Title: How optimally foraging predators promote prey coexistence in a variable environment

Authors:

Simon Maccracken Stump (University of Arizona; Present address: W. K. Kellogg Biological Station- Michigan State University)

Peter Chesson (University of Arizona)

Contact Author:

Simon Maccracken Stump, stumpsim@msu.edu,

W.K. Kellogg Biological Station

3700 East Gull Lake Drive

Hickory Corners, MI 49060

ABSTRACT

Optimal foraging is one of the major predictive theories of predator foraging behavior. However, how an optimally foraging predator affects the coexistence of competing prey is not well understood either in a constant or variable environment, especially for multiple prey species. We study the impact of optimal foraging on prey coexistence using an annual plant model, with and without annual variation in seed germination. Seed predators are modeled using Charnov's model of adaptive diet choice. Our results reveal that multiple prey species can coexist because of this type of predator, and that their effect is not greatly modified by environmental variation. However, in diverse communities, the requirements for coexistence by optimal foraging alone are very restrictive. Optimally foraging predators can have a strong equalizing effect on their prey by creating a competition-predation trade-off. Thus, their main role in promoting diversity may be to reduce species-average fitness differences, making it easier for other mechanisms, such as the storage effect, to allow multiple species to coexist. Like previous models, our model showed that when germination rates vary, the storage effect from competition promotes coexistence. Our results also show that optimally foraging predators can generate a negative storage effect from predation, undermining coexistence, but that this effect will be minor whenever predators commonly differentiate their prey.

Key Words: Optimal foraging theory, storage effect, apparent competition, coexistence, annual plant model, Type II functional response

1. Introduction

Optimal foraging theory is one of the major predictive theories of animal foraging behavior (Perry and Pianka, 1997). Optimal foraging theory encompasses a variety of different models, but all are united by the assumption that a forager will maximize some fitness proxy under some constraint (Pyke et al., 1977). For example, the Charnov model of adaptive diet choice (Charnov, 1976) – the focus of this paper – shows how predators would alter their diet breadth to maximize their calorie intake per unit time. The model assumes that predators are constrained because they must spend time handling their prey; therefore, a predator that consumes low-calorie prey has less time to search for high-calorie prey (Charnov, 1976). The model predicts that predators should always consume high-calorie prey, but should only consume low-calorie prey when high-calorie prey are scarce (Charnov, 1976). Like many optimal foraging models, the Charnov model includes unrealistic assumptions, such as perfect information and perfectly rational behavior (Pierce and Ollason, 1987). However, like many optimal foraging models, it provides an adequate approximation for foraging behavior in many systems (reviewed in Jaenike, 1990; Krebs and McCleery, 1984), such as insectivorous birds (Krebs et al., 1977), crabs (Elner and Hughes, 1978), and coyotes (Hernández et al., 2002). In particular, it incorporates several well-documented behaviors: preference hierarchies (Inouye et al., 1980), predator satiation (Kelly and Sork, 2002), and malleable diet choice (Hernández et al., 2002). Such behaviors can cause a predator to affect its prey differentially, and differential effects are a basic requirement for any mechanism that promotes coexistence (Chesson, 2000). Beyond these differential effects, much is unknown about how an optimally foraging predator will affect its prey's ability to coexist

in a complex community. In this paper, we analyze how an optimally foraging granivore can affect prey coexistence in a diverse community of annual plants.

Many previous studies have shown that an optimally foraging predator can allow two prey species to coexist if there is a competition-predation trade-off (Abrams and Matsuda, 1996; Genkai-Kato and Yamamura, 1999; Gleeson and Wilson, 1986; Krivan, 2003); however, this result is not unique to optimal foraging. Rather, a competition-predation trade-off can allow two species to coexist, even if the predators consume prey at constant per capita rates, i.e. have a linear or Type I functional response (Armstrong, 1979; Holt et al., 1994; Levin, 1970). However, if every species has a linear functional response, then two species is an upper limit to the number of prey that can coexist (Levin, 1970). But, if any species have nonlinear functional responses or malleable behavior, additional prey species may be able to coexist (Levin, 1970). Hambäck (1998) considered a community of three prey species, but did not find three-species coexistence without invoking an additional mechanism. As far as we are aware, no study has examined if optimal foraging can allow more than two species to coexist.

Optimal foraging leads to a form of frequency-dependent predation, which has been shown in other circumstances to be a strong promoter of species coexistence (Chesson and Kuang, 2010). For example, when frequency-dependent predation arises due to a learning constraint, predators will attack abundant prey species disproportionately more (McNair, 1980; Murdoch, 1969). This generates a low-density advantage for prey species, potentially allowing them to recover if they fall to low densities (Chesson and Kuang, 2010; Kuang and Chesson, 2010). Such behavior can allow a potentially unlimited number of prey species to coexist (Chesson and Kuang,

2010). However, there is an important distinction between frequency-dependence arising from learning constraints and frequency-dependence arising from optimal foraging. An optimally foraging predator does not reduce its attack rate on a prey species because that species is rare. Instead, it excludes a prey-species from its diet based on the abundance of higher-calorie prey (Charnov, 1976). Such behavior creates important asymmetries, as high-calorie prey are never ignored.

A deeper understanding of optimal foraging will be particularly important for understanding communities of desert annual plants. Seed predation is thought to play a major role in allowing desert annuals to coexist (Brown and Heske, 1990; Davidson et al., 1984). For example, long-term experiments near Portal, AZ, have shown that when rodents are excluded, the annual community becomes dominated by plants with large seeds (Allington et al., 2013; Brown and Heske, 1990). Granivorous rodents show strong preference hierarchies based on seed size (Brown and Heske, 1990; Inouye et al., 1980), and thus models of optimal foraging, or adaptive diet choice more generally, are likely applicable. Environmental variation is also thought to drive coexistence in these systems (Angert et al., 2009; Chesson et al., 2013; Pake and Venable, 1996). Thus, a model for annual plants provides an opportunity to study how predators interact with yearly variation in the environment. Annual plant models have previously been used to study a diverse set of interactions between consumers and the environment (e.g., Chesson and Kuang, 2010; Kuang and Chesson, 2008; Kuang and Chesson, 2009; Mordecai, 2014).

In previous models of desert annual communities, environmental variation promotes coexistence through the storage effect (Chesson, 1994; Chesson et al., 2013). Seeds of different species have different germination rates each year due to variation in

the weather (Adondakis and Venable, 2004; Facelli et al., 2005). Only individuals who germinate can reproduce. However, when an abundant species has a high germination rate, competition will be high; thus, very abundant species are unable to take advantage of favorable years for germination (Chesson, 1994). Species can gain a low-density advantage by germinating under different conditions, because they are more likely to germinate in years when competition is low, and remain dormant in the seed bank when competition is high (Chesson, 1994).

In a variable environment, natural enemies can generate a storage effect that is analogous to the storage effect from competition (Chesson and Kuang, 2010). Generalist pathogens and predators with a Type III functional response will become more active when prey are abundant (Chesson and Kuang, 2010; Mordecai, 2014). Thus, abundant species will face high consumption rates in years where they have a high germination rate. In this case, species at low-density gain an advantage because they are likely to germinate when consumption rates are low, and are likely to remain dormant when consumption rates are high (Chesson and Kuang, 2010). Thus, the storage effect from consumers is similar to the storage effect from competition, but it is generated by apparent competition instead of resource competition.

In this paper, we study how seed predators that behave according to the Charnov model of adaptive diet choice affect the coexistence of annual plants (Charnov, 1976). We examine the effect of predators both when germination rates are constant, and when they vary. This model allows us to analyze how a major form of predator behavior interacts with environmental variation, and how it affects prey coexistence in a diverse community. Our work suggests that unlike frequency dependent predation due to a

learning constraint (Chesson and Kuang, 2010; Kuang and Chesson, 2010), optimal foraging promotes coexistence mainly by making species competitively similar, rather than by generating a low-density advantage. Our model also suggests a new mechanism through which predators can undermine coexistence: a negative storage effect caused by predator satiation.

2. Model and Analysis

Our model is based upon the life history of desert annual plants, which are competing in the presence of seed predators (Kuang and Chesson, 2008). All variables are listed in Table 1. Our population variable, $N_j(t)$, is the number of seeds of species j at the start of year t , before germination. At the beginning of each year, some fraction of the seeds from each species germinate, $G_j(t)$. A fraction s of the ungerminated seeds will survive and be present in the seed bank the following year. Seeds that germinate compete for resources and grow into adult plants that produce new seeds. Adults of species j produce $Y_j e^{-C(t)}$ seeds on average, where Y_j is proportional to seed yield in the absence of competition, and $C(t)$ is the effect of resource competition defined as the reduction in $\ln$ seed yield due to competition. After seeds are produced, the new seeds are exposed to predators, and have the chance $\exp\{-A_j(t)\}$ of surviving predation. Surviving seeds enter the seed bank, where they are protected from predators and competition, and can germinate in future years. Taken together, the yearly finite rate of increase of species j , $\lambda_j(t)$, is

$$\lambda_j(t) = (1 - G_j(t))s + Y_j G_j(t) e^{-C(t) - A_j(t)}, \quad (1)$$

and the population growth rate is $r_j(t) = \ln \lambda_j(t) = \ln N_j(t+1) - \ln N_j(t)$.

Resource competition is modeled as

$$C(t) = \ln \left\{ \alpha_1 + \alpha_2 \sum_{j=1}^n G_j(t) N_j(t) \right\}, \quad (2)$$

where α_1 and α_2 are competition parameters, and n is the number of competing species. For small population densities, each germinating seed produces approximately Y_j/α_1 seeds; for high population densities, seed production is inversely proportional to the number of plants. Modeling competition with two competition parameters allows us to consider both lottery competition (i.e., when $\alpha_1 = 0$, which assumes no maximum reproductive output and complete resource use), and forms of competition where species have a maximum reproductive output (i.e., when $\alpha_1 > 0$). However, this parameter flexibility leads to slight awkwardness in the defining of Y_j , as it is not exactly seed yield, but merely proportional to it, and zero competition is not $C(t) = 0$, but $\ln\{\alpha_1\}$, except in the lottery case when competition cannot be set to 0. Each species has an identical effect on every other species; thus, in the absence of environmental variation and predators, this form of competition will not allow species to coexist stably (Chesson, 2000; Levin, 1970). We use differences in Y_j to represent competitive differences, but in Appendix E we show that our results would be similar if species differed in the ability to take up resources.

Environmental variation is modeled as variability in the germination rate, $G_j(t)$. We assume that the mean of $G_j(t)$ is $E[G]$ for all species (we will use the notation $E[X]$ to signify the time average value of X), and there is no temporal autocorrelation. The environmental response, used below for calculating the impact of variability, is defined as $E_j(t) = \ln G_j(t)$. The variance of $E_j(t)$ is σ^2 for every species, and the correlation between $E_j(t)$ and $E_k(t)$ is ρ for $j \neq k$.

In the results presented here, the number of predators, P , is held constant so that we can focus on the behavioral response of predators, rather than changes in their abundance. According to computer simulations, the results are qualitatively similar when the predator density has a numerical response to prey, provided that large predator-prey oscillations do not occur and the predators do not drive their prey extinct. Kuang and Chesson (2009, 2010) showed that the numerical response can, however, greatly weaken the storage effect due to competition when the predators are highly efficient. The same outcome occurs here, but our focus is on the effects of the functional response under optimal foraging, which has not been considered previously.

