of the analytical approximations, especially when these assumptions are seriously violated. We compare the coexistence regions that are implied by the analytical approximations (expressions (C.19), (C.24), (C.25) and (C.31)) with those found from simulations. At the lower left hand side of Fig. C.1A, all of the above assumptions are satisfied, and the analytical approximation is seen to yield the same coexistence region as simulation. In the upper right hand side of Fig. C.1A, a moderate difference in the coexistence regions occurs as the difference in Y 's increases, and the assumptions are violated.

In Fig. C.1B, the variance of environmental fluctuations and the degree of frequency-dependent predation are increased tenfold and fivefold respectively, giving very large violations of the assumptions. However, as we can see, the difference between the approximate and accurate coexistence regions remains small or moderate. Large w seems to cause overestimation of the coexistence region, while large Y differences tend to cause underestimation. Although quantitative differences are present, the true and approximate coexistence regions give essentially the same message, giving confidence in our analytical tools.

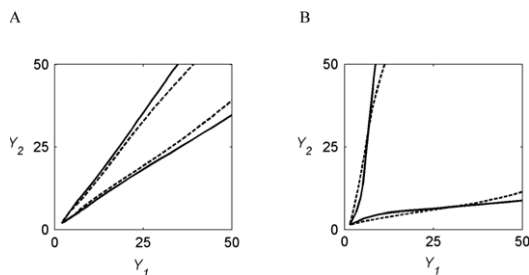


Fig. C.1. Comparison of true (between the two solid lines) and approximate (between the two dashed lines) coexistence regions when the environmental fluctuations and degree of frequency-dependent predation (w) are both small (left) and both large (right). Y is the seed yield. Parameters in panel A: $s_1 = s_2 = 0.8$, $a_1 = a_2 = 0.2$, $s_p = 0.8$, $w = 0.1$, G is a beta random variable with parameters (2, 2) independent between species; panel B: $s_1 = s_2 = 0.8$, $a_1 = a_2 = 0.2$, $s_p = 0.8$, $w = 0.5$. G is a beta random variable with parameters (0.5, 0.5) independent between species.

References

Abrams, P.A., Matsuda, H., 2004. Consequences of behavioral dynamics for the population dynamics of predator–prey systems with switching. *Population Ecology* 46, 13–25.

Abrams, P.A., Shen, L., 1989. Population-dynamics of systems with consumers that maintain a constant ratio of intake rates of 2 resources. *Theoretical Population Biology* 35, 51–89.

Adonakis, S., Venable, D.L., 2004. Dormancy and germination in a guild of Sonoran Desert annuals. *Ecology* 85, 2582–2590.

Almany, G.R., et al., 2007. Predators target rare prey in coral reef fish assemblages. *Oecologia* 152, 751–761.

Ben-Natan, G., et al., 2004. Seeds redistribution in sand dunes: A basis for coexistence of two rodent species. *Oikos* 105, 325–335.

Bond, A.B., 1983. Visual-search and selection of natural stimuli in the pigeon — The attention threshold hypothesis. *Journal of Experimental Psychology—Animal Behavior Processes* 9, 292–306.

Bond, A.B., Kamil, A.C., 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* 415, 609–613.

Bonsall, M.B., Hassell, M.P., 1999. Parasitoid-mediated effects: Apparent competition and the persistence of host–parasitoid assemblages. *Researches on Population Ecology* 41, 59–68.

Brown, J.S., 1989. Desert rodent community structure — A test of 4 mechanisms of coexistence. *Ecological Monographs* 59, 1–20.

Brown, J.S., Venable, D.L., 1991. Life-history evolution of seed-bank annuals in response to seed predation. *Evolutionary Ecology* 5, 12–29.

Brown, J.S., et al., 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. *Ecology* 75, 2286–2300.

Celis-Diez, J.L., Bustamante, R.O., 2005. Frequency-dependent seed size selection on *Cryptocarya alba* (Mol.) Looser (Lauraceae): Testing the effect of background. *Biological Journal of the Linnean Society* 84, 137–142.

