



The storage effect due to frequency-dependent predation in multispecies plant communities

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ARTICLE INFO

Article history:

Received 22 February 2010

Available online 17 June 2010

Keywords:

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

ABSTRACT

Frequency-dependent seed predation (FDP) has been shown to be a powerful coexistence mechanism in models of annual plant communities. However, FDP undermines the competition-based coexistence mechanism called the storage effect (SEC), which relies on temporal environmental fluctuations that drive fluctuations in competition. Although environmental fluctuations also drive fluctuations in predation, a storage effect due to predation (SEp) may not arise due to a time lag between a change in the environment and the resulting change in the predation rate. Here we show how SEp can arise with multispecies FDP, and in a two-species setting with density-dependent frequency-dependence, partially compensating for the reduction in SEC, in the presence of predation. These outcomes occur when predatory behavior is flexible, and can accommodate to changes in prey abundances on a within-year time scale, leading to changes in predator preferences in response to prey abundances in a given year. When predator preferences are determined by average prey abundances over several years, FDP is still a strong coexistence mechanism but undermines SEC without creating SEp.

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1. Introduction

Interest in the role of predation in species coexistence mechanisms has a long history in ecology (Chase et al., 2002). Much focus has been placed on how predation can alter the outcome of competition (Chase et al., 2002), or combine with competition to create new mechanisms (Holt et al., 1994; Grover and Holt, 1998). However, beginning with Holt (1984) there has been a developing understanding of how predation can create coexistence mechanisms independently of competition. This idea then leads to the concepts of predation-based and competition-based coexistence mechanisms (Chesson and Kuang, 2008), and to the question of how competition-based and predation-based coexistence mechanisms interact with one another when present together (Chesson and Kuang, 2008; Kuang and Chesson, 2008, 2009, 2010). Studies like these show that predation-based mechanisms (for example, predator partitioning) and competition-based mechanisms (for example, resource partitioning) tend to interact negatively, with the result that the combined effect of two mechanisms is in fact weaker than the stronger separate mechanism (Chesson and Kuang, 2008; Kuang and Chesson, 2010). Competition-based mechanisms promote species coexistence by intensifying intraspecific competition

relative to interspecific competition, while predation-based mechanisms intensify intraspecific apparent competition relative to interspecific apparent competition (Chesson and Kuang, 2008). Thus, the strength of each of these two sorts of mechanism is limited by the strength of the interaction on which it is based. Because each of these interactions can limit the strength of the other, coexistence mechanisms based on each interaction can be limited by the strength of the other interaction (Chesson and Kuang, 2008; Kuang and Chesson, 2010).

As the relative strengths of predation and competition are varied, other features of the system change in their importance also. For example, the storage-effect coexistence mechanism based on competition (SEC), depends on an interaction between competition and environmental fluctuations (Chesson, 2008). With the introduction of predation, the role of environmental fluctuations in promoting species coexistence can be much reduced (Kuang and Chesson, 2010). This raises the question of why no predation-based coexistence mechanism arises from the interaction between predation and environmental fluctuations, retaining a role for environmental fluctuations in species coexistence. In our previous work (Kuang and Chesson, 2009, 2010), we considered two different situations. In the first situation, predation was non selective and the single predator species led to no predation-based coexistence mechanism (Kuang and Chesson, 2009). The absence of an effective interaction between predation and environmental fluctuations was traced to a time lag between an environmental change and the response of predators through the numerical response to the changed environmental conditions. In the second

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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
\mathcal{C}	Standardized limiting factor, combining competition and apparent competition
E	The environmental response: $\ln(G)$
\mathcal{E}	Standardized environmental response
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	Number of annual plant species
N	Density of an annual plant species
P	Density of the predator
r	Index for the resident when used as a subscript; population growth rate, when not a subscript
S	Simpson's index of diversity
s	Seed survival in the seed bank
s_p	Survival of the predator between years
w	Proportion of predation that is frequency-dependent
Y_j	Per capita seed yield of species j before accounting for competition and predation
β	$= 1 - s(1 - G)$, the mean fraction of seeds lost from the seed bank per unit time
ΔP	Magnitude of the coexistence promoting effect of frequency-dependent predation (FDP)
ΔN	Magnitude of nonlinear competitive variance (NCV)
ΔI_c	Magnitude of the storage effect due to competition (SEc)
ΔI_p	Magnitude of the storage effect due to predation (SEp)
η	$= \ln(GY / [1 - s(1 - G)])$, \ln mean seed production per unit seed loss
λ	Finite rate of increase, $N(t + 1)/N(t)$
ρ	Correlation between the environmental responses, E_j 's, of different species
σ^2	The common variance, $\text{Var}(E)$, of the environmental responses

situation, predators changed their prey preferences as prey relative abundances changed (frequency-dependent predation, FDP), potentially leading to a strong predation-based coexistence mechanism, but environmental fluctuations had a negative effect by decreasing average predator density, thereby decreasing the strength of this predation-based mechanism (Kuang and Chesson, 2010).

Changes in predator behavior can be much quicker than changes in predator population density, suggesting that there need be no lag between changes in the environment and changes in predation intensity when these changes are driven by behavior changes. However, in our previous two-species model (Kuang and Chesson, 2010) such changes were not able to influence coexistence because coexistence mechanisms function by enabling the recovery of species that fall to low density (Chesson, 2008). In a two-species system with FDP, perturbation of one species to low density renders the relative abundance of the other species close to 100%, maximizing predation on that species, a situation not sensitive to environmental fluctuations. Thus, predation rates could not vary in a manner that creates a coexistence mechanism. This raises the question of whether in multispecies systems coexistence can arise from frequency-dependent behavior and environmental fluctuations: although one species may be at low density, the relative abundances of the other species can still change in response to environmental change. We answer this question here in the affirmative and present also a variation on the standard model of FDP that allows predation rates to respond to environmental fluctuations in two-species models when one species is at low abundance. This variation on the standard model realistically makes predation rates density dependent as well as frequency dependent.

The particular system that we consider here is the annual plant guild of arid environments, which is an important field system for understanding the role of environmental fluctuations (Chesson et al., 2004). In this system, environmental fluctuations cause species' absolute and relative abundances to vary greatly from year to year, potentially driving coexistence by the storage effect

(Angert et al., 2009; Chesson et al., 2010). Seed predation is also an important phenomenon in desert annual communities and it has been suggested that it contributes to diversity maintenance (Davidson et al., 1985). Thus, this system is ideal for exploration of the issues discussed here.

In the developments below, we first present several alternative forms of multispecies frequency-dependent behavior. We then show how the total coexistence promoting effect of all the mechanisms present can be divided into specific contributions from each mechanism.

These mechanisms include the fluctuation-independent contribution of frequency-dependent predation, as well as the storage effect, which is fluctuation-dependent. The storage effect, then, divides into the storage effect due to competition (SEc) and the storage effect due to predation (SEp). Approximate formulae for the magnitudes of these mechanisms allow them to be understood, and this understanding is backed up by simulations. The formulae for the mechanism magnitudes show when SEp is expected, and they allow its magnitude and interaction with SEc to be studied. Although these issues are complex, our approach via measures of mechanism magnitude leads to a strong understanding of the issues involved.

2. Model and methods

We use the model of annual plant dynamics with predation of Kuang and Chesson (2010). The symbols defining this model are given in Table 1. Briefly, the model is as follows: desert 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, and that the actual number of seeds produced with competition is Ye^{-C} per

seedling. 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 over time in accordance with studies of germination in annual plant communities (Adondakis and Venable, 2004; Chesson et al., 2010; Facelli et al., 2005). Variation in germination fraction is the clearest means by which coexistence by the storage effect arises in annual plant systems (Chesson et al., 2004), and so it is the basis of our study of the effects of environmental fluctuations.

Predation is represented similarly by specifying e^{-A_j} as the fraction of seed of species j surviving seed predation. The quantity A_j represents the magnitude of predation, and is given by different formulae in different settings. As noted above, we assume seed predation applies to the newly produced seed. Nongerminating seeds are not subject to seed predation, as they are dispersed in surface layers of the soil. However, they are subject to mortality, and are assumed to have a survival rate s_j 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 (Kuang and Chesson, 2010):

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

$$j = 1, \dots, n \tag{1a}$$

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

with

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

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 can be thought of as predator growth on resources that are poorer than those provided by annual plant seeds (Kuang and Chesson, 2010). 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.

Kuang and Chesson (2010) use McNair's (1980) model of foraging subject to learning constraints to derive the following formula for frequency-dependent predation:

$$A_j = a \left((1 - w) + w G_j Y_j N_j / \sum_k G_k Y_k N_k \right) P. \tag{2}$$

In this formula, the absolute abundance of seed of species j susceptible to predation is $G_j Y_j N_j e^{-C}$ and so $G_j Y_j N_j / \sum_k G_k Y_k N_k$ is the relative abundance of species j . The effect of this relative abundance on the foraging rate A_j is controlled by the parameter w . When $w = 0$, predation is frequency independent, and A_j reduces to aP . With $w = 1$, frequency dependent behavior is maximal, and in particular the predation rate on a species declines to zero as its relative abundance decreases, giving a species at low abundance a boost, strongly promoting coexistence (Kuang and Chesson, 2010).

In the form (2) the predator responds directly to current seed production. We call this instantaneous FDP (iFDP). Because the germination fraction G_j fluctuates over time in response to environmental conditions, the predation rate changes immediately as G_j changes. To understand timescale effects on predation as a coexistence mechanism, we consider also the case where predator

Table 2

Types of frequency-dependent predation arising from foraging constraints.

Type of FDP	Formula for A_j/aP
gFDP	$(1 - w) + w \frac{N_j}{\sum_k N_k}$
iFDP	$(1 - w) + w \frac{G_j Y_j N_j}{\sum_k G_k Y_k N_k}$
ddFDP	$(1 - w) + w \frac{G_j Y_j N_j}{\sum_k G_k Y_k N_k} \left[\frac{B \sum_k G_k Y_k N_k e^{-C}}{1 + B \sum_k G_k Y_k N_k e^{-C}} \right]$

Notation: A_j is the predation rate experienced by species j , w is the degree of frequency dependence, a is the maximum value of the attack rate; N_j , G_j , and Y_j , are respectively species j 's density, germination fraction, and seed yield. P is predator density. B is a parameter determining the degree of density dependence of predation.

behavior does not respond immediately to changes in seed production, but instead represents a weighted moving average of past seed production. The actual density of seed in the seed bank, $N_j(t)$, at the beginning of year t is one such weighted average of seed produced prior to year t . For simplicity, we use this weighted average to analyze the case of FDP that responds more gradually to changes in seed abundance and refer to this case as gFDP. In this case the predation rate, A_j , is given as

$$A_j = a \left((1 - w) + w N_j / \sum_k N_k \right) P. \tag{3}$$

Both types of FDP are summarized in Table 2.

For both iFDP and gFDP, the average value of A_j over species is equal to $a(1 - w + w/n)$, where n is the number of prey species. Thus, the average per capita predation rate on individual prey species declines as the number of prey species increases, and this decline is stronger with greater frequency dependence, w . Although this property might be seen as a weakness of the model, it is found in nature, and is explained by foraging behavior observed in nature (Bernays, 2001; Bernays et al., 2004). Moreover, in Appendix A we show how these properties are to be expected when FDP arises from foraging constraints, and are inevitable for any model where A_j is strictly a function of the relative abundance of prey species j . For comparison, we consider also a model where Eq. (2) is modified to maintain the average foraging rate as the number of species increases (Appendix A.3).