2.1 The effect of seed predation, $A_j(t)$

We assume that predators have access to seeds for a window of time in their year of production. We call this the vulnerable period, and use the variable u to denote time during this period. We define $u = 0$ as the time of seed production (i.e., when seeds are first available to the predators), and $u = 1$ as the time when seeds enter the seed bank (i.e., are mixed into the soil) and are no longer available to seed predators. We define $b_j(u)$ as the number of seeds of species j at time u . The number of species j seeds at the start of the vulnerable period, $b_j(0)$, is

$$b_j(0) = Y_j G_j(t) N_j(t) e^{-\int_0^t C_j(t) dt}. \quad (3)$$

We assume that the predators forage randomly (thus encountering seeds in proportion to their density), and every seed found interrupts searching for seeds by a constant amount of time (the handling time), depending on the seed species. This means that the predators have a Type II functional response, the most common response found in nature (Holling,

1959). We define the handling time here to be h and for simplicity assume that it does not depend on the prey species. It follows that the change in $b_j(u)$ during the vulnerable period is

$$\frac{db_j(u)}{du} = -P \frac{ap_j(u)b_j(u)}{1 + ah \sum_{k=1}^n p_k(u)b_k(u)} \quad (4)$$

where a is the attack rate, and $0 \leq p_j(u) \leq 1$ is the probability that a predator will attack seeds of species j if it encounters the seed. The number of seeds that survive to the end of the year, $b_j(1)$, can be calculated by integrating $db_j(u)/du$ over the vulnerable period (Appendix A). The effect of predation, $A_j(t)$, which was defined such that $\exp\{-A_j(t)\}$ is the probability that a seed is not consumed in the year it is produced, can then be written as

$$A_j(t) = \ln \left\{ \frac{b_j(0)}{b_j(1)} \right\}. \quad (5)$$

The Charnov model assumes that a predator will dynamically change its diet to maximize its calorie intake at any given time (Charnov, 1976). We use the symbol e_j for the energy content of a seed and assume throughout that $e_1 > e_2 > \dots > e_n$. Charnov (1976) showed that the probability of consuming a seed encountered at a particular time, $p_j(u)$, is

$$p_j(u) = \begin{cases} 1 & \text{if } \frac{e_j}{h} > \frac{a \sum_{k=1}^{j-1} b_k(u)e_k}{1 + ah \sum_{k=1}^{j-1} b_k(u)} \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

Simply, if a predator encounters a seed of species j , then it can gain e_j/h calories per unit time by eating that seed, or an average of $\left(a \sum_{k=1}^{j-1} b_k(u) e_k \right) / \left(1 + ah \sum_{k=1}^{j-1} b_k(u) \right)$ calories per unit time by searching for higher-calorie seeds. Thus, it is either optimal to consume a species or not, and therefore $p_j(u)$ will either be 0 or 1 (Charnov, 1976). The term $p_1(u)$ will always equal 1 (since it is always optimal to consume the highest-calorie seed), and $p_j(u)$ will equal 1 when $(b_1(u) + b_2(u) + \dots + b_{j-1}(u))$ is lower than the critical switching density, $\tilde{b}_j$, calculated as

$$\tilde{b}_j = \left(\frac{1}{ah} \right) \frac{e_j}{\overline{e_{j-1}} - e_j}, \quad (7)$$

where $\overline{e_{j-1}}$ is the density-weighted mean value of e_k for species 1 through $j - 1$,

$$\overline{e_{j-1}} = \frac{\sum_{k=1}^{j-1} e_k b_k(u)}{\sum_{k=1}^{j-1} b_k(u)}, \quad (8)$$

(we will be using the overline $\overline{X}$ to mean the across-species average of X) (Charnov, 1976). The critical switching density represents a level of scarcity that would cause that predator to broaden its diet: it is optimal to ignore species j only when there are at least $\tilde{b}_j$ higher-calorie seeds.

Three important properties of $A_j(t)$ should be noted. First, because predators forage randomly, any seeds that the predator is willing to consume will be at the same risk of predation. As a result, if the predators consume both species throughout the year, then $A_j(t) = A_k(t)$. Second, a predator that accepts species j at time u would also accept any of species 1, 2, ..., and $j - 1$ at that time (Charnov, 1976); therefore, $A_1(t) \geq A_2(t) \geq$

$\dots \geq A_n(t)$. Third, because predators are limited by handling time, an individual seed is less likely to be eaten when seed density is high; therefore, $A_j(t)$ is a decreasing function of $b_k(0)$ whenever the predator accepts both species j and k , independent of the relative ranking of e_j and e_k .

2.2 Model analysis

The model was analyzed using invasion analysis, a standard approach for determining stable coexistence (Chesson, 2000; Schreiber et al., 2011). In invasion analysis, one species is chosen to be an invader (indicated by the subscript i in place of j or k), and its density is set to zero. The remaining species (referred to as residents, subscript r) are allowed to come to an equilibrium or a stochastic steady state (i.e., $E[r_r]=0$, where $E[r_r]$ is $r_r(t)$ averaged over time). The invader's average growth rate, $E[r_i]$, is then calculated. Species can coexist if there exists some vector of constants $\mathbf{p}$ with entries p_j , such that $\sum p_i E[r_i] > 0$ (summation over all invaders in the community) for all possible subcommunities (Schreiber et al., 2011); thus, a sufficient (but not necessary) condition is that every species has a positive invader growth rate (i.e., if $E[r_i] > 0$) in every possible subcommunity. In our variable environment case below, we use the weaker criteria of mutual invasibility (i.e., if $E[r_i] > 0$ when all other species are residents, rather than in every possible subcommunity); however, computer simulations suggest that in this model, mutual invasibility is sufficient for coexistence.

To understand how competition, predation, and variable germination affect the invader rate growth rates, and ultimately stabilizing mechanisms, we approximated $r_j(t)$ as a quadratic function of $E_j(t)$, $A_j(t)$, and $C(t)$ (Appendix C). Our methods are based on

the general approach of Chesson (1994) for quantifying the contributions of mechanisms to the invasion rate, and closely follow the developments of Kuang and Chesson (2010) and Chesson and Kuang (2010) for seed predation models. Our approximations are based on the assumption that σ^2 , and between-species differences in $\ln Y_j$ and $A_j(t)$, are small (Appendix C). Computer simulations were used to check the quality of our approximations when these values were not small (Appendix F). Generally, we found that our approximations held very well over a wide range of parameter values (Appendix F, Fig. F.2).

The results take the most understandable forms if we use a time unit of a seed generation. Then $r_j(t)$ is redefined as $(\ln N_j(t+1) - \ln N_j(t)) / \beta$, where $\beta = 1 - s(1 - E[G])$ is the average probability that a seed leaves the seed bank in any year. These are the natural units of Chesson (2008). The invader growth rate then takes the following generic form

$$E[r_i] \approx \mu_i - \bar{\mu} + \Delta P_i + \Delta I_{Ci} + \Delta I_{Pi} \quad (9)$$

where μ_i here is the contribution of competitive ability to fitness, $\ln Y_i$, $\bar{\mu}$ is the average $\ln Y_r$ for the resident species, and ΔP_i , ΔI_{Ci} and ΔI_{Pi} , are respectively the contributions to invasion by species i from specific coexistence mechanisms: differential predation, the storage effect due to competition, and the storage effect due to predation (Appendix C). Each is described in detail in the following sections. In the absence of these mechanisms, invasion of species i is governed by $\mu_i - \bar{\mu}$, which is the average fitness difference of Chesson (2000). As this difference must sum to zero across species, not all species would be able to invade as it must be negative for some of them. Indeed, in that case, only the species with the largest value of μ , i.e. largest yield Y_j , would persist. All the others would be driven extinct. Coexistence therefore requires the other terms, i.e.

coexistence requires the coexistence mechanisms. In particular, if the coexistence mechanisms sum to sufficiently large positive numbers, they will offset negative average fitness terms, $\mu_i - \bar{\mu}$, allowing all species to invade and hence coexist with each other.

The coexistence mechanisms in equation (9) have been mostly positive and of similar magnitude for all species in many other studies using these methods (e.g. Chesson, 1994; Kuang and Chesson, 2010), meaning that they unambiguously contribute to the invasion of each species and hence their stable coexistence. However, optimal foraging imposes strong asymmetries on the species: as we will show, the critical predation contribution to the invasion rate, ΔP_i , is positive for some species but zero or negative for others. This means it could act as an equalizing mechanism, offsetting negative values of $\mu_i - \bar{\mu}$ while reducing the invasion rate for species with positive values of $\mu_i - \bar{\mu}$. This outcome is to be expected here if species with larger yields Y_j , and hence larger μ , are more valuable prey and hence always part of the predators' diet. However, equalizing mechanisms cannot alone stabilize coexistence (Chesson 2000). Stabilizing mechanisms are necessary for that. However, an individual mechanism may have both stabilizing and equalizing roles (Chesson 2000, 2003, Mathias and Chesson 2013, Holt and Chesson 2014, Yuan and Chesson 2015). For example, differential predation has a stabilizing role if the average of ΔP_i across species, $\overline{\Delta P}$, is positive. Its equalizing role is assessed by the difference $\Delta P_i - \overline{\Delta P}$. These considerations then lead to a rearrangement of the formula (9) to give

$$E[r_i] \approx \xi_i + \overline{\Delta P} + \overline{\Delta I_c} + \overline{\Delta I_p} \quad (10)$$

in terms of the community average measures of the mechanisms and the modified average fitness comparison

$$\xi_i = (\mu_i - \bar{\mu}) + (\Delta P_i - \overline{\Delta P}) + (\Delta I_{Ci} - \overline{\Delta I_C}) + (\Delta I_{Pi} - \overline{\Delta I_P}) \quad (11)$$

From (10) we can see that a positive value of the sum of the stabilizing components, $\overline{\Delta P} + \overline{\Delta I_C} + \overline{\Delta I_P}$ means that there is a non empty set of $\xi = (\xi_1, \xi_2, \dots, \xi_n)$ values compatible with coexistence (Chesson, 2003). This set becomes larger as these stabilizing components become larger, along with coexistence becoming more stable, because recovery from low density occurs more rapidly (Chesson 2000).

3. Results

First, we present our results in a constant environment. In this case, the optimal foragers are the only effect that can allow species to coexist. Second, we present our results in a community where germination rates vary from year to year.

3.1 Coexistence in a constant environment

In a constant environment, the invader's growth rate (9) reduces to

$$E[r_i] \approx \mu_i - \bar{\mu} + \Delta P_i, \quad (12)$$

where the effect of predation takes the form

$$\Delta P_i = \left(\frac{1}{n-1} \sum_{r \neq i} A_r^{*\{-i\}} \right) - A_i^{*\{-i\}}, \quad (13)$$

and $A_j^{*\{-i\}}$ denotes $A_j(t)$ evaluated at the equilibrium for the resident community when species i is the invader. Hundreds of computer simulations have suggested that when P is fixed and the environment is constant, that the system will reach a globally stable

equilibrium. The value of $A_j^{*\{-i\}}$ differs between species under optimal foraging because $A_j(t) \geq A_k(t)$ whenever $e_j > e_k$. Thus, the term ΔP_i will tend to be nonpositive for species with a high e_i , and nonnegative with a low e_i .

In the two species case, $\Delta P_1 = 0$ because species 1 has the more valuable seeds, and so both species are automatically included in the diet when species 1 is at zero density. Hence both species have the same value of $A^{*\{-1\}}$ (i.e., species 1 and 2 in Fig. 1). The value of ΔP_2 is positive if species 1 is sufficiently abundant at its equilibrium density for species 2 to be excluded from the predator's diet at the beginning of the foraging season ($u = 0$), as determined by condition (6). Then $A_1^{*\{-1\}} > A_2^{*\{-1\}}$ meaning $\Delta P_2 > 0$.

With one ΔP_i positive and the other zero, the community average measure $\overline{\Delta P}$ is necessarily positive, demonstrating a stabilizing effect of optimal foraging. However, the differences between the values of ΔP_i for $i = 1$ and 2, mean that the $\Delta P_i - \overline{\Delta P}$ values are nonzero, altering fitness inequality. The effect is to increase fitness inequality if more desired species is also the weaker competitor (i.e., $Y_1 < Y_2$), but decrease it if $Y_1 > Y_2$ and $\Delta P_2 < 4(\ln Y_1 - \ln Y_2)$, in which case optimal foraging acts an equalizing mechanism. In these terms, the condition for coexistence is very simple. It is merely

$$0 < \mu_1 - \mu_2 < \Delta P_2 \quad (14)$$

where, as defined earlier, $\mu_j = \ln Y_j$. The lower inequality is simply the condition for species 1 to invade and the upper inequality is the condition for species 2 to invade. Now ΔP_2 can be simply be written as the $\ln$ of the fraction of newly produced seed, b_2 , surviving the vulnerable period for species 2 in the invader state, which is calculated from equations (4) and (6) above (Appendix B). Whether or not condition (14) will be

satisfied depends on the relationship between seed yield, Y_j , and seed energy, e_j , as illustrated in Figure 2a.