Charnov, E.L., 1976. Optimal foraging — Attack strategy of a mantid. *American Naturalist* 110, 141–151.

Chase, J.M., et al., 2002. The interaction between predation and competition: A review and synthesis. *Ecology Letters* 5, 302–315.

Chesson, P., 1978. Predator–prey theory and variability. *Annual Review of Ecology and Systematics* 9, 323–347.

Chesson, P.L., 1984. Variable predators and switching behavior. *Theoretical Population Biology* 26, 1–26.

Chesson, P., 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45, 227–276.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31, 343–366.

Chesson, P., 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology* 64, 345–357.

Chesson, P., 2008. Quantifying and testing species coexistence mechanisms. In: Valladares, F., Camacho, A., Elosegui, A., Gracia, C., Estrada, M., Senar, J.C., Gili, J.M. (Eds.), *Unity in Diversity: Reflections on Ecology after the Legacy of Ramon Margalef*. Fundacion BBVA, Bilbao, pp. 119–164.

Chesson, P.L., Ellner, S., 1989. Invasibility and stochastic boundedness in monotonic competition models. *Journal of Mathematical Biology* 27, 117–138.

Chesson, P.L., Huntly, N., 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology & Evolution* 4, 293–298.

Chesson, P., Kuang, J.J., 2008. The interaction between predation and competition. *Nature* 456, 235–238.

Chesson, P., et al., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141, 236–253.

Comins, H.N., Hassell, M.P., 1976. Predation in multi-prey communities. *Journal of Theoretical Biology* 62, 93–114.

Davidson, D.W., et al., 1985. Granivory in the Chihuahuan Desert: Interactions within and between trophic levels. *Ecology* 66, 486–502.

Elliott, J.M., 2004. Prey switching in four species of carnivorous stoneflies. *Freshwater Biology* 49, 709–720.

Ellner, S., 1989. Convergence to stationary distributions in 2-Species stochastic competition models. *Journal of Mathematical Biology* 27, 451–462.

Facelli, J.M., et al., 2005. Differences in seed biology of annual plants in arid lands: A key ingredient of the storage effect. *Ecology* 86, 2998–3006.

Garb, J., et al., 2000. Foraging and community consequences of seed size for coexisting Negev Desert granivores. *Oikos* 88, 291–300.

Goss-Custard, J.D., 1977. Optimal foraging and size selection of worms by redshank. *Tringa totanus*, in field. *Animal Behaviour* 25, 10–29.

Gould, S.J., Lewontin, R.C., 1979. Spandrels of San-Marco and the Panglossian paradigm — A critique of the adaptationist program. *Proceedings of the Royal Society of London Series B—Biological Sciences* 205, 581–598.

Hassell, M.P., 2000. Host–parasitoid population dynamics. *Journal of Animal Ecology* 69, 543–566.

Hobbs, R.J., 1985. Harvester ant foraging and plant-species distribution in annual grassland. *Oecologia* 67, 519–523.

Hofbauer, J., et al., 1987. Coexistence for systems governed by difference-equations of Lotka–Volterra type. *Journal of Mathematical Biology* 25, 553–570.

Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124, 377–406.

Holt, R.D., Kotler, B.P., 1987. Short-term apparent competition. *American Naturalist* 130, 412–430.

Hughes, R.N., Croy, M.I., 1993. An experimental-analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. *Journal of Animal Ecology* 62, 341–352.

Hughes-Hallett, D., 2000. *Calculus: Single Variable*, 2nd ed. Wiley.

Hulme, P.E., Hunt, M.K., 1999. Rodent post-dispersal seed predation in deciduous woodland: Predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* 68, 417–428.

Kotler, B.P., Holt, R.D., 1989. Predation and competition — The interaction of 2 types of species interactions. *Oikos* 54, 256–260.

Krebs, J.R., Inman, A.J., 1992. Learning and foraging — Individuals, groups, and populations. *American Naturalist* 140, S63–S84.