One further issue with these models is in fact the strict frequency dependence of the predation, which arises from McNair's model from the assumption that the previous encounters of the predator determine its current preference, without any effect of the spacing of those encounters. Thus, skill gained from a given prey encounter does not decay with time. It seems more likely that when prey are scarce it would be more difficult for predators to maintain skill in capturing specific prey species. Thus, a further modification of McNair's model (Appendix A.4) considers effectiveness of learning to increase with the absolute abundance of prey (Table 2), making the frequency dependence density dependent (ddFDP).

These equations make the specific assumption that competition equally affects all species, 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 that seed production is a function of $F_j = C + A_j$.

To analyze this model, we introduce some simplifying assumptions. We assume that the germination fractions of different species fluctuate randomly over time according to the same probability distribution. These germination fractions may be correlated between species, but are independent over time. The survival rate 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.

Table 3
Mechanism quantification.

Mechanism	Notation	Magnitude from quadratic approximation
Frequency-dependent predation (FDP)	ΔP	$aw\bar{P}^{(-i)}/(n-1)$ (gFDP and iFDP) $\frac{awP^{(-i)}}{n-1} \left(\frac{B \sum_r M_r}{1+B \sum_r M_r} \right)$ (ddFDP)
Nonlinear competitive variance (NCV)	ΔN	$\frac{(1-\beta)}{2} \sum_{r \neq i} [\text{var}(F_r^{(-i)}) - \text{var}(F_i^{(-i)})]/(n-1)$
Storage effect due to competition (SEC)	ΔI_c	$s \sum_{r \neq i} [\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})]/(n-1)$ $\approx s\sigma^2(1-\rho)\bar{G} \sum_{r \neq i} \bar{N}_r/(n-1)$
Storage effect due to predation (SEp) (nonzero only for iFDP and ddFDP)	ΔI_p	$s \sum_{r \neq i} \text{cov}(E_r, A_r^{(-i)})/(n-1)$ $\approx saw\sigma^2(1-\rho)\bar{S} \cdot \bar{P}/(n-1)$ (iFDP) $\approx \frac{sawP\sigma^2}{n-1} \{U[(1-\rho)\bar{S}] + V[(1-\rho)(1-\bar{S}) + \rho]\}$ (ddFDP)

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), and the bar over a variable means a temporal average, which is the same as the expected value over the stationary distribution defined by resident species. $\bar{P}^{(-i)}$ 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_j is the joint combined effect of resource and apparent competition, and equals $C + A_j$. $\beta = 1 - s(1 - \bar{G})$ is the rate at which seeds are lost from the seed bank. The quantity, ρ , is the correlation between residents and invader. $U = B \sum M_u / (1 + B \sum M_u)$ and $V = B \sum M_u / (1 + B \sum M_u)^2$, with $M_u = G_u Y_u N_u e^{-C}$.

3. Model analysis

We use invasibility analysis (Chesson and Ellner, 1989; Ellner, 1989; Turelli, 1978) to define coexistence of competitors, as in our previous work (Kuang and Chesson, 2009, 2010). Coexistence by the invasibility criterion guarantees that coexisting species recover from low density. Moreover, with stochastic environment models of the sort considered here, the invasibility criterion has been shown in some circumstances to imply convergence of the stochastic processes describing population densities on a stationary stochastic process with all species having positive population sizes (Ellner, 1989). Although this outcome has been demonstrated only in limited circumstances, and does have some exceptions in extreme cases (Chesson, 1982), simulation studies suggest that it applies broadly, and in particular to the circumstances considered in this article (pers. obs.). To evaluate the invasibility criterion, each species i is set in turn at zero density, and its time average growth rate, \bar{r}_i , is calculated while the other species are unconstrained and converge on the stationary distribution they have in the absence of this species. If each \bar{r}_i is positive, then the system satisfies the criterion. A species set to zero density is called an invader, and the other species are termed residents. Any quantity measured when species i is the invader takes the superscript $\{-i\}$. For example, apparent competition for a resident species r , when i is invader, is denoted $A_r^{(-i)}$.

With an invasibility analysis, it is possible to partition the invasion rate \bar{r}_i into contributions from different coexistence mechanisms. For the model given here, this has been done for the two-species case (Kuang and Chesson, 2010), and is extended for the multispecies situation in Appendix B. This procedure identifies several mechanisms of coexistence whose strengths are given by formulae in Table 3. A key quantity is the maximum productivity, η , which is the natural log of average life-time production of new seed from a given seed in the absence of competition and predation (Table 1). This quantity has a critical role in the growth rate formulae. To get rid of an awkward scaling factor, we measure population growth on the time scale of seed generations. The probability of a seed leaving the seed bank in any given year is $\beta = 1 - s(1 - \bar{G})$, and so a seed generation is $1/\beta$. In these units, we show that \bar{r}_i takes the form

$$\bar{r}_i \approx \eta_i - \bar{\eta}_r + \Psi_i \tag{4}$$

where $\bar{\eta}_r$ is average productivity for resident species (Appendix B), and Ψ_i defines the combined magnitudes of the coexistence mechanisms. Fundamentally, in the absence of coexistence mechanisms,

the invasion rate would simply be $\eta_i - \bar{\eta}_r$, which means that the species with the largest value of η would exclude the other species (Chesson, 2009). In the presence of stabilizing coexistence mechanisms, the Ψ_i take positive values. Then, species i can invade the system if

$$\eta_i > \bar{\eta}_r - \Psi_i. \tag{5}$$

Thus, the minimum value of η_i allowing species i to invade is equal to the average resident productivity less Ψ_i . A positive value of Ψ_i means that a species with productivity less than the average of the residents 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 four different mechanisms, depending on the circumstances (Appendix B), which combine additively to determine the value of Ψ_i :

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

These mechanisms are defined in Table 3, 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); ΔI_c is the storage effect due to competition, and ΔI_p is the storage effect due to predation. All these mechanisms, with the exception of ΔI_p , are discussed in detail in Kuang and Chesson (2010) for the two-species case, but are reviewed briefly below. The multispecies measures can be understood as averages over resident species of the formulae applying in the two-species case for a given pair of resident and invader species. Given this fact, it should not be surprising that these multispecies measures share many properties with their two-species counterparts, but their behavior as the number of species increases is especially informative, and in some cases undergoes qualitative change between two-species and multispecies cases.

3.1. Properties of the mechanisms

ΔP : The fluctuation-independent component of frequency dependent predation

This term is the fluctuation-independent effect of FDP on coexistence, i.e. it is an effect that is present independently of environmental fluctuations. Environmental fluctuations do affect this term through the magnitude of average predator density $\bar{P}^{(-i)}$.

This quantity is also inversely proportional to $n - 1$, which is the number of resident species in an invasion analysis. Fundamentally, ΔP is the average excess predation that residents experience compared to an invader, and this quantity decreases in inverse proportion to $n - 1$ as the number of residents increases at fixed predator density. However, as we shall see $\bar{P}^{(i)}$ itself depends on $n - 1$ in ways that depend greatly on other factors. Hence ΔP as a whole is not inversely proportional to $n - 1$.

ΔN : Nonlinear competitive variance

The growth of any species depends nonlinearly on the combination of competition and predation, $F_j = C + A_j$, which fluctuates over time. Specifically, the growth rate is a concave up function of F_j , and so fluctuations in F_j make a positive contribution to the long-term growth rate (Kuang and Chesson, 2008). However, this contribution is greater for residents than invaders because resident F is more variable than invader F , giving a negative effect on coexistence. Conventionally, ΔN is entered with a negative sign, and so a negative effect on coexistence means a positive value of ΔN . In simulations, the trend in $\Delta P - \Delta N$ has followed that in ΔP alone, and so ΔN can be viewed as a correction to ΔP for fluctuating F . For simplicity we combine these mechanisms in the figures.

ΔI : The storage effect

The storage effect gives the contribution to species coexistence of temporal partitioning of the environment. It involves the average over time of the interaction between the species responses to the environment, here G_j , and the density-dependent factors, $F_j = C + A_j$. Here we mean density-dependence in a multispecies sense: C and A_j both depend on the densities of all annual plant species in the system. As defined here, competition, C , is explicitly a function of N_1, \dots, N_n . Apparent competition, A_j , depends on densities in two ways, explicitly through the FDP contributions, and implicitly and indirectly through predator density, P , which depends on past prey densities.

As G_j and F_j fluctuate over time, the growth rate, $r_j(t)$, fluctuates in a way that reflects their interaction. In particular, when G_j is low, $r_j(t)$ is relatively insensitive to the value of F_j . Most important, high values of F_j are prevented from having strongly negative effects on population growth, provided survival of ungerminated seed is not low: $r_j(t)$ can never be less than $\ln[s(1 - G_j)]$. On the other hand, when G_j is high, $r_j(t)$ depends greatly on F_j , and $r_j(t)$ can vary widely. To understand this phenomenon quantitatively, we put germination fraction on the log scale, defining $E_j = \ln G_j$. Then, quadratic expansion of the growth rate (Appendix B) shows that the interactive change in the growth rate as E_j and F_j deviate from their average values is approximately

$$-s(E_j - \bar{E}_j)(F_j - \bar{F}_j) \quad (7)$$

on a timescale of seed generations. Note that this product takes a positive value, representing a positive effect on population growth, when E_j is below average (below average germination) and F_j is above average. This interaction results from persistence of seed in the seed bank, and indeed is proportional to the seed survival fraction s . It has the effect of reducing the impact on population growth of the negative circumstances that result from simultaneous poor germination and high competition or predation. The opposite circumstances, i.e. above average E_j and below average predation and competition, represent an opportunity that is enhanced by long-term persistence of the fruits of such favorable circumstances in the seed bank. These benefits from the interactive component (7) of population growth are more available to invaders than residents, which then promotes coexistence. To measure the total magnitude of these benefits, Eq. (7) is averaged over time to give

$$-s \text{cov}(E_j, F_j). \quad (8)$$

The average resident–invader difference in expression (8) then defines the magnitude of the storage effect (Appendix B.2):

$$\Delta I = \overline{s[\text{cov}(E_r, F_r) - \text{cov}(E_i, F_i)]}^{\{r \neq i\}}, \quad (9)$$

where the over bar superscripted by $\{r \neq i\}$ means the average over resident species r .

As the density-dependent factor, F_j , depends additively on two distinct factors, the covariance $\text{cov}(E_j, F_j)$ divides into two components,

$$\text{cov}(E_j, F_j) = \text{cov}(E_j, C) + \text{cov}(E_j, A_j), \quad (10)$$

and hence the storage effect, ΔI , divides into two components. The storage effect due to competition, SEc, arises from the first covariance and the storage effect due to predation from the second covariance. In our previous work (Kuang and Chesson, 2009, 2010), $\text{cov}(E_j, A_j)$ was zero in a resident–invader scenario, and so there was no storage effect due to predation. Without frequency-dependent predation, $A_j = aP$ and the independence of the environment over time means that $P(t)$ is uncorrelated with $E_j(t)$ (Kuang and Chesson, 2009). That remains true here. With all forms of FDP considered here, the zero abundance of an invader species i means that $\text{cov}(E_i, A_i)$ is always zero. With two species, the single-species resident is fixed at 100% relative abundance, and this means that resident $A_r(t)$ does not vary with the $E_r(t)$ for both iFDP and gFDP. Thus, there is no storage effect due to predation in the two-species case for either iFDP or gFDP. But as we shall see below, a storage effect due to predation does arise in the two-species case with ddFDP because then resident $A_r(t)$ does vary with the $E_r(t)$.