A feature of two-species coexistence is that the more valuable species also has to have higher yield Y_j . More generally for multiple species to coexist, the ranking of seed yields must be the same as the rankings of seed's caloric content, i.e., $Y_1 > Y_2 > \dots > Y_n$ whenever $e_1 > e_2 > \dots > e_n$ as we assume here. This makes sense because, as we have noted above, under optimal foraging, predation mortality A_j^* is ranked in the same order as seed value, and so without some compensating advantage, high seed value species would go extinct. With this assumption, we have found coexistence of as many as nine species (Appendix F) for specific parameter sets, and we see no reason why there should be a limit on the possible number of species coexisting with suitable relationships between e_j and Y_j . However, these relationships become more constrained as the number of species increases, as we illustrate here in Fig. 2 where the coexistence region in terms of the parameters for the least valuable species is much narrower for three species compared with two species. The conditions for three species coexistence are also much more complex than for two species. These conditions are deriving in Appendix B for lottery competition as

$$\begin{aligned}
(1) \quad P &> \frac{1}{a} \ln \left(\frac{b_1(0)\tilde{b}_3}{\tilde{b}_2(b_2(0) + \tilde{b}_2)} \right)^{\{-3\}} + h(b_1(0) + b_2(0) - \tilde{b}_3)^{\{-3\}} \\
(2) \quad Y_2 &> Y_3 \frac{e_2}{e_1 - e_2} \frac{e_1 - e_3}{e_3} \\
(3) \quad Y_2 &< Y_3 \left(ah \frac{\bar{e}_3^{\{-3\}} - e_3}{e_3} \right) (b_2(0)^{\{-3\}} + \tilde{b}_2) \\
(4) \quad Y_3 &> \frac{\alpha_2}{ah} \frac{e_3}{e_2 - e_3}
\end{aligned} \tag{15}$$

(Fig. 1). Thus, four rather complex conditions replace the simple pair of conditions (14) in the two species case.

3.2 Coexistence in a variable environment

When germination rates vary, the invader growth rate is

$$E[r_i] \approx \mu_i - \bar{\mu} + \Delta P_i + \Delta I_{Ci} + \Delta I_{Pi}, \quad (16)$$

where the mean difference in predation is now

$$\Delta P_i = \left(\frac{1}{n-1} \sum_{r \neq i} E[A_r(t)^{\{-i\}}] \right) - E[A_i(t)^{\{-i\}}], \quad (17)$$

(i.e., it is similar to (13) with the $A_j(t)^{\{-i\}}$'s averaged over time), and ΔI_{Ci} and ΔI_{Pi} are the storage effect from competition and predation, described below. Using community average mechanisms, we can rewrite (16) as

$$E[r_i] \approx \xi_i + \overline{\Delta P} + \overline{\Delta I_C} + \overline{\Delta I_P}. \quad (18)$$

Our analysis and computer simulations suggest that environmental variation generally has little effect on $E[A_j(t)^{\{-i\}}]$, and therefore little effect on ΔP_i and $\overline{\Delta P}$, except through its influence on $\bar{N}_j$ (Fig. 3, Appendix C and F). Thus, it appears that the impact of environmental variation can simply be added on to the constant environment case.

3.2.1 The storage effect from competition, ΔI_{Ci}

As in previous studies of the annual plant model, annual variation in germination rates promotes coexistence through the storage effect from competition, ΔI_{Ci} (Chesson, 1994). The functioning of the storage effect has been described in great detail elsewhere (e.g., Chesson, 1994; Chesson, 2000; Kuang and Chesson, 2009; Kuang and Chesson, 2010);

here we present the main results of our model. The storage effect from competition boosts the invader's mean growth rate by an amount

$$\Delta I_{Ci} = s \left[\left(\frac{1}{n-1} \sum_{r \neq i} \text{cov}(E_r(t), C(t)^{\{-i\}}) \right) - \text{cov}(E_i(t), C(t)^{\{-i\}}) \right], \quad (19)$$

(Appendix C) (Chesson, 1994). The factors affecting the magnitude of ΔI_{Ci} can be seen more clearly though the approximation (which is based on a Taylor series)

$$\Delta I_{Ci} \approx s \frac{\sigma^2 (1-\rho) C'_i}{n-1}, \quad (20)$$

(Chesson, 1994) where $C'_i/(n-1)$ is the average sensitivity of $C(t)^{\{-i\}}$ to changes in $E_r(t)$,

$$C'_i = \sum_{r \neq i} \frac{\partial C(t)^{\{-i\}}}{\partial E_r(t)} \Big|_{G_r(t)=E[G]} \quad (21)$$

(Kuang and Chesson, 2009). In our model,

$$C'_i = \frac{\alpha_2 \sum_{r \neq i} E[G] E[N_r^{\{-i\}}]}{\alpha_1 + \alpha_2 \sum_{r \neq i} E[G] E[N_r^{\{-i\}}]} \quad (22)$$

(Appendix C). Thus, we see that ΔI_{Ci} depends on the amount that germination rates vary, σ^2 , correlation between the germination rates of each species, ρ , the seed survival rate, s , and the amount that germination affects competition, C'_i . ΔI_{Ci} is always non-negative; therefore $\overline{\Delta I_C}$ is always non-negative and greater than $(\Delta I_{Ci} - \overline{\Delta I_C})$. Thus, the storage effect from competition will never reduce $\overline{r}_i$, but instead will increase the invader growth rate of all species, hence promoting coexistence regardless of the number of species.

This increases the parameter range over which species can coexist, and can even allow species to coexist without a strict competition-predation trade-off (Fig. 4). This result is qualitatively the same as previous models that used different forms of competition (e.g.,

Chesson, 1994; Kuang and Chesson, 2010), as expected from general theory (Chesson, 2003).

3.2.2 The storage effect from predation, ΔI_{Pi}

Dormant seeds are protected from predators; thus, a population can benefit by staying dormant through years of high apparent competition. This produces a storage effect from predation, ΔI_{Pi} , that is analogous to the storage effect from competition (Chesson and Kuang, 2010). It affects invader growth rates by an amount

$$\Delta I_{Pi} = s \left[\left(\frac{1}{n-1} \sum_{r \neq i} \text{cov}(E_r(t), A_r(t)^{\{-i\}}) \right) - \text{cov}(E_i(t), A_i(t)^{\{-i\}}) \right], \quad (23)$$

(Appendix C) (Chesson and Kuang, 2010).

Our results suggest that when predators commonly differentiate their prey (i.e., $A_1(t) \neq A_k(t)$ for some k and most t), then the storage effect from predation will be insignificant compared to the mean difference in predation, i.e., $\Delta I_{Pi} \ll \Delta P_i$. We outline technical reasons for this in Appendix C and D, but in essence, the benefit that an invader gains by germinating in years of low predation is small compared to the benefit it gains by being excluded from the predator's diet. This occurs in part because $A_j(t)$ is limited in how much it can vary from year to year, so the benefit an invader gains by germinating more in years of low predation is small (Appendix C and D). As a result, the storage effect from predation will have a negligible effect on coexistence when predators regularly exclude some prey from their diet (Appendix C and F).

Interestingly, if the predators do not differentiate their prey (i.e., $A_j(t) = A_k(t)$ for all t), or if they do it rarely (i.e., $A_j(t) = A_k(t)$ for most t , Appendix D), then the storage effect from predation can appreciably affect coexistence. Analogous to our

approximation of ΔI_{Ci} , (20), the factors affecting ΔI_{Pi} can be seen through its approximation

$$\Delta I_{Pi} \approx s \frac{\sigma^2 (1 - \rho) A_i'}{n - 1}, \quad (24)$$

(Chesson and Kuang, 2010) where A_i' , analogous to C_i' , is the sensitivity of $A_i(t)^{\{-i\}}$ to changes in $E_r(t)$,

$$A_i' = (1 - C_i') \left(1 - \frac{1 + ha \sum b_r(0)}{1 + ha \sum b_r(1)} \bigg|_{G_r(t) = E[G]} \right)^{\{-i\}} \quad (25)$$

(Appendix D). Like the storage effect from competition, the storage effect from predation is proportional to four factors: the amount that germination varies, σ^2 , the amount that germination differs between species, $(1 - \rho)$, the amount that a change in $E_r(t)$ changes predation rates, $A_i'/(n - 1)$, and the seed bank survival rate, s .

Unlike ΔI_{Ci} , the term ΔI_{Pi} is non-positive. This difference occurs because $C(t)$ is an increasing function of seed germination (i.e., more germinating seeds leads to more competition), whereas $A_i(t)$ is a decreasing function of seed germination (i.e., due to predator satiation). Thus, when an abundant resident has a year of high germination, the high density of seeds it produces will satiate the predators, and the per-seed predation risk will be reduced. Thus, $\text{cov}(E_r(t), A_r(t)^{\{-i\}})$ will be negative (Appendix D). Invaders are too rare to satiate the predators, and as a result, $E_i(t)$ will not affect $A_i(t)^{\{-i\}}$. Thus, $\text{cov}(E_i(t), A_i(t)^{\{-i\}})$ will be less negative than $\text{cov}(E_r(t), A_r(t)^{\{-i\}})$, and ΔI_{Pi} will be negative (Appendix D). Because the residents gain an advantage that the invader does not, the storage effect from predation will act as a destabilizing mechanism, and thus undermine coexistence.

4. Discussion

Although a many previous studies have examined the effect of optimal foragers on prey coexistence, such studies have mainly focused on two-species coexistence in a constant environment (e.g., Abrams and Matsuda, 1996; Genkai-Kato and Yamamura, 1999; Gleeson and Wilson, 1986; Krivan, 1996; Krivan, 2003), and on the dynamics of predator-prey oscillations (e.g., Gleeson and Wilson, 1986; Krivan, 1996; Ma et al., 2003). Similarly, many recent studies of prey coexistence in a variable environment have not studied optimal foraging or adaptive diet choice (Chesson and Kuang, 2010; Kuang and Chesson, 2009; Kuang and Chesson, 2010; Mordecai, 2014; Stump and Chesson, 2015). In this paper, we unite these fields by analyzing the effect of adaptive diet choice on multispecies coexistence a variable environment. Our results indicate that adaptive diet choice can promote coexistence in two distinct ways: it can create a competition-predation trade-off, which has an equalizing effect, and it can lead to reduced apparent competition for invaders, which has a stabilizing effect. We show that multiple prey species can coexist because of an optimally foraging predator without the need for other mechanisms. Additionally, our model shows that under most circumstances, the effects of predators will not be strongly modified by environmental variation. However, variation in germination rates can powerfully promote coexistence via a storage effect from competition (Chesson, 1994). Thus, optimal foragers and variable germination will make separate contributions to coexistence. Adaptive foragers can also undermine coexistence in two distinct ways: if the weakest competitors produce the most desirable seeds, then predators will undermine coexistence by increasing mean fitness differences;

and, if it is optimal for the predators to be generalists, then they can undermine coexistence by creating a negative storage effect from predation.

4.1 The role of adaptive diet choice in coexistence

In our model, prey can coexist due to optimal foraging alone when there is a strict competition-predation trade-off, such that more competitive plants produce more desirable seeds. This could happen, for example, if there is a trade-off between producing more seeds and better defended seeds (Dalling et al., 2011). Alternatively, a competition-predation trade-off could occur if predators prefer larger seeds, but plants that produce larger seeds are stronger competitors (e.g., Lebrija-Trejos et al., 2016); such a trade-off could be represented using the competition model in Appendix E. Under any such competition-predation trade-off, the predator will begin each year consuming only the most desirable seed species. As these seeds are depleted, it becomes advantageous for the predator to include additional prey species in its diet. As a result, the most competitive species have the highest risk of predation (because their seeds are consumed throughout the year), and the least competitive species have the lowest risk of predation (because their seeds are only consumed at the end of the year). Although the effect of the competition-predation trade-off is mainly equalizing, it is necessary for the stabilizing effects to allow species to coexist. For coexistence to occur, each species must be consumed relatively less when they become very rare (Fig. 1). This can occur because, when a species' population declines, it is less able to satiate the predators, and its competitors are more able to satiate the predators. The net result is that predation risk is

reduced for the species at low density relative to the more abundant species. In our model, an unlimited number of species can coexist through this form of predation.