Krivan, V., 1996. Optimal foraging and predator–prey dynamics. *Theoretical Population Biology* 49, 265–290.

Krivan, V., 2003. Competitive co-existence by adaptive predators. *Evolutionary Ecology Research* 5, 1163–1182.

Kuang, J.J., Chesson, P., 2008. Predation–competition interactions for seasonally recruiting species. *American Naturalist* 171, E119–E133.

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

Kuang, J.J., Chesson, P., The storage effect due to predation in multispecies plant communities with frequency-dependent predator behavior (unpublished manuscript).

- Kunin, W.E., 1994. Density-dependent foraging in the harvester ant *Messor ebeninus*- 2 experiments. *Oecologia* 98, 328–335.
- Lawton, J.H., et al., 1974. Switching in invertebrate predators. In: Usher, M.B., Williamson, M.H. (Eds.), *Ecological Stability*. Chapman and Hall, pp. 141–158.
- Leibold, M.A., 1996. A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147, 784–812.
- Levin, S.A., 1970. Community equilibria and stability, and an extension of competitive exclusion principle. *The American Naturalist* 104, 413–423.
- Longland, W.S., et al., 2001. Seedling recruitment in *Oryzopsis hymenoides*: Are desert granivores mutualists or predators? *Ecology* 82, 3131–3148.
- Ma, B.O., et al., 2003. Dynamic versus instantaneous models of diet choice. *American Naturalist* 162, 668–684.
- MacArthur, R.H., Levins, R., 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101, 377–385.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *American Naturalist* 100, 603–609.
- Marini, M.A., Weale, M.E., 1997. Density- and frequency-dependent predation of artificial bird nests. *Biological Journal of the Linnean Society* 62, 195–208.
- McNair, J.N., 1980. A stochastic foraging model with predator training effects. 1. Functional-response, switching, and run lengths. *Theoretical Population Biology* 17, 141–166.
- Murdoch, W.W., 1977. Stabilizing effects of spatial heterogeneity in predator–prey systems. *Theoretical Population Biology* 11, 252–273.
- Murdoch, W.W., Bence, J., 1987. General predators and unstable prey populations. In: Kerfoot, W.C., Sih, A. (Eds.), *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, London, pp. 17–30.
- Murdoch, W.W., et al., 1975. Switching in predatory fish. *Ecology* 56, 1094–1105.
- Pake, C.E., Venable, D.L., 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success. *Ecology* 76, 246–261.
- Persson, L., 1985. Optimal foraging – The difficulty of exploiting different feeding strategies simultaneously. *Oecologia* 67, 338–341.
- Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11, 559–623.
- Ripa, J., Ives, A.R., 2003. Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology* 64, 369–384.
- Roughgarden, J., Feldman, M., 1975. Species packing and predation pressure. *Ecology* 56, 489–492.
- Schmidt, K.A., Brown, J.S., 1996. Patch assessment in fox squirrels: The role of resource density, patch size, and patch boundaries. *American Naturalist* 147, 360–380.
- Simpson, S.J., et al., 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68, 1299–1311.
- Snyder, R.E., Chesson, P., 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *American Naturalist* 164, 633–650.
- Snyder, R.E., et al., 2005. Examining the relative importance of spatial and nonspatial coexistence mechanisms. *American Naturalist* 166, E75–E94.
- Tansky, M., 1978. Switching effect in prey–predator system. *Journal of Theoretical Biology* 70, 263–271.
- Turelli, M., 1978. Does environmental variability limit niche overlap. *Proceedings of the National Academy of Sciences of the United States of America* 75, 5085–5089.
- Veech, J.A., 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behavioral Ecology* 12, 467–474.
- Warburton, K., et al., 1998. Generalists as sequential specialists: Diets and prey switching in juvenile silver perch. *Environmental Biology of Fishes* 51, 445–454.
- Warburton, K., Thomson, C., 2006. Costs of learning: The dynamics of mixed-prey exploitation by silver perch, *Bidyanus bidyanus* (Mitchell, 1838). *Animal Behaviour* 71, 361–370.