With gFDP, $A_r(t)$ is uncorrelated with $E_r(t)$, regardless of the number species, as $A_r(t)$ reflects only past values of the environmental responses. However, with multispecies iFDP, a storage effect due to predation (SEp) appears. With two or more resident species, $A_r(t)$ increases directly as a function of $E_r(t)$ because an increase in $E_r(t)$ increases the relative abundance of the seed of species r . Thus, a positive value of $\text{cov}(E_r, A_r)$ results. However, for an invader i , $\text{cov}(E_i, A_i)$ remains zero because at zero relative abundance $A_i(t)$ cannot change as a function of $E_i(t)$, and $P(t)$ is uncorrelated with $E_i(t)$ regardless. Hence, an invader–resident difference in $\text{cov}(E, A)$ is guaranteed in this case. So the immediate behavioral response of the predator to prey relative abundances in a given year creates SEp with multispecies iFDP.

The measures of the magnitudes of SEc and SEp are denoted respectively by ΔI_c and ΔI_p (Table 3). For iFDP, they are both proportional to $\sigma^2(1 - \rho)$, where σ^2 is the common variance of $E_j(t)$, and ρ is the common correlation between species. It follows that $\sigma^2(1 - \rho)$ is that component of the variance of E that is independent between species. An interesting feature of the measure ΔI_p of SEp is that it is proportional to the time average value, \bar{S} , of Simpson's index of diversity for resident species, divided by $n - 1$, the number of resident species. Simpson's index is the probability that two individuals chosen at random will be different species. It is thus zero when there is only one resident species, rendering SEp absent in this case. For any fixed number of residents, this formula says that SEp is stronger when residents are more equal in abundance. This outcome reflects the fact that even abundances in the seedbank lead to a dominant influence of the current environment on seedling relative abundances, maximizing the covariance between environment and apparent competition for residents. However, as the number of resident species, $n - 1$, increases, $\bar{S}/(n - 1)$ declines, and so like ΔP and ΔI_c , ΔI_p weakens as the number of resident species increases.

The dependence on Simpson's index in the case of iFDP emphasizes that if the residents have no diversity, there is no SEp. In particular, in the two-species case, SEp cannot occur with iFDP. With

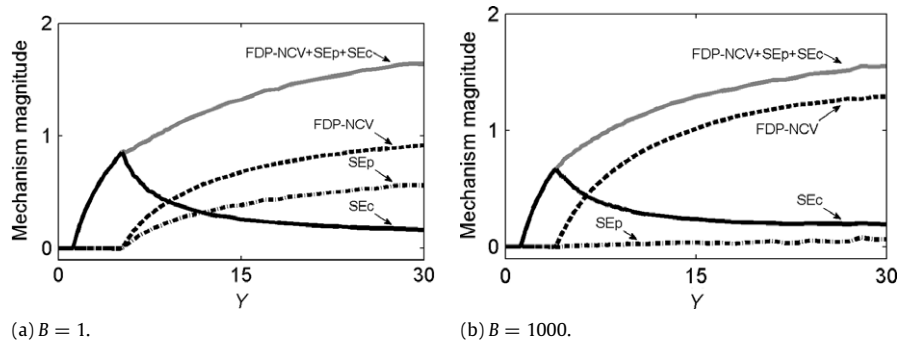


Fig. 1. Mechanism magnitudes with ddFDP. The separate mechanisms, FDP – NCV ($\Delta P - \Delta N$, dashed line), SEc (ΔI_c , solid line), and SEp (ΔI_p , dash-dot line), and the combined magnitudes of all mechanisms (gray line), plotted against the seed yield parameter, Y . Without the predator, SEc is the only mechanism. The predator enters at sufficiently high seed yield, at which point SEc declines in importance. Panel (a), parameter $B = 1$ (strong density dependence), allowing SEp to be an important mechanism. Panel (b), parameter $B = 1000$ (weak density dependence), allowing only weak SEp. Common parameters: $a = 0.2$, $s = 0.8$, $s_p = 0.8$, $w = 0.5$; G is beta(0.5, 0.5), independent between species.

ddFDP, however, there is no requirement for diversity in the prey. The formula for ΔI_p in the case of ddFDP (Table 3) consists of two components. The component multiplied by the positive quantity U , is the quantity defining ΔI_p in the case of iFDP, but the component multiplied by V is unique to ddFDP and has the interesting property that it is a decreasing function of Simpson's index. Moreover, this component is maximized when $\rho = 1$, i.e. when the annual plant species respond identically to the physical environment. Thus, it also has the unique feature that it does not require species-specific responses to the environment. This outcome reflects the fact that with density-dependent predation, low density weakens any correlation between the environment and apparent competition without reliance on species having different responses to the physical environment, thus rendering invader $\text{cov}(E, A)$ zero. With iFDP, resident $\text{cov}(E, A)$ still cannot be nonzero with $\rho = 1$ because the factor elevating predation rates of residents is repeated encounters with the same prey alone. However, with ddFDP, predation rates also vary with the time since the previous encounter, which then reflects the overall abundance of prey, not just the identity of the previous prey encountered. Relative to iFDP, a predator with ddFDP pays a penalty in ability to catch prey as prey absolute abundances go down. This penalty is partially recovered by $\text{cov}(E, A)$ because it accounts for higher overall capture rates when the environment makes a prey species more abundant. This effect is only strong for a prey species that is abundant in the seed bank, for only then can A strongly reflect E . Thus, a contrast between residents and invaders arises, driving the storage effect.

4. Magnitudes and interactions of coexistence mechanisms

As we have seen above, there are differences between the three sorts of FDP depending on the number of annual plant species present. Thus, we distinguish between the two-species case and the multispecies case in our discussion.

4.1. Interacting coexistence mechanisms in the two-species case

The two-species cases with iFDP and gFDP are fully described in Kuang and Chesson (2010). Our chief concern here is how ddFDP differs from these two other forms of FDP. The outstanding distinction is that SEp is positive in the two-species case of ddFDP. Fig. 1 shows how the magnitudes of the mechanisms vary with the yield Y . In panel (a), with a low value of B , the spacing of prey encounters has a major effect and so SEp occurs. At low yield, the predator is not supported. As yield is increased, the predator is able to enter, sharply reducing SEc, but replacing it with SEp. SEc is never completely zero, and the combined effects of SEc and SEp increase as the yield increases. The parameter B decreases the sensitivity of predator learning to prey density, and as B becomes

large, the situation applying for iFDP and gFDP is approached. Thus, SEp disappears for large B (ΔI_p approaches zero).

4.2. Interacting coexistence mechanisms with many species

In a multi-species setting in a variable environment, gFDP is strongly distinguished from iFDP and ddFDP, because gFDP never leads to SEp. We assess the multiple species coexistence region in terms of the minimum productivity (η) required for invasion, which we determine by simulation. For simplicity, resident productivities are assumed equal. However, simulations show that resident differences in seed yield do not affect the critical patterns. The mechanism NCV (ΔN) is present in all cases, but its role seems to be to reduce the effects of FDP, without changing trends, as we have seen above, and so we mention it no further below.

We first discuss the difference between iFDP and gFDP, as shown in Fig. 2. In a constant environment, there is no distinction between these two while residents have the same productivity and germination rate. As the numbers of residents increase, the minimum invasion requirement increases. In a variable environment, patterns are qualitatively similar for both iFDP and gFDP. In a variable environment, and 5% FDP, SEc is dominant and predation has a negative effect on coexistence, indicated by the higher minimum productivity requirements compared with SEc alone. At 50% FDP, predation not only compensates for its negative impact on SEc, but also allows coexistence of species with lower productivity compared to the case without predation. Thus, at $w = 0.5$, both types of FDP have more effect than SEc as a coexistence mechanism for the chosen set of parameters.

Fig. 2 also shows more complex effects occurring with 100% FDP. With only few residents in the system, the minimum productivity for invasion is the lowest compared with any other level of FDP and also compared with no predation. This outcome is not surprising, because at 100% FDP, the predator ignores the invader, and preys only on the residents, greatly advantaging the invader. However, as the number of residents increases, eventually the invasion requirement jumps sharply with iFDP and gFDP, associated with a drop in foraging efficiency (Appendix B.2) and a reduction in predator density (Fig. 3). This occurs earliest with no environmental variation, when mean predation rates are too low to sustain the predator in the system. With environmental fluctuations, SEp not only benefits the invader by slowing the increase in the minimum invasion requirement, it also benefits the predator. Environmental fluctuations maintain uneven relative abundances of the prey. With FDP, this means average prey intake rates are higher (Appendix A). However, for more than 10 residents (not shown), FDP has no or very low effect in all cases, and

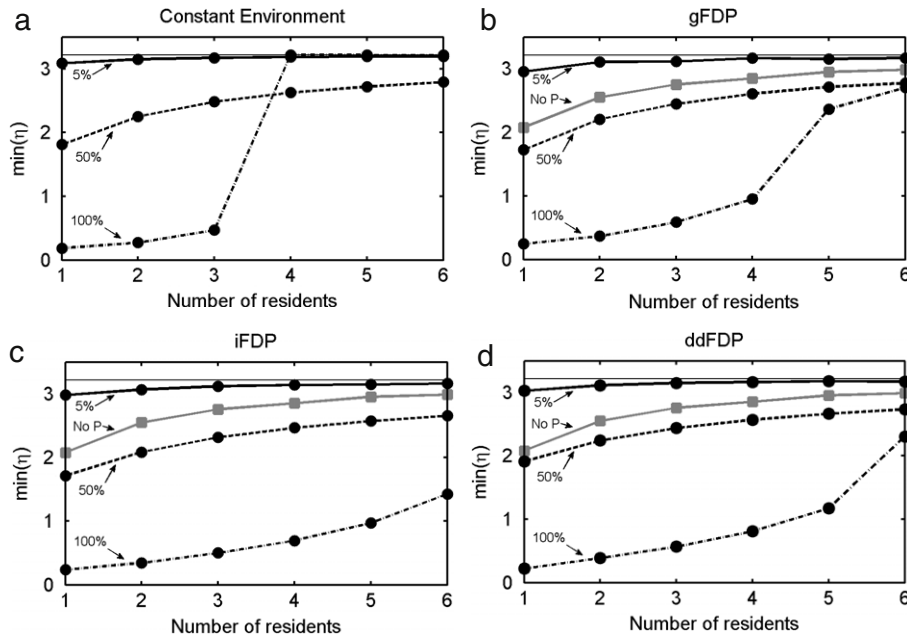


Fig. 2. Minimum invasion requirements as a function of number of residents. The minimum invasion requirement, η , is a direct measure of the combined strength of all coexistence mechanisms, with lower values meaning greater strength. The horizontal solid line gives the resident η , set the same for each resident species. When $\min(\eta)$ has this value, the combined mechanisms have zero strength. The gray line defines the case without the predator. The percentages define the percent FDP (the quantity $100w\%$). Thus, $w = 1$, dash-dot line; $w = 0.5$, dashed line; $w = 0.05$, solid line. (a) No environmental variation, which also means no coexistence without a predator. (b) Gradual frequency-dependent predation (gFDP). (c) Instantaneous frequency-dependent predation (iFDP). (d) Combined density-dependent and frequency-dependent predation (ddFDP). Parameter: $s = 0.8$, $Y_r = 30$, $s_p = 0.8$, $a = 0.2$, $G = \text{beta}(0.5, 0.5)$ independent between species.