Our results suggest that it is fairly easy for a small number of prey species to coexist due to adaptive diet choice alone. However, adaptive diet choice, by itself, seems unlikely to be the sole mechanism promoting coexistence in diverse communities. As more prey species are added to the community, the proportion of parameter space that will allow species to coexist shrinks (Fig. 2). A similar relationship has been found in many other models (e.g., Chesson and Kuang, 2010; Holt and Chesson, 2014; Stump and Chesson, 2015); however, in those models, many species can coexist by having similar competitive ability. In this model, species must differ in their yields, and yield must trade-off with seed energy content along a particular relationship (Fig. 2). It seems unlikely that yield (or competitive ability more generally) will trade off so perfectly with energy content (or desirability more generally) in a real community. Thus, it is probably not realistic to expect adaptive diet choice to be the only factor promoting coexistence in diverse communities. Similar criticisms have been made of the competition-colonization trade-off (Levine and Rees, 2002). And, like the competition-colonization trade-off, the more important role of adaptive foragers in diverse communities may be how they affect mean fitness differences. If optimally foraging predators generate an equalizing effect, then they could promote coexistence in combination with other stabilizing mechanism (Chesson, 2000). This is consistent with the observation that competition-predation trade-offs are widespread, but models predict that they should have a weak stabilizing effect (Chase et al., 2002).

This result of our model suggests an explanation for how annual plant communities in the southwestern United States can coexist. Annual plant diversity is thought to be maintained by variable germination (Angert et al., 2009; Chesson et al., 2013). However, large seeded plants become dominant when rodents are excluded (Allington et al., 2013; Brown and Heske, 1990). In this community, rodents have been shown to strongly prefer large seeds (Inouye et al., 1980), and some large-seeded plants have been shown to be strong competitors (Ignace and Chesson, 2014). These results suggest that rodents generate a competition-predation trade-off in this system. Thus, one possibility is that if rodents are present, differences in species-average fitness are small and diversity can be maintained by a storage effect from competition; if rodents are excluded, large-seeded plants have a large advantage, and the storage effect is inadequate to maintain diversity.

We have focused on how adaptive foragers could promote coexistence, but it is also possible that they could undermine coexistence. For example, studies have shown that there is a trade-off between producing large seeds and producing many seeds (Henery and Westoby, 2001; Muller - Landau et al., 2008). If large seeds do not have a significant competitive advantage, but granivores prefer large seeds, then a seed size-seed number trade-off would be unequalizing: species with the high reproductive output would have their fitness advantage boosted further by lower granivory.

4.2 The storage effect from competition and predation

Like previous models (e.g., Chesson, 1994; Kuang and Chesson, 2009), our results indicate that variable germination can strongly promote coexistence via a storage effect

from competition. The storage effect can even allow species to coexist in the absence of a strict competition-predation trade-off, even though this is a requirement for coexistence with only an optimally foraging predator (Fig. 4). In this case, species coexist if the benefit of the storage effect outweighs the disadvantage of being both a weaker competitor and a target for predators. Thus, this paper joins several recent articles in suggesting the importance of both competition-based mechanisms and consumption-based mechanisms in promoting coexistence (e.g., Chesson and Kuang, 2010; Kuang and Chesson, 2010; Mordecai, 2014).

Interestingly, we found that generalist predators with a Type II functional response can produce a negative storage effect (ΔI_{Pi}), undermining coexistence. This is the first study we know of showing that predators can produce a negative storage effect. Our result differs from previous models of pathogen outbreaks and predators with a Type III functional response, which can create a positive storage effect (Chesson and Kuang, 2010; Mordecai, 2014). The difference is that those types of predators become more efficient when prey are common, whereas predators with a Type II functional response become less efficient when prey are common. In previous studies, abundant species are self-limiting because they cause attack rates to increase in years of high germination (Chesson and Kuang, 2010; Mordecai, 2014). In our study, high seed density will satiate the predators and increase seed survival. This process gives abundant species an advantage because they can satiate predators by germinating in high numbers. Very rare species cannot do this. As a result, variation in germination produces a low-density disadvantage, and thus coexistence is undermined.

Our model also indicates that the storage effect from predation will be inconsequential if predators regularly exclude certain prey from their diet, because the storage effect will always be much smaller than the mean difference in predation (ΔP_i). Intuitively, a benefit that occurs infrequently (such as predator satiation during an extreme germination event) must be much stronger than a benefit that occurs every year (such as being excluded from a predator's diet) for both to have the same effect. When the predators commonly differentiate between prey species, such high variation in predation risk is not possible in this model. For example, consider the case where the predator consumes only the resident: the resident gains a small benefit from occasionally satiating the predators, but the invader gains a major benefit because it is never consumed. As a result, yearly variation in predator satiation would have a trivial effect on coexistence. Thus, we expect the storage effect from predation to be mainly important in communities with generalist predators.

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Appendix A. Derivation of $A_j(t)$, the risk of predation

Here we derive $A_j(t)$. First, we will consider the case of a single prey. Equation (4) rearranges to

$$-\frac{1+ahb_j(u)}{aPb_j(u)}db_j(u) = du. \quad (26)$$

We integrate this between times u_0 and u_1 ,

$$-\int_{b_j(u_0)}^{b_j(u_1)} \frac{1+ahb_j(u)}{aPb_j(u)}db_j(u) = \int_{u_0}^{u_1} du. \quad (27)$$

Solving this integral, we get

$$-\frac{1}{aP} \ln(b_j(u)) - \frac{h}{P} b_j(u) \Big|_{b_j(u_0)}^{b_j(u_1)} = u_1 - u_0, \quad (28)$$

which simplifies to

$$ahb(u_1)e^{ahb(u_1)} = ahb(u_0)e^{ahb(u_0)-aP(u_1-u_0)}. \quad (29)$$

Because the left side of equation (29) takes the form Ze^Z , where $Z = ahb(u_1)$,

$$ahb_j(u_1) = W\left(ahb_j(u_0)e^{ahb_j(u_0)-aP(u_1-u_0)}\right), \quad (30)$$

where W is the Lambert W function. Thus,

$$b_j(u_1) = \frac{W\left(ahb_j(u_0)e^{ahb_j(u_0)-aP(u_1-u_0)}\right)}{ah}, \quad (31)$$

and

$$A_j(t) = \ln\left\{\frac{b_j(0)}{b_j(1)}\right\} = \ln\left\{\frac{ahb_j(0)}{W\left(ahb_j(0)e^{ahb_j(0)-aP}\right)}\right\}. \quad (32)$$

Under our interpretation of optimal foraging theory, it is possible that a predator will begin the year consuming only species 1, and then add additional species to its diet. We will derive this for a two species system. Seeds of species 1 will be consumed from the beginning of the year until only $\tilde{b}_2$ seeds remain, where $\tilde{b}_2$ is the critical switching density defined in equation (7) (originally derived in Charnov, 1976). This occurs at the

time $\tilde{u}_2$, derived below. Thus, the chance that a species 1 seed survives from $u = 0$ to $u = \tilde{u}_2$ is

$$P(\text{spp. 1 seed survives to } \tilde{u}_2) = \frac{\text{seeds at time } \tilde{u}_2}{\text{seed at time 0}} = \frac{\tilde{b}_2}{b_1(0)} \quad (33)$$

After time $\tilde{u}_2$, the predator will consume species 1 and 2 at an equal rate until the end of the year ($u = 1$). Because species 2 has not been consumed up to that point, there will be $b_2(0)$ seeds of species 2 at time $\tilde{u}_2$. If we define $b_{final} = b_1(1) + b_2(1)$, then

$$P(\text{seed survives from } \tilde{u}_2 \text{ to } 1) = \frac{\text{seeds at time 1}}{\text{seed at time } \tilde{u}_2} = \frac{b_{final}}{\tilde{b}_2 + b_2(0)}. \quad (34)$$

We can calculate b_{final} using (31), where $u_0 = \tilde{u}_2$, $u_1 = 1$, and $b_i(u_0) = \tilde{b}_2 + b_1(0)$. Thus,

$$P(\text{seed survives from } \tilde{u}_2 \text{ to } 1) = \frac{W\left(ah\left(\tilde{b}_2 + b_2(0)\right)e^{ah\left(\tilde{b}_2 + b_2(0)\right) - aP(1 - \tilde{u}_2)}\right)}{ah\left(\tilde{b}_2 + b_2(0)\right)}. \quad (35)$$

Because $A_j(t)$ can be written as $-\ln(\text{probability of surviving to time } 1)$,

$$A_1(t) = \ln \left\{ \frac{b_1(0)}{\tilde{b}_2} \frac{ah\left(\tilde{b}_2 + b_2(0)\right)}{W\left(ah\left(\tilde{b}_2 + b_2(0)\right)e^{ah\left(\tilde{b}_2 + b_2(0)\right) - aP(1 - \tilde{u}_2)}\right)} \right\} \quad (36)$$

and

$$A_2(t) = \ln \left\{ \frac{ah\left(\tilde{b}_2 + b_2(0)\right)}{W\left(ah\left(\tilde{b}_2 + b_2(0)\right)e^{ah\left(\tilde{b}_2 + b_2(0)\right) - aP(1 - \tilde{u}_2)}\right)} \right\} \quad (37)$$

Because it will be useful later, we now calculate $\tilde{u}_2$, the amount of time it takes to reduce the density of species 1 seeds from $b_1(0)$ to $\tilde{b}_2$. By our integral in (27),

$$-\int_{b_1(0)}^{\tilde{b}_2} \frac{1 + ahb_1(u)}{aP(t)b_1(u)} db_1(u) = \int_0^{\tilde{u}_2} du \quad (38)$$

Integrating this, we find that

$$\tilde{u}_2 = \frac{1}{aP} \ln \left(\frac{b_1(0)}{\tilde{b}_2} \right) + \frac{h}{P} (b_1(0) - \tilde{b}_2) \quad (39)$$

In a system with three or more species, $A_j(t)$ can be calculated using identical methods. In this case, if the predator consumes species 1 through j , then for $k \leq j$,

$$A_k(t) = \ln \left\{ \frac{ah(\tilde{b}_j + b_j(0))}{W \left(ah(\tilde{b}_j + b_j(0)) e^{ah(\tilde{b}_j + b_j(0)) - aP(1 - \tilde{u}_j)} \right)} \right\} + \sum_{l=k}^{j-1} \ln \left\{ \frac{b_l(0) + \tilde{b}_l}{\tilde{b}_{l+1}} \right\}, \quad (40)$$

and

$$\tilde{u}_k = \tilde{u}_{k-1} + \left(\frac{1}{aP} \ln \left(\frac{b_{k-1}(0) + \tilde{b}_{k-1}}{\tilde{b}_k} \right) + \frac{h}{P} (b_{k-1}(0) + \tilde{b}_{k-1} - \tilde{b}_k) \right). \quad (41)$$

Appendix B. Two and three-species coexistence in a constant environment

In this section, we show general conditions for species to coexist in a constant environment. In section B.1 we define necessary and sufficient conditions for 2 species to coexist. In section B.2, we show sufficient conditions for 3 species to coexist under lottery competition. To emphasize that the environment is constant, in this section we will write terms such as G , C , and A_j without the (t) .

Species can coexist if each species has a positive growth rate as an invader while each resident is at equilibrium, i.e.

$$\begin{aligned} \lambda_i &= (1 - G)s + Y_i G e^{-C - A_i^*} > 1 \\ \lambda_r &= (1 - G)s + Y_r G e^{-C - A_r^*} = 1 \quad \forall r \neq i \end{aligned}, \quad (42)$$

where A_j^* and C^* are the values of A_j and C when the residents are at equilibrium.

Combining these, we see that a species can invade if

$$\ln Y_i + (A_r^{*\{-i\}} - A_i^{*\{-i\}}) > \ln Y_r \quad (43)$$

for each residents in the system, r (Kuang and Chesson, 2010). If this holds when every species is an invader, then $\overline{\Delta P}$ will be positive, and $\overline{\Delta P} > -\min(\xi_j)$. This inequality illustrates that competition-predation trade-off (i.e., $e_1 > e_2 > \dots > e_n$ whenever $Y_1 > Y_2 > \dots > Y_n$) is a necessary condition for species to coexist.

B.1 Two species coexistence

We first consider a two species community where $e_1 > e_2$. If species 1 is the invader, the predators will consume both species equally: it is optimal for the predators to consume species 1, but because species 1 is so rare, the predator should also consume species 2. As a result, $A_1^{*\{-1\}} = A_2^{*\{-1\}}$. Thus, (43) holds if and only if $Y_1 > Y_2$.