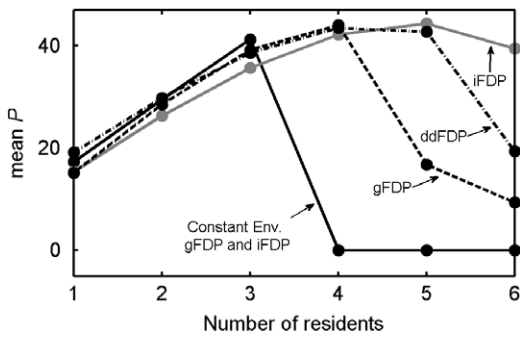


Fig. 3. Changes in mean predator density with changes in species richness. Time averages of predator density at 100% FDP. The curves correspond to the four panels of Fig. 2, with the same parameter values and show changes in predator density underlying the patterns in Fig. 2.

coexistence is promoted almost entirely, or completely, by SEc alone.

Fig. 2 also shows the outcomes for ddFDP. It shows a similar pattern to iFDP. For the same values of other parameters, the quantity B , which determines the closeness of the model to iFDP, shows that ddFDP is slightly less effective at maintaining diversity than is iFDP, but that is at least partly the effect of lower overall average predation rates due to the reduced efficacy of learning. The biggest effect occurs as the number of residents reaches 6 with 100% FDP, for then a low value of B leads to a sharp increase in the minimum η for invasion, reflecting a strong decline in predator abundance in that case (Fig. 3).

5. Discussion

Although frequency-dependent predation has long been known in models to be a powerful mechanism of species coexistence (Roughgarden and Feldman, 1975; Krivan, 2003), it has not previously been understood as a component of fluctuation-dependent

coexistence. Here we have seen how frequency-dependent behavior can lead to the fluctuation-dependent coexistence mechanism, the storage effect due to predation (SEp). In our previous work with models having just two prey species (Kuang and Chesson, 2010), we found that although frequency-dependent predation could promote coexistence, the presence of predation undermined the storage effect due to competition (SEc). Thus, it undermined the role of environmental fluctuations in promoting species coexistence. The net outcome from predation could be an enhancement of the abilities of annual plant species to coexist if frequency dependence were strong enough, but it could also be a net undermining of coexistence if frequency dependence were weaker. Here, we have seen how the ability of predators to respond behaviorally to annual fluctuations in the relative and absolute abundances of annual plant seed can create SEp, maintaining a strong role for environmental fluctuations in species coexistence even though predation still undermines SEc.

Critical to the presence of SEp is temporal covariance between the mortality rate due to predation and the response of annual plant seed production to environmental conditions. Invader resident-differences in this covariance, along with persistence of dormant seed in the seed-bank, create SEp. When frequency-dependent predation reflects densities in the seed bank (gFDP), rather than current seed production (iFDP and ddFDP), this covariance does not occur and SEp is absent. However, predators that adjust their seed preferences to the current relative abundances of plant seed (iFDP and ddFDP) do create this covariance, and hence SEp. A peculiar feature of SEp compared with SEc is that there is never any covariance between predation and the invader environmental response. It follows that the magnitude of SEp reflects entirely the extent to which resident species are attacked more heavily when the environment favors them (i.e. $\text{cov}(E, A)$ for residents) rather than a comparison between residents and invaders in this regard. Thus, unlike SEc, the correlation between resident and invader responses to the environment is irrelevant to the magnitude of SEp.

When predation is strictly frequency-dependent on current seed production, i.e. when the per capita mortality due to predation on a species is strictly a function of the relative abundance of new seed of the species (iFDP), SEp only occurs when at least three annual plant species are present. The technical reason is that in an invasibility analysis with two species, the resident is at 100% relative abundance (the invader is at 0%), regardless of the environment, and so the per capita predation rates are fixed and unresponsive to the environment. We do not have to think of this in terms of an invasibility analysis, however, because it also has meaning for the dynamics of two species following the decline of one of them to low abundance. A large disparity in species abundances cannot be quickly changed by an environmental change, and so the relative predation rates are insensitive to the environment in such cases. Thus, fluctuations in per capita predation rates become less important as one species declines in abundance. In this case of two annual plant species, however, the fluctuation-independent component of predation, measured here through ΔP , is maximal. This outcome means that although SEp does not arise, strong FDP still has a strong effect on coexistence. In this case, it is the role of fluctuations in coexistence that becomes diminished when a predator is introduced, not the overall ability of species to coexist.

With more than two plant species, and iFDP with one species at low density, new seed production of the remaining species can vary greatly in relative magnitude as the environment varies. This tendency depends on two factors. First is the relative abundances of the species in the seed bank, from which relative abundances of new seed production can deviate, both positively and negatively. These deviations occur most readily when species are at similar relative abundances in the seed bank. Second is the correlation between species in germination fraction. If germination fractions do not show relative fluctuations (the case with high correlation), environmental fluctuations do not create relative variation in seed production. These two factors both appear explicitly in the formula for the magnitude of SEp (ΔI_p) as the product $\bar{S}(1 - \rho)$, where \bar{S} is the time average of Simpson's diversity index for resident species (measuring evenness when n is fixed), and ρ is the correlation between species' environmental responses. Fundamentally, when species' relative abundances can be moved easily to extreme values by environmental fluctuations, strong covariance between mortality rates and the environment arise. This covariance promotes coexistence because it prevents abundant species from gaining full advantage of favorable environmental conditions, providing a relative advantage to species at low density, promoting their recovery. It is also worthwhile noting that with frequency-dependent predation and many species, average relative abundance is necessarily low. Without environmental fluctuations, FDP would mostly be responsible for checking the growth of the more abundant species. With strong environmental fluctuations affecting species differentially, all species are checked by FDP, but at different times, and it is this effect that is captured by SEp.

Although strict frequency dependence of per capita predation rates requires more than two plant species to create SEp, with density dependence as well, this is not necessary. We introduced density-dependent frequency-dependent predation (ddFDP) by modifying our iFDP model with the assumption that prey capture ability depends not just on the relative frequency with which a prey is encountered (which leads to strict FDP), but also on the absolute rate of prey encounters. This means that the growth of even a single species resident is checked when the environment favors it because predation rates go up with the total seed production, not just with relative seed production. In terms of storage-effect theory, covariance between environment and apparent competition ($\text{cov}(E, A)$) arises. The formula for ΔI_p

(the magnitude of SEp) in that case has two components to it. One of these reflects frequency dependence and involves the same term $\bar{S}(1 - \rho)$, discussed above, showing how coexistence is enhanced by evenness of residents in the seed bank and low correlation between their environmental responses. This term is zero for a guild of only two annual plant species. However, another term is present that varies quite differently because it depends on absolute prey abundances, not relative prey abundances. It decreases as a function of Simpson's index, and increases as a function of the correlation between environmental responses, exactly the opposite of the first term. Thus, a storage effect due to predation is possible with ddFDP under quite different circumstances to iFDP. The conditions for ddFDP to create SEp are much broader than for iFDP, and since it is more realistic, it is the preferred model.

Another factor in these effects is the numerical response of the predator, and especially the average density (\bar{P}) that it maintains. The mechanism measures ΔP and ΔI_p are both proportional to \bar{P} , but the behavior of \bar{P} is not so easy to predict. Interestingly, in the presence of frequency-dependent predation, although environmental fluctuations can depress \bar{P} slightly for low diversity annual plant guilds, for high diversity guilds, environmental fluctuations can prevent collapse of the predator population, presumably by ensuring that new seed production is mostly dominated by a few species in any given year, as has been observed in nature in annual plant guilds (Chesson et al., 2010). This effect, which creates SEp, helps maintain predator abundance by increasing foraging efficiency. High predator abundance, however, depresses plant densities, with the result that competition and the competition-based mechanism, SEc, are reduced. It is this reduction in plant densities that causes coexistence to be dramatically undermined with the introduction of a frequency-independent predator (Kuang and Chesson, 2009).

These developments are framed in terms of annual plant species and temporal variation in seed germination. The key features of this analysis clearly generalize, as inspection of the derivations in Appendix B.2 reveals. Several broad principles are involved. First, as we have emphasized elsewhere (Chesson and Kuang, 2008; Kuang and Chesson, 2009, 2010) and in the introduction to this article, the overall magnitudes of competition and predation limit the potential magnitudes respectively of competition-based and predation-based mechanisms. That is seen here in the decline of SEc as a predator is introduced and limits prey density, limiting competition, and in the collapse of predation-based mechanisms as the predator density falls as a consequence of increasing prey diversity. Second, for environmental fluctuations to lead to coexistence, some form of storage or buffered population growth is required. That occurs here through persistence of dormant seed in the seed bank, but can occur in perennial organisms by high survival of adult organisms. Buffered population growth makes the population growth rate an interactive function of the environmental responses and the density-dependent processes of competition and apparent competition. It then follows that long-term population growth is dependent on the covariances between the environmental response and the responses to competition and apparent competition. The storage effect, in the various forms that we have discussed, is the outcome, and that is certainly not limited to this annual plant model.

It is worthwhile considering how the storage effect might arise also with specific variations on the annual plant model. We considered environmental variation driving seed germination, as that is a clear way in which covariance between environment and competition arises. Had we considered instead temporal variation in the seed yield parameter, Y , then there would have been no covariance between environment and competition, and no SEc. However, covariance between environment and apparent

competition would still have occurred with iFDP and ddFDP, generating SEp. In making these distinctions, however, it is important to be clear what the parameter Y means biologically. In Chesson et al. (2005) and Angert et al. (2009) it is given as the product of seed production per unit biomass and a parameter V representing average mass of an individual plant, which is therefore reflective of seedling growth and survival. Higher growth is associated with higher demand for resources and therefore more competition. Thus, the magnitude of competition, C , depends on V . For this reason, temporal variation in V would lead to SEc (Angert et al., 2009) and also SEp with iFDP and ddFDP. On the other hand, temporal variation in seed production per unit biomass reflects processes occurring after competition has occurred. Thus, C does not depend on seed production per unit biomass, and temporal variation in seed production per unit biomass would not lead to SEc, but SEp would still occur.

As with most analytical model analyses, simplifying assumptions were used here to obtain clear easily understood formulae. These are special cases of the more complex general formulae developed in Chesson (1994, 2008). Here, assumptions of equal mean germination fractions, and small differences between species in the seed yield parameter, Y , meant that Simpson's index, S , was calculated simply on the density of seed in the seed bank. It is clear from the derivation (Appendix B.2), however, that in more complex cases it would need to be not the crude densities in the seed bank but densities weighted by average germination fraction and seed yield. Moreover, it is clear that further weightings would be necessary with a more general form of frequency-dependent predation where species are not favored equally by the predator at equal relative abundances (formula A.6 of Kuang and Chesson, 2010). Although these would seem to be complications, a little reflection indicates that they make perfect sense ecologically.