There are two cases to consider for determining if species 2 can invade: the predator never consumes species 2, and the predator consumes it for only part of the year. First, if the predators never consume species 2, then $A_2^{*\{-2\}} = 0$, and $\Delta P_2 = A_1^{*\{-2\}} = \ln b_1(0) - \ln b_1(1)$. Thus, inequality (43) will hold, and species 2 will have a positive invader growth rate if

$$\ln Y_2 + \ln b_1(0)^{\{-2\}} - \ln b_1(1)^{\{-2\}} > \ln Y_1 \quad (44)$$

Second, if the predator only consumes species 2 for part of the year, then by definition, it will add species 2 to its diet at time $u = \tilde{u}_2$ (i.e., when $b_1(\tilde{u}_2) = \tilde{b}_2$). In this case, both prey species experience the same risk of predation between times $\tilde{u}_2$ and 1, which can be

calculated as $b_1(1)/\tilde{b}_2$. $A_1^{\{-2\}} = \ln b_1(0) - \ln b_1(1)$, $A_2^{\{-2\}} = \ln \tilde{b}_2 - \ln b_1(1)$, and thus $\Delta P_2 = \ln b_1(0) - \ln \tilde{b}_2$. Thus, (43) will hold, and species 2 will have a positive invader growth rate, if

$$\ln Y_2 + \ln b_1(0)^{\{-2\}} - \ln \tilde{b}_2 > \ln Y_1. \quad (45)$$

It is simple to show that in either case that $\overline{\Delta P}$ will be positive, and $\overline{\Delta P} > -\min(\xi_j)$

B.2 Three species coexistence

In this section, we derive sufficient conditions for 3 species to coexist in a constant environment. We assume that $e_1 > e_2 > e_3$ and $Y_1 > Y_2 > Y_3$. We will assume the special case of $\alpha_1 = 0$ (i.e., lottery competition), so that predators cannot drive the prey species extinct, and so that knowing the proportional relationship of N_1 , N_2 , and N_3 , rather than their exact values, is sufficient to calculating the number of seeds produced.

We will show that the conditions in equation (15) allow three species to coexist in a constant environment. In short, condition **(1)** guarantees that predators have a large enough effect to actually maintain diversity, **(2)** is that species 2 can invade a community with species 1 and 3 as residents, **(3)** is that species 3 can invade a community with species 1 and 2 as residents, and **(4)** is that species 3 can invade a community with only species 2 as a resident.

We first derive condition **(1)**,

$$P > \frac{1}{a} \ln \left(\frac{b_1(0)\tilde{b}_3}{\tilde{b}_2(b_2(0) + \tilde{b}_2)} \right)^{\{-3\}} + h(b_1(0) + b_2(0) - \tilde{b}_3)^{\{-3\}}. \text{ The coexistence region will be}$$

the largest, and simplest to calculate, when the number of species 1 and 2 seeds are reduced to below $\tilde{b}_3$ in all cases. It may be possible for coexistence to occur with fewer predators, and thus our result here show conditions that are sufficient but not necessary. It will be the most difficult for predators to reduce the number of species 1 and 2 seeds below $\tilde{b}_3$ when both species 1 and 2 are residents. By equation (41), species 3 will be added to the predator's diet at time

$$\tilde{u}_3 = \tilde{u}_2 + \left(\frac{1}{aP} \ln \left(\frac{b_2(0) + \tilde{b}_2}{\tilde{b}_3} \right)^{\{-3\}} + \frac{h}{P} (b_2(0) + \tilde{b}_2 - \tilde{b}_3)^{\{-3\}} \right). \quad (46)$$

where, by equation (39),

$$\tilde{u}_2 = \frac{1}{aP} \ln \left(\frac{b_1(0)}{\tilde{b}_2} \right)^{\{-3\}} + \frac{h}{P} (b_1(0) - \tilde{b}_2)^{\{-3\}}. \quad (47)$$

Combining these,

$$\tilde{u}_3 = \frac{1}{aP} \ln \left(\frac{b_1(0)\tilde{b}_3}{\tilde{b}_2(b_2(0) + \tilde{b}_2)} \right)^{\{-3\}} + \frac{h}{P} (b_1(0) + b_2(0) - \tilde{b}_3)^{\{-3\}}. \quad (48)$$

Thus, $\tilde{u}_3 < 1$ whenever

$$P > \frac{1}{a} \ln \left(\frac{b_1(0)\tilde{b}_3}{\tilde{b}_2(b_2(0) + \tilde{b}_2)} \right)^{\{-3\}} + h(b_1(0) + b_2(0) - \tilde{b}_3)^{\{-3\}}; \quad (49)$$

This is condition **(1)**.

Next, we derive condition **(2)**, $Y_2 > Y_3 \frac{e_2}{e_1 - e_2} \frac{e_1 - e_3}{e_3}$. By equation (43), species 2

will have a positive invader growth rate if

$$\ln Y_2 - \ln Y_3 > A_3^{*\{-2\}} - A_2^{*\{-2\}}. \quad (50)$$

Species 2 will be added to the predator's diet when the number of species 1 seeds, $b_1(u)$, has been reduced to

$$\tilde{b}_2^{\{-2\}} = \left(\frac{1}{ah} \right) \frac{e_2}{e_1 - e_2}. \quad (51)$$

Since species 2 is the invader, $b_2(0) = 0$, and therefore it will have no effect on the predator's behavior. Thus, species 3 will added to the predator's diet when $b_1(u)$ has been reduced to

$$\tilde{b}_3^{\{-2\}} = \left(\frac{1}{ah} \right) \frac{e_3}{e_1 - e_3}, \quad (52)$$

By our previous derivation of for A_j^* , equation (40), we see that

$$\begin{aligned} A_2^{*\{-2\}} &= \ln \frac{\tilde{b}_2^{\{-2\}}}{\tilde{b}_3^{\{-2\}}} - \ln \left(P(\text{survival after time } \tilde{u}_3) \right) \\ A_3^{*\{-2\}} &= -\ln \left(P(\text{survival after time } \tilde{u}_3) \right) \end{aligned} \quad (53)$$

Thus, substituting (53) into (50), we see that species 2 will be able to invade when

$$Y_2 > Y_3 \left(\frac{\tilde{b}_2^{\{-2\}}}{\tilde{b}_3^{\{-2\}}} \right). \quad (54)$$

Substituting (51) and (52) into this reduces our inequality to condition **(2)**.

Next, we consider condition **(3)**, $Y_2 < Y_3 \left(ah \frac{\bar{e}_3^{\{-3\}} - e_3}{e_3} \right) (b_2(0)^{\{-3\}} + \tilde{b}_2)$. Species 3

will have a positive growth rate as an invader if

$$\ln Y_2 - \ln Y_3 < A_3^{*\{-3\}} - A_2^{*\{-3\}}. \quad (55)$$

Now, species 2 will be added to the predator's diet when the number of species 1 seeds, $b_1(u)$, has been reduced to $\tilde{b}_2^{\{-3\}}$ (which is the same as $\tilde{b}_2^{\{-2\}}$, equation (51)), and species 3 will added to the predator's diet when $b_1(u) + b_2(u)$ has been reduced to

$$\tilde{b}_3^{\{-3\}} = \left(\frac{1}{ah} \right) \frac{e_3}{\bar{e}_3^{\{-3\}} - e_3}, \quad (56)$$

where $\bar{e}_3^{\{-3\}}$, the mean weighted value of e_1 and e_2 when species 3 is an invader, is

$$\bar{e}_3^{\{-3\}} = \left(\frac{e_1 \tilde{b}_2 + e_2 b_2(0)^{\{-3\}}}{\tilde{b}_2 + b_2(0)^{\{-3\}}} \right). \quad (57)$$

The probability a seed will be consumed between when species 2 and species 3 are added to the predator's diet is $\tilde{b}_3^{\{-3\}} / (\tilde{b}_2^{\{-3\}} + b_2(0))$. Thus, (55) will hold when

$$Y_2 < Y_3 \left(\frac{b_2(0)^{\{-3\}} + \tilde{b}_2}{\tilde{b}_3^{\{-3\}}} \right). \quad (58)$$

By our definition of $\tilde{b}_3^{\{-3\}}$, this reduces to condition **(3)**.

Here we show that conditions **(2)** and **(3)** can both hold. Equations (54) and (58) can be combined to

$$Y_3 \left(\frac{\tilde{b}_2^{\{-2\}}}{\tilde{b}_3^{\{-2\}}} \right) < Y_2 < Y_3 \left(\frac{b_2(0)^{\{-3\}} + \tilde{b}_2^{\{-3\}}}{\tilde{b}_3^{\{-3\}}} \right), \quad (59)$$

which reduces to

$$\frac{\tilde{b}_2^{\{-2\}}}{\tilde{b}_3^{\{-2\}}} < \frac{b_2(0)^{\{-3\}} + \tilde{b}_2^{\{-3\}}}{\tilde{b}_3^{\{-3\}}}, \quad (60)$$

The term $\tilde{b}_2^{\{-j\}}$ depends only on e_1 , e_2 , a , and h , none of which change when resident-invader states change. Thus $\tilde{b}_2^{\{-3\}} = \tilde{b}_2^{\{-2\}}$, and we will write both as simply $\tilde{b}_2$,

$$\frac{\tilde{b}_2}{\tilde{b}_3^{\{-2\}}} < \frac{b_2(0)^{\{-3\}} + \tilde{b}_2}{\tilde{b}_3^{\{-3\}}}. \quad (61)$$

Using Charnov's (1976) derived value of $\tilde{b}_j$, equation (7), will write each $\tilde{b}_3$ in terms of e_j values,

$$\left(ah \frac{e_1 - e_3}{e_3} \right) \tilde{b}_2 < \left(ah \frac{\bar{e}_3^{\{-3\}} - e_3}{e_3} \right) (b_2(0)^{\{-3\}} + \tilde{b}_2) . \quad (62)$$

With some rearranging, this simplifies to

$$e_1 \tilde{b}_2 < \bar{e}_3^{\{-3\}} (b_2(0)^{\{-3\}} + \tilde{b}_2) - e_3 b_2(0)^{\{-3\}} . \quad (63)$$

By our definition of $\bar{e}_3^{\{-3\}}$, (57),

$$e_1 \tilde{b}_2 < \left(\frac{e_1 \tilde{b}_2 + e_2 b_2(0)^{\{-3\}}}{\tilde{b}_2 + b_2(0)^{\{-3\}}} \right) (b_2(0)^{\{-3\}} + \tilde{b}_2) - e_3 b_2(0)^{\{-3\}} , \quad (64)$$

which simplifies to

$$e_1 \tilde{b}_2 < e_1 \tilde{b}_2 + e_2 b_2(0)^{\{-3\}} - e_3 b_2(0)^{\{-3\}} , \quad (65)$$

which reduces very simply to

$$e_3 < e_2 , \quad (66)$$

which is true by assumption. Thus, conditions **(2)** and **(3)** can hold for some Y_2 .

Finally, we consider condition **(4)**, $Y_3 > \frac{\alpha_2}{ah} \frac{e_3}{e_2 - e_3}$. For species 2 and 3 to coexist

as in the absence of species 1, it must be the case that species 3 can invade when only species 2 is the resident. By condition (43), this will occur when

$$Y_3 > Y_2 \left(\frac{\tilde{b}_3^{\{-1,3\}}}{b_2(0)^{\{-1,3\}}} \right) , \quad (67)$$

(where superscript $\{-1,3\}$ indicates that species 1 and 3 are absent). When species 2 is the resident, and $\alpha_1 = 0$,

$$b_2(0) = \frac{Y_2 N_2^{\{-1,3\}} G}{\alpha_2 N_2^{\{-1,3\}} G} = \frac{Y_2}{\alpha_2} . \quad (68)$$

By our equation for $\tilde{b}_j$, equation (7),

$$\tilde{b}_3^{\{-1,3\}} = \left(\frac{1}{ah} \right) \frac{e_2}{e_3 - e_2}. \quad (69)$$

Combining these, species 2 and 3 can coexist if

$$Y_3 > \frac{\alpha_2}{ah} \frac{e_3}{e_2 - e_3}. \quad (70)$$

This is condition **(4)**.

When species 1 is an invader, it will be able to invade any subcommunity. In short, it will never be beneficial for the predator to consume only species 1, and thus since $A_1^{*\{-1\}} = A_2^{*\{-1\}}$ if species 2 is present (Fig. 1), and $A_1^{*\{-1\}} = A_3^{*\{-1\}}$ if only species 3 is present. Thus, since $Y_1 > Y_2 > Y_3$, it will have a positive invader growth rate. The other conditions are sufficient to allow species 2 or 3 to invade a community with only species 1.

Appendix C. Species coexistence in a variable environment

In Appendix C, we derive conditions necessary for species to coexist when there is year-to-year variation in germination. Our derivation follows the framework of Chesson (1994), and the derivation of Kuang and Chesson (2010).

C.1 Size assumptions

Our analysis relies on small effect assumptions. These are described in detail in Chesson (1994). We assume that σ^2 , the variance in $E_j(t)$, is small enough that $r_j(t)$ can be approximated by a second-order Taylor series. A function $f(\sigma)$ is $O(\sigma)$ if there exists a k such that $|f(\sigma)| < k\sigma$ as $\sigma \rightarrow 0$. We assume that $E_j(t)$ varies over a finite range of $O(\sigma)$ and that $|\ln Y_j - \ln Y_k|$ and $E[A_j(t) - A_k(t)]$ are $O(\sigma^2)$. In order to guarantee that $E[A_j(t) - A_k(t)]$

is at most $O(\sigma^2)$, we assume that P is $O(\sigma^2)$, and thus $A_j(t)$ is at most $O(\sigma^2)$; we relax this assumption in Appendix D. Because $C(t)$ is a linear combination of $E_j(t)$ values, any two $C(t)$ values will be within $O(\sigma)$, and the variance in $C(t)$ will be $O(\sigma^2)$. We show that, as with previous models (e.g., Chesson, 1994; Kuang and Chesson, 2010), these assumptions lead to $E[r_i] = O(\sigma^2)$. In our analysis, we ignore terms that are smaller than $O(\sigma^2)$, which we refer to as $o(\sigma^2)$, as these will not generally impact the sign of $E[r_i]$. Computer simulations suggest that they will have little effect, even when σ^2 is reasonably large (Appendix D).

In this analysis, we use the symbol $\approx$ to indicate that terms differ by no more than $o(\sigma^2)$.

C.2 Partitioning $r_j(t)$ into the effects of environment and density-dependence

Our model was almost identical to the one studied in Kuang and Chesson (2010) and Chesson and Kuang (2010), except that $A_j(t)$ is much different. Thus, our basic analysis closely follows those papers, which are based on Chesson (1994). The basic derivation is written in this section for the reader's convenience, and the novel contributions of this work are included in section C.3.

Each species' growth rate can be written as a function of environmental and density dependent effects, $E_j(t)$ and $D_j(t) = C(t) + A_j(t)$,

$$r_j(t) = g_j(E_j(t), D_j(t)) = \ln\left(\left(1 - e^{E_j(t)}\right)s + Y_j e^{E_j(t) - D_j(t)}\right). \quad (71)$$

The long-term average growth rate, $E[r_j]$, can be determined by taking the average of $g_j(E_j(t), D_j(t))$ over t . As shown in Chesson and Kuang (2010), (71) can be approximated as

$$\bar{r}_j \approx E[\mathcal{E}_j] - E[\mathcal{D}_j] + \gamma E[\mathcal{E}_j \mathcal{D}_j]. \quad (72)$$

where $\mathcal{E}_j$ and $\mathcal{D}_j$ represent the standardized effect of the environment and density-dependent factors in the units of $r_j(t)$,

$$\begin{aligned} \mathcal{E}_j &= \ln \left(\left(1 - e^{E_j(t)} \right) s + \frac{e^{E_j(t)}}{E[G]} \left(1 - (1 - E[G])s \right) \right), \\ \mathcal{D}_j &= -\ln \left((1 - E[G])s + Y_j E[G] e^{-D_j(t)} \right) \end{aligned} \quad (73)$$

and

$$\gamma = \frac{\partial^2 g_j}{\partial \mathcal{E}_j \partial \mathcal{D}_j} \bigg|_{\mathcal{E}_j = \mathcal{D}_j = 0} = -\frac{s}{1-s} \quad (74)$$

(Chesson and Kuang, 2010; Kuang and Chesson, 2010). Note that the variables D_j and $\mathcal{D}_j$ were previously called F_j and $\mathcal{E}_j$, though the rest of variables were similar to Chesson and Kuang (2010) and Kuang and Chesson (2010).

Since $E[r_r] = 0$ for all residents, but each expected value term in (72) may not be zero, we write $E[r_r]$ as a comparison between the resident and invader growth rate,

$$\begin{aligned} \frac{E[r_i]}{\beta} &= \frac{E[r_i]}{\beta} - \frac{1}{n-1} \sum_{r \neq i} \frac{E[r_r]}{\beta} \\ &\approx \frac{1}{\beta} (E[\mathcal{E}_i] - E[\mathcal{D}_i] + \gamma E[\mathcal{E}_i \mathcal{D}_i]) - \frac{1}{\beta(n-1)} \sum_{r \neq i} (E[\mathcal{E}_r] - E[\mathcal{D}_r] + \gamma E[\mathcal{E}_r \mathcal{D}_r]) \end{aligned} \quad (75)$$

(Chesson and Kuang, 2010; Kuang and Chesson, 2010). As derived in Kuang and Chesson (2010) and Chesson and Kuang (2010), this can be simplified to

$$\begin{aligned} \frac{E[r_i]}{\beta} &\approx \left(\ln \left(\frac{E[G] Y_i}{1 - s(1 - E[G])} \right) - \frac{1}{n-1} \sum_{r \neq i} \ln \left(\frac{E[G] Y_r}{1 - s(1 - E[G])} \right) \right), \\ &\quad + \Delta E_i - \Delta N_i + \Delta P_i + \Delta I_{Ci} + \Delta I_{Pi} \end{aligned} \quad (76)$$

where the effect of the environment, ΔE_i , is

$$\Delta E_i = \frac{E[\mathcal{C}_i^{\{-i\}}]}{\beta} - \frac{1}{n-1} \sum_{r \neq i} \frac{E[\mathcal{C}_r^{\{-i\}}]}{\beta}, \quad (77)$$

the relative nonlinearity, ΔN_i , is

$$\Delta N_i \approx \frac{(1-\beta)}{2} \text{var}(D_i(t)^{\{-i\}}) - \frac{(1-\beta)}{2} \frac{1}{n-1} \sum_{r \neq i} \text{var}(D_r(t)^{\{-i\}}). \quad (78)$$

the mean difference in predation, ΔP_i , is

$$\Delta P_i = \left(\frac{1}{n-1} \sum_{r \neq i} E[A_r(t)^{\{-i\}}] \right) - E[A_i(t)^{\{-i\}}], \quad (79)$$

the storage effect from competition, ΔI_{Ci} , is

$$\Delta I_{Ci} \approx -s \text{cov}(E_i(t), C(t)^{\{-i\}}) + \frac{s}{n-1} \sum_{r \neq i} \text{cov}(E_r(t), C(t)^{\{-i\}}), \quad (80)$$

and the storage effect from predation, ΔI_{Pi} , is

$$\Delta I_{Pi} \approx -s \text{cov}(E_i(t), A_i(t)^{\{-i\}}) + \frac{s}{n-1} \sum_{r \neq i} \text{cov}(E_r(t), A_r(t)^{\{-i\}}). \quad (81)$$

Because s and $E[G]$ are the same between species, the parenthetical term in (76)

can be simplified to $\left(-\ln Y_i + \frac{1}{n-1} \sum_{r \neq i} \ln Y_r \right)$, or $\mu_i - \bar{\mu}$. By our definition of $\mathcal{C}_j$, $E[\mathcal{C}_j]$

will be the same between species, and therefore $\Delta E_i = 0$ (Chesson and Kuang, 2010). As

shown in Kuang and Chesson (2010), ΔI_{Ci} can be approximated as

$$\Delta I_{Ci} \approx s \frac{\sigma^2 (1-\rho) C_i'}{n-1}, \quad (82)$$

where C_i' is the sum of the $\partial C(t)^{\{-i\}} / \partial E_r(t)$ terms across the residents (and thus, $C_i' / (n-1)$

is the average value of $\partial C^{\{-i\}}(t) / \partial E_r(t)$). Our model of competition differs slightly from

the one in Kuang and Chesson (2010), and we find that

$$C'_i = \sum_{r \neq i} \frac{\partial C(t)^{\{-i\}}}{\partial E_r(t)} \Big|_{E_j(t) = \ln E[G]} = \frac{\alpha_2 E[G] \sum_{r \neq i} E[N_r^{\{-i\}}]}{\alpha_1 + \alpha_2 E[G] \sum_{r \neq i} E[N_r^{\{-i\}}]} . \quad (83)$$

We show below that ΔN_i and ΔI_{Pi} are $o(\sigma^2)$, and thus ≈ 0 , when P and σ^2 are small. With these simplifications, the invader growth rate will take on the forms presented in equations (9), (12), and (16). Additionally, our equations for invader growth which consider community-average values, equation (10) and (18), can be calculated by determining the species average mean values of each mechanism and rearranging (76).

C.3 The effect of optimally foraging predators

In this section, we will present our novel results by determining ΔP_i , ΔN_i , and ΔI_{Pi} for an optimally foraging predator.

C.3.1 ΔP_i due to optimally foraging predations

Simulations suggest that under the size assumptions described in C.1, the predator's diet range will not change between years for most parameter sets (Appendix F, Fig. F.3).

Rather, the predator will consume a set number of species throughout the year, every year. Below, we will show under this scenario, ΔP_i will not be affected by environmental variation. In Appendix F, we show using simulations that even under less restrictive cases, environmental variation tends to have little effect on ΔP_i .

We will assume that the predator consumes species 1 through m throughout the year (i.e., $p_j(u) = 1$ for all u for $j \leq m$ and $p_j(u) = 0$ for all $j > m$). Under this case, $A_1(t)^{\{-i\}} = \dots = A_m(t)^{\{-i\}}$ and $A_{m+1}(t)^{\{-i\}} = \dots = A_n(t)^{\{-i\}} = 0$. Thus,

$$\Delta P_i = \begin{cases} \frac{m\beta}{n-1} E[A_1(t)^{\{-i\}}] & i > m \\ -\frac{\beta(n-m-2)}{n-1} E[A_1(t)^{\{-i\}}] & i \leq m \end{cases}. \quad (84)$$

Because $A_r(t)$ is a nonlinear function of $E_r(t)$, $E[A_1(t)^{\{-i\}}]$ will be affected by variation in $E_r(t)$. However, as we will show, these effects are $o(\sigma^2)$, and thus can be ignored.

The term $A_1(t)^{\{-i\}}$ can be approximated using a Taylor series around the point $E_r(t) = \ln E[G]$ for all r ,

$$\begin{aligned} A_1(t)^{\{-i\}} &\approx A_1(t)^{\{-i\}} \Big|_{E_j(t)=\ln E[G]} + \\ &\sum_{j=1}^m \left((E_j(t) - \ln E[G]) \frac{\partial A_1(t)^{\{-i\}}}{\partial E_j(t)} + \frac{1}{2} \sum_{k=1}^m (E_j(t) - \ln E[G]) (E_k(t) - \ln E[G]) \frac{\partial^2 A_1(t)^{\{-i\}}}{\partial E_j(t) \partial E_k(t)} \right) \end{aligned} \quad (85)$$

Because $\ln E[G] \neq E[\ln G]$, the mean value of $E_j(t) - \ln E[G]$ is $-\sigma^2/2$ rather than 0. The mean of $(E_j(t) - \ln E[G])^2 \approx \text{var}(E_j(t)) = \sigma^2$, and the mean of $(E_j(t) - \ln E[G])(E_k(t) - \ln E[G]) \approx \text{cov}(E_j(t), E_k(t)) = \rho\sigma^2$. Thus, we can approximate $E[A_1(t)]$ as

$$\begin{aligned} E[A_1(t)^{\{-i\}}] &\approx A_1(t)^{\{-i\}} \Big|_{E_j(t)=\ln E[G]} + \\ &\sum_{j=1}^m \left(\left(-\frac{\sigma^2}{2} \right) \frac{\partial A_1(t)^{\{-i\}}}{\partial E_j(t)} + \frac{\sigma^2}{2} \frac{\partial^2 A_1(t)}{\partial E_j(t)^2} + \sum_{k \neq j} \frac{\rho\sigma^2}{2} \frac{\partial^2 A_1(t)}{\partial E_j(t) \partial E_k(t)} \right) \end{aligned} \quad (86)$$

We will next show all but term $A_1(t)^{\{-i\}}$ are $o(\sigma^2)$.