Frequency-dependent predation is far from the only way that predation-based coexistence mechanisms can arise. In a seminal work, Holt (1984) demonstrated predation-based species coexistence resulting from various interactions between predation and spatial variation, some of which correspond to spatial versions of SEp. A recent focus of theoretical work has been predation-competition tradeoffs (Chesson and Kuang, 2008; Grover and Holt, 1998; Holt et al., 1994; Kuang and Chesson, 2008), but a serious weakness of this mechanism is that acting alone it cannot stabilize the coexistence of more than two prey species. Predator partitioning is a much more viable possibility (Chesson and Kuang, 2008). A related idea, recently termed "differential sensitivity", suggests that species differ in their sensitivities to predation or other natural enemies, and that natural enemy effects fluctuate substantially in time or space (Kelly and Bowler, 2009). These natural enemy effects are incorporated in a density-independent way. In particular, no numerical response is assumed. In effect, the natural enemies act like the physical environment, as modeled here, because they are not involved in feedback loops with plant species. They do not create predation-based mechanisms (Chesson and Kuang, 2008) because, in the absence of any density-dependent component of predation, apparent competition cannot occur. Instead predation drives fluctuations in competition, and treating mortality due to predation as the environmental response, covariance between environment and competition, and ultimately SEc, result. Thus, in a terminology where predation-based mechanisms arise from the pattern of apparent competition, and competition-based mechanisms from the pattern of competition (Chesson and Kuang, 2008), the role of predation in Kelly and Bowler (2009), and also in the spatial model of Pacala and Tilman (1994), is to mediate competition-based coexistence.

All mechanisms discussed so far rely on just a single predator species. However, natural systems generally have a multiplicity

of predators. Coexistence by predator partitioning occurs when different predators focus on different prey species (Chesson and Kuang, 2008). Acting alone, predator-partitioning can only maintain as many prey species as there are predators, yet predators are normally regarded as less species rich than their prey. Broadening the category of predators to include all natural enemies breaks this restriction, although it is unknown how effective different sorts of natural enemies might be in promoting diversity by natural enemy partitioning. In some guilds, for example tropical forests, natural enemy partitioning is an attractive possibility as developed in the Janzen–Connell hypothesis (Adler and Muller-Landau, 2005; Connell, 1970; Janzen, 1970; Petermann et al., 2008). Regardless, FDP has the attractive feature that it has the potential to maintain prey species diversity with many fewer effective natural enemies than prey species.

The form of FDP here is based on learning constraints (Kuang and Chesson, 2010). An alternative origin of FDP is optimal diet selection (Abrams and Matsuda, 2004; Krivan, 2003; Ma et al., 2003), which has been found to promote coexistence of two prey species (Krivan, 2003). However, it remains to be considered more generally. As it is based on asymmetries between species it has an intrinsic asymmetry that constraint-based FDP does not have. With optimal diet selection, FDP arises from the inclusion of species in the diet as more preferred species become rare. This mechanism would seem to limit the extent of any low-density advantage that it might provide, especially in multispecies systems. One feature of FDP based on foraging constraints that is not so intuitive is that foraging efficiency necessarily goes down with diversity. This feature has been found in nature (Bernays, 2001; Bernays et al., 2004), and means that FDP as a coexistence mechanism weakens as diversity is increased, tending to place a limit on the diversity that can be maintained. However, most mechanisms have this property, as we see here with SEc. If FDP is prevented from weakening as diversity increases, as in Appendix A.3, FDP does not weaken as a coexistence mechanism, promoting diversity extremely powerfully (Appendix A.3), but this situation seems fanciful. Appendix A provides an extended discussion of these issues.

There is much to be learned about the actual sorts of FDP present in nature and their strengths. Surprisingly, despite initial enthusiasm for field studies of FDP, and numerous lab studies, this important phenomenon has been investigated to only a limited degree in nature (Kuang and Chesson, 2010). Although FDP has been found among seed predators, and in several other systems in these studies, the generality of this phenomenon is poorly understood. The potential for important roles of FDP in diversity maintenance, with different forms of FDP potentially having rather different effects, implies there is much to be gained by renewed empirical emphasis on this phenomenon.

Acknowledgments

We thank the Chesson Lab discussion group, Bob Holt and an anonymous reviewer for helpful comments on this work. Larry Bai-lian Li generously provided office space for JJK at University of California (UC), Riverside. This work was supported by National Science Foundation grant DEB-0717222.

Appendix A. Models of frequency-dependent predation

The model of frequency-dependent predation (FDP) used in the text is derived in Kuang and Chesson (2010) from a model of foraging under learning constraints due to McNair (1980). Models of frequency-dependent behavior are often written down on intuitive grounds, but then often have unintended and questionable consequences for predator efficiency (Holt, 1983).

For this reason derivation from a behavioral submodel with clearly defined assumptions is vitally important. McNair's model applies to asymptotic consumption rates in continuous time, with replenishment of the prey so that prey encounter rates do not change over the period in question. In the text we use an integrated form of this equation (the depletion rate A_j is replaced by the survival probability $\exp(-A_j)$). This approach in effect assumes that per capita predation rates are fixed at the beginning of the interval of time in question rather than being continuously updated as prey depletion occurs. Simulations have revealed only quantitative, not qualitative differences in the results from this assumption.

In the multispecies case, the formula that we use for FDP differs distinctly from a more commonly used formula of Comins and Hassell (1976), based not on a foraging model, but on intuitive grounds. In the text we find that the strength of FDP declines at the number of species decreases, which might be regarded as a weakness of our model formulation. However, the formula of Comins and Hassell (1976) becomes inconsistent when a prey species goes extinct, and cannot be used to study the effects of the number of prey species on species coexistence. In Appendix A.1, we show that our formulae are fully consistent as the number of prey species changes. In Appendix A.2, we show that average foraging efficiency must decline with the number of prey species and with the degree of frequency dependence whenever the attack rate is strictly a function of prey relative abundances. Thus, this decline in foraging efficiency is inevitable with a consistent model of FDP, at least under symmetry conditions where only the relative abundance of a prey species determines the attack rate on it. In Appendix A.3, we present a formula for frequency-dependent attack rates that remains consistent when extinctions occur, but is free from the constraints that are a natural part of McNair's (1980) foraging model. In this model, foraging efficiency does not depend on the frequency of an individual prey species alone, and the average foraging efficiency on an individual prey species does not decline with the number of prey species and the degree of frequency dependence. We argue, however, that this outcome is unrealistic. Finally in Appendix A.4, we show how McNair's (1980) model can be modified to provide the model of density-dependent frequency-dependence used in the text.

A.1. The formulae for frequency dependent predation used here

Prey species j 's relative frequency is $u_j = N_j / (N_1 + \dots + N_n)$, where N_j is either the density of the seeds of the prey species in the seed bank or its current seed crop. The quantity n is the number of species. The text provides a very simple attack-rate formula for FDP which we write here as

$$A_j/P = a(1 - w + wu_j). \quad (\text{A.1})$$

Note that this attack rate is a function of relative abundance only. The parameter w determines the degree of frequency dependence. This formula does not depend on the number of species, and does not depend on absolute abundances of the species. It has two critical features. First, as we have emphasized, it follows from reasonable postulates about foraging behavior under learning constraints (Kuang and Chesson, 2010), as embodied in McNair's (1980) foraging model. Second, this formula applies consistently as the number of species is changed. For example, when the relative abundance of a given species approaches zero in (A.1) it is natural to expect the formula to converge on that applying with one fewer species. This formula does that trivially because the formula itself does not include n as a parameter, and is just a continuous function of u_j . In contrast, a formula for frequency-dependent predation that has been used a number of times in the literature (Bonsall and

Hassell, 1999; Hassell and Comins, 1976), without this important property, is given in our notation as

$$A_j/P = a(1 - w + nwu_j). \quad (\text{A.2})$$

Note that the only change in the formula is the n in front of w . Formula (A.2) has the intuitively attractive feature that averaging across species gives the constant value a . So regardless of the level of frequency dependence in the system, the average attack rate remains the same. However, given the frequent counter-intuitive nature of science, what at first sight makes sense intuitively need not make sense with further information. This formula embodies inconsistencies which mean that it should not be used to determine the effect of the number of species on the consequences of FDP. As the relative abundance of some species i , (not equal to j) goes to zero, the formula (A.2) for the attack rate on species j does not change, but the system approaches an $n - 1$ species system. It makes sense that when $u_i = 0$, and the system is truly $n - 1$ species, the formula for the attack rate on species j should in fact be

$$A_j/P = a[1 - w + (n - 1)wu_j]. \quad (\text{A.3})$$

However, formula (A.2) does not convert to formula (A.3) as a species drops out of the system, and so it is inconsistent. It says that although one prey has negligible abundance, formula (A.2) applies, but as soon as it becomes zero, formula (A.3) applies, and there is a sudden drop in the attack rates on other prey species. This discontinuous behavior makes no sense in an invasion analysis with any number of prey species. In that case, it is important that the model used for residents be continuous with that applying after invasion when the number of species has increased by 1.

The formula (A.1) that we use, however, does not maintain average foraging efficiency as the number of species increases. Nor does it maintain average foraging efficiency as the degree of frequency dependence increases (i.e. as w increases). Instead, in both cases, that efficiency must fall. Although these facts may appear to be deficiencies, as mentioned in the text there is evidence from nature that foraging efficiency is lower when more choices are to be made. These facts are discussed by Bernays et al. (2004), primarily for insects, and by Warburton and Thomson (2006) for fishes. In Appendix A.2 we go on to show that such decreasing efficiencies are necessary properties of models of predation where changes in attack rates are functions of frequency alone.

A.2. Strict frequency-dependent predation and decline in foraging efficiency with number of species and choosiness

In this work, it is critical also that the model behave sensibly as the number of species increases. This entails decreasing efficacy of the coexistence mechanism as the number of species increases, which is a natural property whenever species have overlapping niches, because with more species, species abundances are naturally lower on average, and the distinction between resident and invader is necessarily less. Although our formulae (2) and (3) in the text are particular formulae, the property that we have been discussing is a generic one. If we make that attack rate some arbitrary increasing function, $f(u_j)$, of relative abundance alone, average attack rates must necessarily decrease as diversity increases. For instance in the case where species are exactly even in abundance, the attack rate is $f(1/n)$ and necessarily declines with n . In the specific formula (A.1) that we use here, the attack rate is linear in u_j , which means that the average attack rate is always $f(1/n)$. Uneven abundances, however, lead to higher weighted average attack rates, where the weights are the prey densities. A little algebra shows this weighted average to be $f(1/n) + nw\text{var}_j(u_j)$, i.e. it is inflated by an amount proportional to the variance between species in relative abundance. This means that

Table A.1
Quantification of the mechanisms with sFDP.

Mechanism	Notation	Mechanism magnitude (natural units)
Frequency-dependent predation (FDP)	ΔP	$aw\bar{p}^{(-i)}$
Nonlinear competitive variance (NCV)	ΔN	$\frac{(1-\beta)}{2} \sum_{r \neq i} [\text{var}(F_r^{(-i)}) - \text{var}(F_i^{(-i)})] / (n-1)$
Storage effect due to competition (SEc)	ΔI_c	$s \sum_{r \neq i} [\text{cov}(E_r, C^{(-i)}) - \text{cov}(E_i, C^{(-i)})] / (n-1)$
Storage effect due to predation (SEp)	ΔI_p	$s \sum_{r \neq i} \text{cov}(E_r, A_r^{(-i)}) / (n-1)$

the instantaneous total food intake of the predator in continuous time is increased by unevenness in prey abundance. The discrete-time formulation of the text does not lead to such a simple quantitative result, but the same qualitative outcome can be seen to apply. Thus, the predator's intake rate declines both with prey species richness and prey species evenness, that is, with the two standard components of species diversity.

Now consider the related problem of the decline in the attack rate as the choosiness parameter w increases. Suppose the attack rate on species j takes the form

$$f(w, u_j) \tag{A.4}$$

where f is any function that increases in u_j (i.e. defines frequency dependence), and w is a parameter determining the degree of frequency dependence. This function must satisfy several properties to be a sensible model of frequency-dependence. These are as follows:

$$\frac{\partial f(w, u_j)}{\partial u_j} > 0 \quad \text{for any positive values of } w \text{ and } u_j \tag{A.5}$$

(the predation rate increases with frequency).

$$\frac{\partial^2 f(w, u_j)}{\partial w \partial u_j} > 0 \tag{A.6}$$

(increasing the parameter w increases the dependence on frequency).

$$f(0, u_j) = \text{constant} \tag{A.7}$$

(there is no frequency dependence when $w = 0$).

$$f(w, 1) = \text{constant} \tag{A.8}$$

(in a monoculture there is no frequency dependence and therefore no effect of the parameter w).

From (A.6) and (A.8), we see that

$$\frac{\partial f(w, u_j)}{\partial w} = - \int_{u_j}^1 \frac{\partial^2 f(w, u)}{\partial w \partial u} du < 0. \tag{A.9}$$

So attack rates must decline as w increases regardless of the precise formula in use. Thus, there is no alternative model. In particular, the model used historically (Eq. (A.2)) is not one such model because it depends in some unclear manner on total prey density. When frequency dependence is strict, that is, depends only on relative, not absolute, abundance, its behavior is quite constrained if it is to maintain logical consistency.

The question of course arises as to how we interpret this outcome biologically. One interpretation is as follows: we expect w to be a predator trait. High w means that predator learning in relation to specific prey is necessary for prey capture. Such learning leads both to frequency dependence, and to costs that lower overall capture rates. A predator that requires less learning has lower costs and is not so frequency-dependent in behavior.

A.3. A model for frequency-dependent predation without learning constraints

Here we modify our model so that foraging efficiency does not decline with number of species and the degree of frequency dependence. We do this without the inconsistencies of the Comins and Hassell (1976) model, but of course by Appendix A.2 the foraging rate on a given species cannot be a function of that species relative abundance alone. However, the desired properties can be achieved by making the foraging rate depend on the relative abundances of all species. For this, we modify Eq. (A.1) by dividing the relative frequency u_j of species j by the summed squared relative abundances of all species, to obtain

$$A_j/P = a \left(1 - w + w u_j / \sum_k u_k^2 \right). \tag{A.10}$$

When the species are equal in relative abundance, $1/\sum_k u_k^2$ is simply n , and so we see that formula (A.10) modifies the Comins and Hassell (1976) formula so that decreasing the number of species by 1, and setting one species to zero density, agree, freeing (A.10) of the inconsistency in the Comins and Hassell (1976) formula. In terms of the notation in the text, this formula can be written

$$A_j = a \left((1 - w) + w \frac{G_j Y_j N_j}{\sum_k G_k Y_k N_k} \cdot \frac{(\sum_k G_k Y_k N_k)^2}{\sum_k (G_k Y_k N_k)^2} \right) P. \tag{A.11}$$

This formula has the intuitively appealing property that the total instantaneous rate of seed consumption by the predator population, $\sum_j A_j Y_j G_j N_j \exp(-C)$, equals $aP \sum_j Y_j G_j N_j \exp(-C)$, i.e. it is simply proportional to the total density of seed available, with no reflection of frequency-dependent behavior and no reflection of the number of species. Thus, this form of FDP involves no cost to foraging efficiency from frequency-dependent behavior. We refer to this situation as “super FDP” (sFDP). Appendix B shows how the invasion rate of a species at low density is partitioned into the fitness comparison term, FDP, nonlinear competitive variance, and two storage effect terms due respectively to competition and predation as follows:

$$\bar{r}_i = \eta_i - \bar{\eta} + \Delta P - \Delta N + \Delta I_c + \Delta I_p, \tag{A.12}$$

regardless of the form of FDP. The formulae for the last four terms in the case of sFDP are given in Table A.1, as derived in Appendix B.

Note that in the two-species case, coexistence conditions for sFDP do not differ from those applying to iFDP and gFDP because then the resident $A_r^{(-i)}$ is always equal to aP , and $A_i^{(-i)}$ is always $a(1 - w)P$ regardless of the form of FDP.

In the multispecies case, sFDP behaves completely differently from iFDP and gFDP. Specifically, the direct contribution of FDP to coexistence (ΔP) remains unchanged as the number of prey, n , increases. Moreover, the magnitude of SEp changes little as n increases. These effects are illustrated by plots of the minimum productivity required for invasion shown in Fig. A.1. This minimum

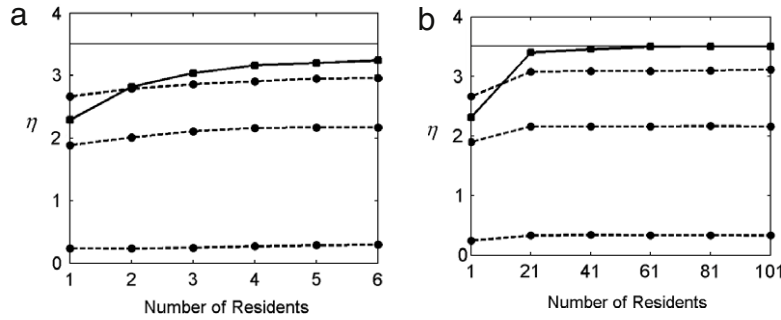


Fig. A.1. Minimum invasion requirements with sFDP. Each panel gives the minimum productivity, η , required for a successful invasion as a function of the number of residents. The solid lines are for a variable environment without predation. The dashed lines are for a variable environment with FDP of 25%, 50% and 100%, from top to bottom in each panel. The horizontal solid line marks the average resident productivity, $\bar{\eta}$. (a) Number of residents ($n - 1$) ranging from 1 to 6. (b) Number of residents ($n - 1$) ranging from 1 to 101 residents. Parameter: $s = 0.8$, $\bar{Y}_r = 40$, $s_p = 0.8$, $a = 0.2$, $G = \text{beta}(0.5, 0.5)$ independent between species.

productivity is asymptotically constant as the number prey species increase, and is almost completely constant with 100% FDP. These facts are unsurprising given that the formula for FDP was chosen to maintain total food intake without any cost associated with complex behavior. We include the case of sFDP for comparison, but in the absence of a derivation from a model of actual predatory behavior, it cannot be taken seriously.

A.4. Density-dependent frequency-dependent predation (ddFDP)

McNair's (1980) stochastic foraging model considers an individual predator repeatedly searching for, encountering, capturing and handling prey. The idea of learning is incorporated by assuming that the predator success rate is higher with repeated encounters of the same species. As prey are not depleted, the stochastic capture process approaches a stationary stochastic process, with asymptotic capture rate, $\Omega^{(j)}$, of prey species j , which is the total rate at which prey of species j are consumed by a unit of predator biomass. If we assume that the prey j are encountered at the rate e_j and that the time to handle prey is negligible, then the asymptotic capture rate of species j is simply

$$\Omega^{(j)} = \sum_k \frac{e_k}{\Sigma e_l} e_j \gamma_{kj}, \quad (\text{A.13})$$

where γ_{kj} is the probability that species j is captured on encounter, given that the previous encounter was with species k . In Kuang and Chesson (2010) γ_{kj} is equal to 1 if the previous encounter was with the same species, and $\alpha < 1$, if the previous encounter was with a different species. The absolute magnitudes of these quantities are of little significance. Only their relative magnitudes are important. The important feature of the previous assumption, which we now modify, is that learning from a previous encounter does not decay with time. The mean spacing of encounters is the reciprocal of the sum, Σe_l , of the individual species' encounter rates. We make the assumption here that γ_{kj} is a decreasing function of the mean spacing of encounters, or equivalently, an increasing function of the species sum of the mean encounter rate. This assumption treats the encounter spacings as deterministic for the purposes of the capture probability. However, this assumption is not likely to change the results qualitatively compared with a full stochastic treatment. The form we choose for capture probability is

$$\gamma_{kj} = \begin{cases} \alpha + (1 - \alpha) \frac{B \sum_l e_l}{1 + B \sum_l e_l}, & k = j \\ \alpha, & k \neq j. \end{cases} \quad (\text{A.14})$$

Thus, as encounter rates approach zero, it does not matter whether the previous encounter was with the same or a different species:

the capture rate is the same. Substituting in (A.13), we get the per encounter capture rate

$$\Omega^{(j)} / e_j = \alpha + (1 - \alpha) \frac{e_j}{\sum_l e_l} \left[\frac{B \sum_l e_l}{1 + B \sum_l e_l} \right]. \quad (\text{A.15})$$

We can now define $w = 1 - \alpha$, so that w measures the failure rate when a predator encounters an unfamiliar prey. Assuming the encounter rates e_l are proportional to prey abundance,

$$e_j = a Y_j G_j N_j e^{-C}. \quad (\text{A.16})$$

Absorbing a into B to simplify the parameterization then leads to the formula for the attack rate,

$$A_j / aP = (1 - w) + w \frac{G_j Y_j N_j}{\sum_k G_k Y_k N_k} \left[\frac{B \sum_k G_k Y_k N_k e^{-C}}{1 + B \sum_k G_k Y_k N_k e^{-C}} \right], \quad (\text{A.17})$$

as used in the text.

Appendix B. Coexistence criteria

We first consider the equilibrium case, and then use that to derive the criteria for the variable environment case by quadratic approximation.

B.1. Criteria for invasion of the resident equilibrium

We first derive the multispecies invasion condition for the equilibrium case. 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 r_i is positive. However, in the equilibrium case, it is easier to work with the finite rate of increase $\exp(r_i)$, which is just the same as $N_i(t + 1) / N_i(t)$. Using Eq. (1a) of the text, the finite rate of increase of any species j is

$$s_j(1 - G_j) + G_j Y_j e^{-C - A_j}. \quad (\text{B.1})$$

The invader species i always has $A_i = a(1 - w)P^{\{-i\}}$, because it is at zero density, and experiences only the frequency-independent component of predation.