First, consider $\partial A_1(t)^{\{-i\}} / \partial E_r(t)$. The term $A_1(t)$, defined in (32), can be rewritten as

$$A_1(t) = \ln \left(\sum_{r=1}^m b_r(0) \right) + \ln(ah) - \ln \left(W \left(\sum_{r=1}^m b_r(0) a h e^{\sum_{r=1}^m b_r(0) a h - a P} \right) \right). \quad (87)$$

By the chain rule, the derivative simplifies to

$$\frac{\partial A_1(t)}{\partial E_r(t)} = \frac{\alpha_1}{\alpha_1 + \alpha_2 E[G] \sum_{k=1}^n E[N_k]} \frac{b_r(0)}{\sum_{k=1}^n b_k(0)} \left(1 - \frac{1 + ah \sum b_r(0)}{1 + W \left(\sum b_r(0) a h e^{\sum b_r(0) ah - aP} \right)} \right). \quad (88)$$

Because $W \left(\sum b_r(0) a h e^{\sum b_r(0) ah - aP} \right) / ah$ is the number of seeds that remain at the end of the year (equation (31)), this can be simplified to

$$\frac{\partial A_1(t)}{\partial E_r(t)} = \frac{\alpha_1}{\alpha_1 + \alpha_2 E[E[N_k]] \sum E[N_k]} \frac{b_r(0)}{\sum b_r(0)} \left(1 - \frac{1 + ah \sum b_r(0)}{1 + ah \sum b_r(1)} \right). \quad (89)$$

With some algebraic manipulation, this becomes

$$\frac{\partial A_1(t)^{\{-i\}}}{\partial E_j(t)} = \left[\frac{\alpha_1}{\alpha_1 + \alpha_2 E[G] \sum_{k=1}^m E[N_k]} \frac{b_j(0)}{\sum_{k=1}^m b_k(0)} \left(\frac{ah \left[\left(\sum_{k=1}^m b_k(1) \right) - \left(\sum_{k=1}^m b_k(0) \right) \right]}{1 + ah \left(\sum_{k=1}^m b_k(1) \right)} \right) \right]^{\{-i\}}. \quad (90)$$

We will now show that $ah[\sum b_m(1) - \sum b_m(0)]/[1 + ah \sum b_m(1)]^{\{-i\}}$ is $O(\sigma^2)$, and therefore $\partial A_1(t)^{\{-i\}}/\partial E_r(t)$ is $O(\sigma^2)$. Because the risk of predation on all species is the same for species 1 through m ,

$$\ln \left(\frac{b_1(0)}{b_1(1)} \right) = \ln \left(\frac{\sum_{j=1}^m b_m(0)}{\sum_{j=1}^m b_m(1)} \right). \quad (91)$$

Thus, $A_1(t)^{\{-i\}} = \ln [\sum b_m(0)/\sum b_m(1)]^{\{-i\}}$. However, because $A_1(t)^{\{-i\}} = O(\sigma^2)$, we can use the approximation

$$\begin{aligned} A_1(t)^{\{-i\}} &\approx \frac{\sum b_r(0)}{\sum b_r(1)} - 1 \\ &= \left[\frac{\sum b_r(0) - \sum b_r(1)}{\sum b_r(1)} \right]^{\{-i\}} > \left[\frac{c_1 (\sum b_r(0) - \sum b_r(1))}{c_2 + c_1 \sum b_r(1)} \right]^{\{-i\}} \end{aligned} \quad (92)$$

for any $c_1, c_2 > 0$. Thus, $\partial A_1(t)^{\{-i\}}/\partial E_r(t)$ is $O(\sigma^2)$, and $(-\sigma^2/2)(\partial A_1(t)^{\{-i\}}/\partial E_r(t)) = O(\sigma^4)$.

Next, we calculate $\partial^2 A_1(t)^{\{-i\}}/\partial E_r(t)^2$. With a great deal of algebraic manipulation, we see that it is

$$\begin{aligned} \frac{\partial^2 A_1(t)^{\{-i\}}}{\partial E_r(t)^2} = & \left[\frac{\partial}{\partial E_j(t)} \left(\frac{\alpha_1}{\alpha_1 + \alpha_2 E[G] \sum_{k=1}^m E[N_k]} \frac{b_j(0)}{\sum_{k=1}^m b_k(0)} \right) \right] \left[\frac{ah \left[\left(\sum_{k=1}^m b_k(1) \right) - \left(\sum_{k=1}^m b_k(0) \right) \right]}{1 + ah \left(\sum_{k=1}^m b_k(1) \right)} \right] + \\ & \left(\frac{\alpha_1}{\alpha_1 + \alpha_2 E[G] \sum_{k=1}^m E[N_k]} \frac{b_j(0)}{\sum_{k=1}^m b_k(0)} \right)^2 \left[\frac{ah \left[1 + ah \sum_{k=1}^m b_k(0) \right]^2 \frac{\sum_{k=1}^m b_k(1)}{\sum_{k=1}^m b_k(0)} - ah \left[1 + ah \sum_{k=1}^m b_k(1) \right]^2}{\left[1 + ah \sum_{k=1}^m b_k(1) \right]^3} \right]. \quad (93) \end{aligned}$$

Though complex, the first term is proportional to $(\sum b_k(1) - \sum b_k(0))/(1 + ah \sum b_k(1))$, which is $O(\sigma^2)$, and the second term is approximately proportional to $-(\sum b_k(1) - \sum b_k(0))^2/(1 + ah \sum b_k(1))^3$, which is also $O(\sigma^2)$. Thus, $(\sigma^2/2)(\partial^2 A_1(t)^{\{-i\}}/\partial E_j(t)^2) = O(\sigma^4)$. Similarly, $\partial^2 A_1(t)^{\{-i\}}/\partial E_j(t)\partial E_k(t)$ will be $O(\sigma^4)$.

Thus, we are left with $E[A_1(t)^{\{-i\}}] \approx A_1(t)^{\{-i\}} \Big|_{E_r(t)=E[G]}$, and we conclude that

variation in $E_j(t)$ has little effect on ΔP_i when P and σ^2 are small.

C.3.2 ΔN_i due to optimally foraging predations

By the rules of probability theory,

$$\text{var}(D_j(t)) = \text{var}(A_j(t) + C(t)) = \text{var}(A_j(t)) + \text{var}(C(t)) + 2 \text{cov}(A_j(t), C(t)). \quad (94)$$

Substituting this into our approximation of ΔN_i , equation (78),

$$\Delta N_i \approx \frac{(1-\beta)}{2} \left(\text{var}(A_i(t)^{\{-i\}}) + \text{var}(C(t)^{\{-i\}}) + 2 \text{cov}(A_i(t)^{\{-i\}}, C(t)^{\{-i\}}) \right) - \frac{(1-\beta)}{2(n-1)} \sum_{r \neq i} \left(\text{var}(A_r(t)^{\{-i\}}) + \text{var}(C(t)^{\{-i\}}) + 2 \text{cov}(A_r(t)^{\{-i\}}, C(t)^{\{-i\}}) \right). \quad (95)$$

To calculate this, we will show that $\text{var}(A_j(t)^{\{-i\}})$ is very small. The rate that seeds are consumed is a decreasing function of h , and an increasing function of $p_j(t)$. When $h = 0$, and $p_j(u) = 1$ for all u , then the predators have a Type I functional response, and each seed has a probability $\exp\{-P\}$ of being consumed (Hassell, 2000). Therefore,

$$A_j(t)^{\{-i\}} = -\ln(P(\text{seed survives})) \approx P(\text{seed eaten}) < P. \quad (96)$$

Thus, $A_j(t)^{\{-i\}}$ will be at most $O(P)$, and therefore $O(\sigma^2)$. Since $A_j(t)^{\{-i\}}$ is strictly non-negative,

$$E[A_j(t)^{\{-i\}}]^2 > E[A_j(t)^{\{-i\}} - E[A_j(t)^{\{-i\}}]]^2 = \text{var}(A_j(t)^{\{-i\}}). \quad (97)$$

Therefore, $\text{var}(A_j(t)^{\{-i\}})$ will be at most $O(\sigma^4)$. Since $\text{var}(C(t)^{\{-i\}}) = O(\sigma^2)$, each $\text{cov}(A_j(t)^{\{-i\}}, C(t)^{\{-i\}})$ will be at most $O(\sigma^3)$. Thus, dropping the $o(\sigma^2)$ terms from (95),

$$\Delta N_i \approx \frac{(1-\beta)}{2} \text{var}(C(t)^{\{-i\}}) - \frac{(1-\beta)}{2(n-1)} \sum_{r \neq i} \left(\text{var}(C(t)^{\{-i\}}) \right) = 0. \quad (98)$$

C.3.3 ΔI_{Pi} due to optimally foraging predations

By equations (96) and (97), $\text{var}(A_j(t)^{\{-i\}})$ will be at most $O(\sigma^4)$. Since $\text{var}(E_j(t)^{\{-i\}}) = \sigma^2$, $\text{cov}(E_j(t)^{\{-i\}}, A_k(t)^{\{-i\}})$ will be at most $O(\sigma^3)$ for every j and k . Thus, by our approximation of ΔI_{Pi} , equation (81), ΔI_{Pi} will be at most $O(\sigma^3)$.

Appendix D. Coexistence in a variable environment- Large P assumption

A critical requirement for our analysis is that $E[A_k(t)^{\{-i\}} - A_j(t)^{\{-i\}}]$ is $O(\sigma^2)$. If this assumption is not met, then we have assumed that ΔP_i will much larger than the other terms, and our results will be rather trivial: the factors we assumed are big will be bigger than the factors we assumed are small. In Appendix C, we guaranteed that $E[A_k(t)^{\{-i\}} - A_j(t)^{\{-i\}}]$ is small by assuming that P is $O(\sigma^2)$, and therefore $A_j(t)$ is $O(\sigma^2)$. However, if $A_j(t)^{\{-i\}} = A_k(t)^{\{-i\}}$ for most years, then such an assumption is not necessary. In this section, we relax the assumption that P is $O(\sigma^2)$, and rather assume that e_j values are close enough that $A_j(t) = A_k(t)$ for all j and k , and for most or all t . Our analysis in C.2 will continue to hold, but our analysis in C.3 will not. In section D.1, we outline conditions under which $E[A_k(t)^{\{-i\}} - A_j(t)^{\{-i\}}]$ is $O(\sigma^2)$ even if $A_j(t)$ is $O(1)$. In section D.2, we show that $\Delta N_i \approx 0$. In section D.3, we calculate ΔI_{P_i} , and show that may not be 0.

D.1 Conditions in which $E[A_k(t)^{\{-i\}} - A_j(t)^{\{-i\}}]$ is $O(\sigma^2)$ for large P

The difference in predation risk between any two species, $A_j(t) - A_{j+k}(t)$, can be expressed as

$$A_j(t) - A_{j+k}(t) = (A_j(t) - A_{j+1}(t)) + (A_{j+1}(t) - A_{j+2}(t)) + \dots + (A_{j+k-1}(t) - A_{j+k}(t)). \quad (99)$$

Thus, we will focus for now on $A_j(t) - A_{j+1}(t)$, and use it later to construct $A_j(t) - A_{j+k}(t)$.

If a predator consumes both species j and $j+1$ during the year,

$$A_j(t) - A_{j+1}(t) = \max\left(0, \ln(\tilde{b}_j + b_j(0)) - \ln \tilde{b}_{j+1}\right). \quad (100)$$

Here, $\tilde{b}_j$, the critical switching density for species j , is the number of seeds $b_1(u) + b_2(u) + \dots + b_{j-1}(u)$ at the time u that a predator adds species j to its diet. Thus, using a Taylor series approximation,

$$A_j(t) - A_{j+1}(t) \approx \max \left(0, \ln \left(\tilde{b}_j + b_j(0) \right) \Big|_{E_r(t)=\ln E[G]} - \ln \tilde{b}_{j+1} \Big|_{E_r(t)=\ln E[G]} + \tau_j(t) \right), \quad (101)$$

where $\tau_j(t)$ is the deviation from average conditions

$$\tau_j(t) = \sum_{k=1}^n \left(E_k(t) - \ln E[G] \right) \left(\frac{\partial b_j(0)}{\partial E_k(t)} + \frac{\partial \tilde{b}_j}{\partial E_k(t)} + \frac{\partial \tilde{b}_{j+1}}{\partial E_k(t)} \right) \Big|_{E_r(t)=\ln E[G]}. \quad (102)$$

By examining equation (3), it is easy to see that $\partial b_j(t)/\partial E_k(t)$ will generally be $O(1)$, and thus term $\tau_j(t)$ will vary by an amount $O(\sigma)$. Thus, the term $E[A_j(t) - A_{j+1}(t)]$ will be $O(\sigma)$, and our assumption will be violated, unless $A_j(t) - A_{j+1}(t) = 0$ for all but a proportion $O(\sigma)$ of years. For our calculations below, we will define p_{dif} as the proportion of years that the predator differentiates its prey (i.e., $A_j(t) \neq A_{j+1}(t)$), and assume that p_{dif} is $O(\sigma)$ or smaller. Our analysis below includes the special case of $p_{dif} = 0$, i.e., the predator consumes all species throughout every year.