For a system with $n - 1$ residents and gFDP, with the invader being species n (so that it is at the end of a list), and equating resident finite rates of increase to one (resident growth rates to zero), we find that the resident joint equilibrium must satisfy the equations

$$\begin{aligned} s_1(1 - G_1) + G_1 Y_1 e^{-C^{*\{-n\}} - aP^{*\{-n\}} \left((1-w) + w N_1^{*\{-n\}} / \sum N_r^{*\{-n\}} \right)} &= 1 \\ \dots & \\ s_{n-1}(1 - G_{n-1}) + G_{n-1} Y_{n-1} & \\ \times e^{-C^{*\{-n\}} - aP^{*\{-n\}} \left((1-w) + w N_{n-1}^{*\{-n\}} / \sum N_r^{*\{-n\}} \right)} &= 1. \end{aligned} \quad (\text{B.2})$$

In this general equilibrium situation, we can define η_j simply as $\ln \{G_j Y_j / [1 - s_j(1 - G_j)]\}$, then (B.2) rearranges to

$$\begin{aligned} C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) + wN_1^{*\{-n\}} / \sum N_r^{*\{-n\}} \right) &= \eta_1 \\ \dots & \\ C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) + wN_{n-1}^{*\{-n\}} / \sum N_r^{*\{-n\}} \right) &= \eta_{n-1}. \end{aligned} \tag{B.3}$$

Summation of the equations in (B.3) gives

$$(n - 1)C^{*\{-n\}} + (n - 1)aP^{*\{-n\}}(1 - w) + aP^{*\{-n\}}w = \sum \eta_r$$

or,

$$C^{*\{-n\}} + a(1 - w)P^{*\{-n\}} = \bar{\eta} - awP^{*\{-n\}} / (n - 1). \tag{B.4}$$

Substituting (B.4) into (B.1) and rearranging (with the invader now designated as usual as species i , instead of n) the condition for invasion is

$$\eta_i > \bar{\eta} - \Delta P, \tag{B.5}$$

with $\Delta P = awP^{*\{-i\}} / (n - 1)$. Simulations show that $P^{*\{-i\}}$ increases with resident $\bar{\eta}$, and ΔP hence is larger when the species with smaller η is the invader.

The calculation of the invasion condition in the case of iFDP is similar to the calculation for gFDP. However, Eqs. (B.3) become

$$\begin{aligned} C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) \right. \\ \left. + wG_1 Y_1 N_1^{*\{-n\}} / \sum G_r Y_r N_r^{*\{-n\}} \right) &= \eta_1 \\ \dots & \\ C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) \right. \\ \left. + wG_{n-1} Y_{n-1} N_{n-1}^{*\{-n\}} / \sum G_r Y_r N_r^{*\{-n\}} \right) &= \eta_{n-1}, \end{aligned} \tag{B.6}$$

which also sum to give (B.4) and (B.5). Thus, in a constant environment, the invasion condition for iFDP is equal to that for gFDP.

The calculation of the invasion condition in the case of sFDP is parallel to that for gFDP, above, with small variations, as follows. For sFDP, the resident joint equilibrium relationship satisfies

$$\begin{aligned} C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) + wG_1 Y_1 N_1^{*\{-n\}} \right. \\ \left. \times \sum G_r Y_r N_r^{*\{-n\}} / \sum (G_r Y_r N_r^{*\{-n\}})^2 \right) &= \eta_1 \\ \dots & \\ C^{*\{-n\}} + aP^{*\{-n\}} \left((1 - w) + wG_{n-1} Y_{n-1} N_{n-1}^{*\{-n\}} \right. \\ \left. \times \sum G_r Y_r N_r^{*\{-n\}} / \sum (G_r Y_r N_r^{*\{-n\}})^2 \right) &= \eta_{n-1}. \end{aligned} \tag{B.7}$$

Summation of the equations in (B.7) gives

$$\begin{aligned} \sum \eta_r &= (n - 1) C^{*\{-n\}} + (n - 1)aP^{*\{-n\}}(1 - w) \\ &+ aP^{*\{-n\}}w \left[\left(\sum G_r Y_r N_r^{*\{-n\}} \right)^2 / \sum (G_r Y_r N_r^{*\{-n\}})^2 \right]. \end{aligned} \tag{B.8}$$

If each species has the same seedling density, $G_k Y_k N_k^{*\{-n\}}$, at equilibrium, expression (B.8) reduces to

$$C^{*\{-n\}} + a(1 - w)P^{*\{-n\}} + awP^{*\{-n\}} = \bar{\eta}. \tag{B.9}$$

Substituting (B.9) into (B.1) and replacing n with i , we get (B.5) once more but with

$$\Delta P = awP^{*\{-i\}}. \tag{B.10}$$

This calculation extends to the case considered below where the η values of the species are assumed to differ from one another by no more than a certain amount. Such an assumption applies to the quadratic approximation that is the mainstay of the analysis for calculating the magnitudes of the coexistence mechanisms in the case of a variable environment. To define what we mean here, we first introduce standard mathematical notation, $O(x)$, to indicate a quantity that remains of comparable magnitude to x as x becomes small (Hughes-Hallett et al., 2009). Below, x is σ^2 , the variance of the environmental response. For consistency, we use that notation throughout for the small quantity intended here. If the magnitudes of the η s differ by no more than $O(\sigma^2)$, subtracting any pair of equations in (B.7) reveals that

$$G_k Y_k N_k^{*\{-n\}} = G_j Y_j N_j^{*\{-n\}} + O(\sigma^2); \quad \text{for } j \neq k. \tag{B.11}$$

Applying this to (B.9) then reveals that Eq. (B.10) remains true with an error equal to $O(\sigma^4)$. It follows that the magnitude of FDP is

$$\Delta P = awP^{*\{-i\}} + O(\sigma^4). \tag{B.12}$$

Thus, we see that in a constant environment, with sFDP, the number of resident species does not appear in the formula for ΔP , in contrast to ΔP for iFDP and gFDP.

B.2. Variable environments and quadratic approximation

Coexistence of annual plant species in the presence of environmental fluctuations is studied in detail in Chesson (1994), and adapted to coexistence of two species in the presence of FDP in Kuang and Chesson (2010). In effect, the multispecies case takes the invasion conditions for the two-species case, and averages over resident species. Our results require certain technical assumptions (Chesson, 1994), 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, they point the way to the larger patterns, and sometimes produce surprisingly accurate results (Kuang and Chesson, 2010). As mentioned in the text, we make some simplifying assumptions, which lead to easily interpreted formulae. The same methods, however, can be used to obtain more complex formulae without these assumptions. Here we assume that the log 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. We use the standard mathematical notation $O(x)$ (see Appendix B.1) to indicate a quantity that remains of comparable magnitude to x as x becomes small. With the assumptions here, 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 . Our development considers the cases of iFDP and gFDP first, and then goes on to consider the modifications necessary for ddFDP and sFDP.

We assume independence of environmental fluctuations over time, but allow the $E_j(t)$'s to be correlated between species with common correlation ρ . For simplicity, we assume also that the seed survival rate is the same for all species, i.e. $s_j = s_k = s$. Thus, it follows that the seed loss rate, $\beta = 1 - s(1 - \bar{G})$, is the same for each species, i.e., $\beta_j = \beta_k$.

To ensure $\bar{r}_i = O(\sigma^2)$, the η 's should not differ between species by more than $O(\sigma^2)$, and w should be $O(\sigma^2)$, which gives $\Delta P = O(\sigma^2)$. To constrain η differences, we must assume that the Y 's for different species differ by at most $O(\sigma^2)$. The final assumption that we make is that the variance in F over time is also $O(\sigma^2)$. More detailed discussions of all these assumptions and their consequences can be found in Kuang and Chesson (2010).

The growth rate of species j takes the form

$$r_j(t) = \ln(s(1 - e^{E_j}) + Y_j e^{E_j - F_j}), \quad (\text{B.13})$$

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 discussed in Kuang and Chesson (2010), viz

$$r_j(t) = g_j(E_j, F_j). \quad (\text{B.14})$$

The analysis begins with a Taylor expansion of $r_j(t)$ in E_j and F_j . This is done about fixed values, E_j^* and F_j^* , of E_j and F_j , which satisfy the equilibrium condition

$$g_j(E_j^*, F_j^*) = 0 \quad (\text{i.e. } \ln(s(1 - e^{E_j^*}) + Y_j e^{E_j^* - F_j^*}) = 0). \quad (\text{B.15})$$

We first choose $F_j^* = \eta_j = \ln(\bar{G}Y_j/[1 - s(1 - \bar{G})])$, and then E_j^* is found from (B.15) to equal $\ln \bar{G}$, and so is the same for all species. Rather than a standard Taylor expansion, it has been found to be more informative to do this expansion in terms of standardized variables that take the same units as r_j . To do this, we define

$$\mathcal{E}_j = g_j(E_j, F_j^*), \quad \text{i.e. } \mathcal{E}_j = \ln\left\{s\left[1 - e^{E_j}\right] + Y_j e^{E_j - F_j^*}\right\}, \quad (\text{B.16})$$

and

$$\mathcal{C}_j = -g_j(E_j^*, F_j), \quad \text{i.e. } \mathcal{C}_j = -\ln\left\{s\left[1 - e^{E_j^*}\right] + Y_j e^{E_j^* - F_j}\right\}. \quad (\text{B.17})$$

These quantities \mathcal{E}_j and \mathcal{C}_j are increasing functions respectively of E_j and F_j , and so are simply nonlinear transformations of these variables into r_j units. The choice of E_j^* so that it is equal to $\ln \bar{G}$ means that it satisfies one of the required technical assumptions of Chesson (1994) mentioned above, viz $E[E_j] = E_j^* + O(\sigma^2)$. Combined with suitable deterministic stability of the combined plant densities and their predator (Chesson, 1994), this implies also $E[F_j] = F_j^* + O(\sigma^2)$. These facts permit changes of variable between E_j and F_j and \mathcal{E}_j and \mathcal{C}_j with control over the errors involved.

In terms of the transformed variables (B.16) and (B.17), the growth rate becomes

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \quad (\text{B.18})$$

where

$$\gamma_j = \frac{\partial^2 r_j}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \Big|_{\mathcal{E}_j = \mathcal{C}_j = 0}, \quad (\text{B.19})$$

(Chesson, 1994).

Long-term growth rates of species in this system are then found by averaging (B.18) over time:

$$\bar{r}_j \approx E[\mathcal{E}_j] - E[\mathcal{C}_j] + \gamma_j E[\mathcal{E}_j \mathcal{C}_j], \quad (\text{B.20})$$

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 (B.20)) 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 rates as follows (Chesson, 1994):

$$\bar{r}_i = \bar{r}_i - \sum_{r \neq i} q_{ir} \bar{r}_r = \Delta E - \Delta C + \Delta I, \quad (\text{B.21})$$

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 , and the terms on the right are as follows:

$$\Delta E = E[\mathcal{E}_i] - \sum_{r \neq i} q_{ir} E[\mathcal{E}_r], \quad (\text{B.22})$$

$$\Delta C = E[\mathcal{C}_i^{\{-i\}}] - \sum_{r \neq i} q_{ir} E[\mathcal{C}_r^{\{-i\}}], \quad (\text{B.23})$$

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

$$\Delta I = \gamma_i E[\mathcal{E}_i \mathcal{C}_i^{\{-i\}}] - \sum_{r \neq i} q_{ir} \gamma_r E[\mathcal{E}_r \mathcal{C}_r^{\{-i\}}]. \quad (\text{B.24})$$

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

$$\Delta C = -\beta(\eta_i - \bar{\eta}) - \Delta P + \Delta N, \quad (\text{B.25})$$

so that the invader growth rate becomes

$$\bar{r}_i \approx \beta(\eta_i - \bar{\eta}) + \Delta P - \Delta N + \Delta I. \quad (\text{B.26})$$

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

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{E}_i with respect to \mathcal{C}_r (Chesson, 1994). Because of FDP here, it is not possible to express \mathcal{E}_i exactly as a function of \mathcal{C}_r in this model, but, as $w = O(\sigma^2)$, it is possible to ignore FDP in deriving q_{ir} because errors no more than $O(\sigma^4)$ would arise. As in Kuang and Chesson (2009), q_{ir} becomes $\beta_i/\beta_r(n-1)$ here, and because the β 's are the same here, as explained above,

$$q_{ir} = 1/(n-1). \quad (\text{B.27})$$

We now derive the approximations for each term in expression (B.26). First of all

$$\Delta E = E[\mathcal{E}_i] - \frac{1}{n-1} \sum_{r \neq i} E[\mathcal{E}_r], \quad (\text{B.28})$$

which is a comparison of mean invader and resident environmental responses. Using definition (B.16) of \mathcal{E}_j , and noting that $F_j^* = \eta_j$, we see that

$$\mathcal{E}_j = \ln\{s + (1-s)G_j/\bar{G}\}, \quad (\text{B.29})$$

exactly as in Kuang and Chesson (2010). Since the G_j have the same distribution for all j , $E[\mathcal{E}_j]$ does not depend on j , and so

$$\Delta E = 0. \quad (\text{B.30})$$

We now establish Eq. (B.25), i.e. $\Delta C = -\beta(\eta_i - \bar{\eta}) - \Delta P + \Delta N$, with

$$\Delta P \approx \beta a w \bar{P}^{(1-i)} / (n - 1), \tag{B.31}$$

and

$$\Delta N \approx \frac{\beta(1 - \beta)}{2} \sum_{r \neq i} \left[\text{var} (F_r^{(1-i)}) - \text{var} (F_i^{(1-i)}) \right] / (n - 1). \tag{B.32}$$

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

$$E[F_i] - F_i^* - \left(\overline{E[F_r]} - \overline{F_r^*} \right) - \frac{1}{2} (1 - \beta) \times \left(E \left[(F_i - F_i^*)^2 \right] - \overline{E \left[(F_r - F_r^*)^2 \right]} \right), \tag{B.33}$$

where the over bar with superscript r in expression (B.33) means the average over resident species. Because $E[F_j]$ is within $O(\sigma^2)$ of F_j^* in Chesson (1994), the expected squares in (B.33) become the variances $\text{Var} (F_i)$ and $\text{Var} (F_r)$. Thus, the quadratic part of (B.33) becomes $\Delta N / \beta$ as given by (B.32) 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, it 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 (B.33) rearranges to

$$- \left(F_i^* - \overline{F_r^*} \right) + E \left[F_i - \overline{F_r} \right]. \tag{B.34}$$

The equilibrium comparison (first term) is simply $-(\eta_i - \bar{\eta})$, and the difference between the resident and average invader expected F values simplifies to $-awE[P^{(1-i)}] / (n - 1)$. Thus, we have established (B.25), i.e. $\Delta C = -\beta(\eta_i - \bar{\eta}) - \Delta P + \Delta N$, with ΔP and ΔN given by (B.31) and (B.32).

The last term in the formula (B.26) for \bar{r}_i is the storage effect, ΔI . Because the quantities $E[\mathcal{C}] = O(\sigma^2)$ (Chesson, 1994), the definition of the storage effect (B.24) is equivalent to

$$\Delta I = \gamma_i \text{cov}(\mathcal{C}_i, \mathcal{C}_i^{(1-i)}) - \sum_{r \neq i} q_{ir} \gamma_r \text{cov}(\mathcal{C}_r, \mathcal{C}_r^{(1-i)}), \tag{B.35}$$

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{C}_j can be linearly approximated as $(1 - s)(E_j - E_j^*)$, and \mathcal{C}_j can be linearly approximated as $\beta(F_j - F^*)$. It follows that the interaction term $\gamma_j \mathcal{C}_j \mathcal{C}_j$ in Eq. (B.18) is equal to

$$\gamma_j \mathcal{C}_j \mathcal{C}_j = -s\beta(E_j - E_j^*)(F_j - F_j^*) + O(\sigma^3). \tag{B.36}$$

Moreover, because E_j^* and F_j^* differ by no more than $O(\sigma^2)$ from their means, (B.36) remains true on substituting means for equilibrium values. Scaling by β then gives the per seed generation interaction term (7) of the text.

To continue our formal development of the storage effect, recall that $q_{ir} = \beta_i / \beta_r (n - 1) = 1 / (n - 1)$, substituting (B.36) into (B.35) gives

$$\Delta I \approx \beta s \left\{ \frac{1}{n - 1} \sum_{r \neq i} \left[\text{cov} (E_r, F_r^{(1-i)}) - \text{cov} (E_i, F_i^{(1-i)}) \right] \right\}. \tag{B.37}$$

Now $F_j = C + A_j$. For the case of gFDP, $A_r = aP((1 - w) + wN_r / \sum N_k)$, 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 for gFDP expression (B.37) reduces to the storage effect due to competition,

$$\Delta I_c \approx \beta s \left\{ \frac{1}{n - 1} \sum_{r \neq i} \left[\text{cov} (E_r, C^{(1-i)}) - \text{cov} (E_i, C^{(1-i)}) \right] \right\}, \tag{B.38}$$

which is reported in natural units in Table 3 (i.e. divided by β following the convention of Chesson, 2008), and is approximately $\approx \beta s(1 - \rho)\sigma^2 \bar{G} \sum_{r \neq i} \bar{N}_r / (n - 1)$ (Kuang and Chesson, 2009).

For iFDP, $A_r = aP((1 - w) + wG_r Y_r N_r / \sum G_k Y_k N_k)$, and $A_i = aP(1 - w)$, so expression (B.37) is the sum of expression (B.38) and the storage effect due to predation (SEp). Since $\text{cov} (E_i, A_i^{(1-i)}) = 0$ due to the fact that the invader only experiences frequency-independent component of predation, $A_i^{(1-i)}(t)$ has no correlation with $E_i(t)$. This means that SEp is simply

$$\Delta I_p \approx \beta s \left\{ \frac{1}{n - 1} \sum_{r \neq i} \text{cov} (E_r, A_r^{(1-i)}) \right\}. \tag{B.39}$$

To estimate ΔI_p to the correct accuracy we linearly expand A_r around the equilibrium value of $E_r = \ln G_r$ for all $r \neq i$ (Chesson, 1994):

$$A_r = A_r^* + \sum_{j \neq i} (E_j - E_j^*) \left(\frac{\partial A_r}{\partial E_j} \right)^* + O(\sigma^2). \tag{B.40}$$

Here, the subscripts j, r and s are all for the residents, and A_r^* and $(\partial A_r / \partial E_j)^*$ are evaluated at E 's equal to the equilibrium values. However, these derivatives still depend on $N(t)$ and $P(t)$, which are statistically independent of $E_j(t)$. The first derivatives are different for different residents,

$$\left(\frac{\partial A_r}{\partial E_j} \right)^* / a w P = \begin{cases} \left[\frac{e^{E_j^*} Y_j N_j \sum_{s \neq i} e^{E_s^*} Y_s N_s - (e^{E_j^*} Y_j N_j)^2}{\left(\sum_{s \neq i} e^{E_s^*} Y_s N_s \right)^2} \right], & \text{if } j = r \\ -e^{E_j^*} Y_j N_j e^{E_r^*} Y_r N_r / \left(\sum_{s \neq i} e^{E_s^*} Y_s N_s \right)^2, & \text{if } j \neq r. \end{cases} \tag{B.41}$$

Substituting expression (B.40) in expression (B.39) gives

$$\begin{aligned} \Delta I_p &= \frac{s\beta}{n - 1} \sum_{r \neq i} \text{cov} (E_r, A_r) \\ &\approx \frac{s\beta}{n - 1} \sum_{r \neq i} \text{cov} \left(E_r, \sum_{s \neq i} E_s \left(\frac{\partial A_r}{\partial E_s} \right)^* \right) \\ &= \frac{s\beta}{n - 1} \sum_{r \neq i} \left\{ \sigma^2 E \left[\left(\frac{\partial A_r}{\partial E_r} \right)^* \right] + \sum_{s \neq r, i} \rho \sigma^2 E \left[\left(\frac{\partial A_r}{\partial E_s} \right)^* \right] \right\}, \end{aligned} \tag{B.42}$$

where σ^2 is the variance of E 's, ρ is the correlation between species E 's, and $E[\cdot]$ is the time average for $N(t)$. Substituting expression (B.41) in (B.42) gives

$$\Delta I_p \approx \frac{s\beta a w \bar{P} (1 - \rho) \sigma^2}{n - 1} \times E \left[1 - \sum_{r \neq i} (e^{E_r^*} Y_r N_r)^2 / \left(\sum_{r \neq i} e^{E_r^*} Y_r N_r \right)^2 \right]. \tag{B.43}$$

Because E_r^* equals $\ln \bar{G}$, and we assume that the Y_r 's differ only by $O(\sigma^2)$, $e^{E_r^*} Y_r = \bar{G} \bar{Y} + O(\sigma^2)$, and expression (B.43) can be simplified to

$$\Delta I_p \approx \frac{s\beta aw\bar{P}(1-\rho)\sigma^2 E[S]}{n-1}, \tag{B.44}$$

where S is the Simpson's diversity (Legendre and Legendre, 1998)

$$S = 1 - \sum_{r \neq i} N_r^2 / \left(\sum_{r \neq i} N_r \right)^2, \tag{B.45}$$

calculated for the resident densities in the seed bank.

B.3. Modifications for ddFDP and sFDP

Most of the calculations above remain the same with these two other forms of FDP. The first of these is the value of ΔP , which comes from $-E[F_i - \bar{F}_r^r]$ in expression (B.34). As C cancels out here in all cases, in fact $\Delta P = -E[A_i - \bar{A}_r^r] = \sum_r E[A_r - A_i]/(n-1)$. In the case of ddFDP

$$\sum_r (A_r - A_i) = awP \left(\frac{B \sum_r M_r}{1 + B \sum_r M_r} \right) \tag{B.46}$$

where $M_r = Y_r G_r N_r e^{-C}$. Taking expected values and dividing by $(n-1)$ gives ΔP , as stated in Table 3.

In the case of sFDP, $\sum_r (A_r - A_i) G_r Y_r N_r / awP = \sum_r G_r Y_r N_r$. If it is now assumed that the resident species have identical parameters, then it is possible to deduce from this equation that $E[(A_r - A_i) / awP | P] = 1 + O(\sigma^2)$, from which it follows that $E[(A_r - A_i)] = awE[P] + O(\sigma^2)$, demonstrating the desired result for the case of sFDP.

The storage effect due to predation satisfies the general expression (B.42) above, regardless of the form of FDP. For ddFDP, the part of A_r / awP that depends on the E_j splits up into the product, $X_r Z$, with

$$X_r = \frac{Y_r G_r N_r}{\sum_s Y_s G_s N_s}, \quad Z = \frac{B \sum_r M_r}{1 + B \sum_r M_r}. \tag{B.47}$$

The derivatives of X_r with respect to the E_j are the same as the derivatives of A_r / awP for iFDP, given by Eq. (B.41) above. For Z , we have simply

$$\left(\frac{\partial Z}{\partial E_j} \right)^* = \frac{BM_j^*}{\left(1 + B \sum_r M_r^* \right)^2} \tag{B.48}$$

where M_j^* is just M_j with the E_i^* replacing E_i . The partial derivatives for A_r are then just found from (B.48) and (B.41) using the product rule. Straightforward calculation then produces the formula in Table 3 for ΔI_p , where at the final stage, M_j is substituted for M_j^* in the formulae for U and V because these lead to equally correct formulae (cannot differ more than $O(\sigma^4)$), and the tabulated formula is simpler to interpret.

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