D.2 Relative nonlinearity for large P

To calculate ΔN_i , we must calculate the variance of $C(t)^{\{-i\}} + A_j(t)^{\{-i\}}$. By making the

substitution $A_j(t) = A_1(t) - \sum_{k=1}^{j-1} (A_k(t) - A_{k+1}(t))$, we see that

$$\begin{aligned} \text{var} \left(A_1(t) - \sum_{k=1}^{j-1} (A_k(t) - A_{k+1}(t)) + C(t) \right) &= \text{var}(A_1(t)) + \text{var}(C(t)) + 2 \text{cov}(A_1(t), C(t)) \\ &+ \sum_{k=1}^{j-1} \text{var}(A_k(t) - A_{k+1}(t)) + \sum_{k=1}^{j-1} \sum_{l \neq k}^{j-1} \text{cov}(A_k(t) - A_{k+1}(t), A_l(t) - A_{l+1}(t)) \\ &- 2 \sum_{k=1}^{j-1} \text{cov}(A_1(t), A_k(t) - A_{k+1}(t)) - 2 \sum_{k=1}^{j-1} \text{cov}(C(t), A_k(t) - A_{k+1}(t)) \end{aligned} \quad (103)$$

To simplify this equation, we need to calculate variance of $A_j(t) - A_{j+1}(t)$. We can write $A_j(t) - A_{j+1}(t)$ as the product of two random variables,

$$A_j(t) - A_{j+1}(t) \approx B(t)\omega(t), \quad (104)$$

where $B(t)$ is a Bernoulli random variable with $\mathbf{P}(B(t)=1) = p_{dif}$, and

$$\omega(t) = \ln\left(\tilde{b}_j + b_j(0)\right)\Big|_{E_r(t)=E_r^*, N_r(t)=E[N_r]} - \ln\tilde{b}_{j+1}\Big|_{E_r(t)=E_r^*, N_r(t)=E[N_r]} + \tau_j(t) \quad (105)$$

In this case,

$$\begin{aligned} \text{var}\left(A_j(t) - A_{j+1}(t)\right) &= \text{var}\left(\omega_j(t)B(t)\right) \\ &= E\left[\omega_j(t)^2 B(t)^2\right] - E\left[\omega_j(t)B(t)\right]^2. \end{aligned} \quad (106)$$

Because $B(t) = 0$ or 1 , $B(t)^2 = B(t)$. Thus,

$$\begin{aligned} E\left[\omega_j(t)^2 B(t)^2\right] &= E\left[\omega_j(t)^2 B(t)\right] \\ &= E\left[\omega_j(t)^2 \mid B(t)=1\right] E[B(t)]. \end{aligned} \quad (107)$$

Because $\omega_j(t)$ is $O(\sigma)$, $E[\omega_j(t)^2 | B(t)=1] = O(\sigma^2)$. Since $B(t)$ is a Bernoulli variable, $E[B(t)] = p_{dif}$, which is at most $O(\sigma)$ by assumption. Thus, $\text{var}[A_j(t) - A_{j+1}(t)]$ is at most $O(\sigma^3)$.

Returning to equation (103), we see that $\text{cov}(A_j(t) + C(t))$ can be greatly simplified. Because each $\text{var}(A_k(t)^{\{-i\}} - A_{k+1}(t)^{\{-i\}})$ term is at most $O(\sigma^3)$, and $\text{var}(C(t)^{\{-i\}})$ and $\text{var}(A_j(t)^{\{-i\}})$ are $O(\sigma^2)$, we see that

$$\begin{aligned} \text{cov}\left(A_k(t)^{\{-i\}} - A_{k+1}(t)^{\{-i\}}, C(t)^{\{-i\}}\right) &\leq O(\sigma^{2.5}) \\ \text{cov}\left(A_k(t)^{\{-i\}} - A_{k+1}(t)^{\{-i\}}, A_l(t)^{\{-i\}}\right) &\leq O(\sigma^{2.5}) \\ \text{cov}\left(A_k(t)^{\{-i\}} - A_{k+1}(t)^{\{-i\}}, A_l(t)^{\{-i\}} - A_{l+1}(t)^{\{-i\}}\right) &\leq O(\sigma^3) \end{aligned} \quad (108)$$

Thus, dropping the $o(\sigma^2)$ terms from equation (103), we are left with

$$\text{var}\left(A_j(t)^{\{-i\}} + C(t)^{\{-i\}}\right) \approx \text{var}\left(A_l(t)^{\{-i\}}\right) + \text{var}\left(C(t)^{\{-i\}}\right) + 2\text{cov}\left(A_l(t)^{\{-i\}}, C(t)^{\{-i\}}\right). \quad (109)$$

This term will be identical between species, and thus $\Delta N_i \approx 0$.

D.3 The storage effect from predation

Next we calculate ΔI_{Pi} . To calculate $\text{cov}(A_j(t), E_j(t))$, we again use the substitution

$$A_j(t) = A_1(t) - \sum_{k=1}^{j-1} (A_k(t) - A_{k+1}(t)), \text{ and find}$$

$$\text{cov}(A_j(t), E_j(t)) = \text{cov}(A_1(t), E_j(t)) - \sum_{k=1}^{j-1} \text{cov}(A_k(t) - A_{k+1}(t), E_j(t)). \quad (110)$$

However, since $\text{var}(E_j(t)) = \sigma^2$ and each $\text{var}(A_k(t)^{\{-i\}} - A_{k+1}(t)^{\{-i\}})$ is at most $O(\sigma^3)$,

$$\text{cov}(A_k(t) - A_{k+1}(t), E_j(t)) \leq O(\sigma^{2.5}). \quad (111)$$

Thus, (110) can be approximated as

$$\text{cov}(A_j(t), E_j(t)) \approx \text{cov}(A_1(t), E_j(t)), \quad (112)$$

and, by equation (81), the storage effect from predation can be approximated as

$$\Delta I_{Pi} \approx s \left[\left(\frac{1}{n-1} \sum_{r \neq i} \text{cov}(E_r(t), A_1(t)^{\{-i\}}) \right) - \text{cov}(E_i(t), A_1(t)^{\{-i\}}) \right]. \quad (113)$$

As shown in Chesson and Kuang (2010),

$$\Delta I_{Pi} \approx \frac{s\sigma^2(1-\rho)}{n-1} \sum_{r \neq i} \frac{\partial A_1(t)^{\{-i\}}}{\partial E_r(t)}. \quad (114)$$

By our derivation of $\partial A_1(t)/\partial E_r(t)$, equation (89), ΔI_{Pi} can be approximated as

$$\begin{aligned} \Delta I_{Pi} &\approx \frac{s\sigma^2(1-\rho)}{n-1} \frac{\alpha_1}{\alpha_1 + \alpha_2 E[G] \sum_{k=1}^n E[N_r^{\{-i\}}]} \left(1 - \frac{1 + ah \sum b_r(0)}{1 + ah \sum b_r(1)} \right)^{\{-i\}} \\ &= \frac{s\sigma^2(1-\rho)}{n-1} (1 - C'_i) \left(1 - \frac{1 + ah \sum b_r(0)}{1 + ah \sum b_r(1)} \right)^{\{-i\}}, \quad (115) \\ &= \frac{s\sigma^2(1-\rho) A'_i}{n-1} \end{aligned}$$

where C'_i is defined in (83), and A'_i is given in the main text as in (25).

Appendix E. Alternative form of competition

In this section, we derive a different form of resource competition, and show that its results are qualitatively similar. Our main model of competition, equation (2), assumed that each germinating seed captured $1/(\alpha_1 + \alpha_2 \sum N_j(t) G_j(t))$ resources, and then converted each unit of resource into Y_j seeds, where Y_j is a species-specific quantity. A species was thus a stronger competitor if it could more efficiently turn resources into seeds. As an alternative, in this appendix we assume that each germinating seed captures $V_j/(\alpha_1 + \alpha_2 \sum V_j N_j(t) G_j(t))$ resources, where V_j is a species-specific competitive vigor, and then converts each unit of resource into Y seeds. In this case, a stronger competitor can take up resources more effectively. Thus, our formula for competition is now

$$\tilde{C}(t) = \ln \left\{ \alpha_1 + \alpha_2 \sum_{j=1}^n V_j G_j(t) N_j(t) \right\}, \quad (116)$$

and the yearly finite rate of increase is

$$\lambda_j(t) = (1 - G_j(t))s + YV_j G_j(t) e^{-\tilde{C}(t) - A_j(t)}. \quad (117)$$

We write $\tilde{C}(t)$ to distinguish this formula for competition from $C(t)$ in equation (2).

Analogous to before (Appendix B), when variation in germination is absent, species i will be able to invade if

$$\begin{aligned} \lambda_i &= (1 - G)s + YV_i G e^{-\tilde{C}^* - A_i^*} > 1 \\ \lambda_r &= (1 - G)s + YV_r G e^{-\tilde{C}^* - A_r^*} = 1 \quad \forall r \neq i \end{aligned}, \quad (118)$$

where $\tilde{C}^*$ is the value of $\tilde{C}$ when the residents are at equilibrium. Combining these, we see that a species can invade if

$$\ln V_i + (A_r^{*\{-i\}} - A_i^{*\{-i\}}) > \ln V_r. \quad (119)$$

Thus, this result is exactly analogous to equation (43), except that V_j now determines the relative competitive ability.

Next, we consider the variable environment case. We will need to assume that $\ln\{V_j\}$ and $\ln\{V_k\}$ will differ by at most $O(\sigma^2)$ (equivalent to our previous assumptions that Y_j values were similar). Our approximation of the invader growth rate in section C.2 will follow identically, and will result in an invader growth rate of

$$\frac{\bar{r}_i}{\beta} \approx \left(\ln \left(\frac{E[G]V_i Y}{1-s(1-E[G])} \right) - \frac{1}{n-1} \sum_{r \neq i} \ln \left(\frac{E[G]V_r Y}{1-s(1-E[G])} \right) \right) + \Delta E_i - \Delta N_i + \Delta P_i + \Delta I_{Ci} + \Delta I_{Pi} \quad (120)$$

The definition of each Δ term will not change, except that they will now include $\tilde{C}(t)$.

The mean fitness difference term is now

$$\mu_i - \bar{\mu} = \ln V_i - \frac{1}{n-1} \sum_{r \neq i} \ln V_r \quad (121)$$

The storage effects will show a few quantitative differences, though be qualitatively similar. First, we can again use the Taylor series to approximate the storage effect from competition as

$$\Delta I_{Ci} \approx s \frac{\sigma^2 (1-\rho) \tilde{C}'_i}{n-1} \quad (122)$$

The sensitivity of competition to germination is now

$$\tilde{C}'_i = \sum_{r \neq i} \left. \frac{\partial \tilde{C}'(t)^{\{-i\}}}{\partial E_r(t)} \right|_{E_j(t)=\ln \bar{G}} = \frac{\alpha_2 E[G] \sum_{r \neq i} V_r E[N_r^{\{-i\}}]}{\alpha_1 + \alpha_2 E[G] \sum_{r \neq i} V_r E[N_r^{\{-i\}}]} \quad (123)$$

This will differ slightly between species; however, differences in V_j will only be $O(\sigma^2)$, and thus will only affect ΔI_{Ci} by $O(\sigma^4)$. We can simplify this term to

$$\tilde{C}'_i \approx \frac{\alpha_2 E[G] \bar{V} \sum_{r \neq i} E[N_r^{\{-i\}}]}{\alpha_1 + \alpha_2 E[G] \bar{V} \sum_{r \neq i} E[N_r^{\{-i\}}]} \quad (124)$$

where $\bar{V}$ is the mean of V_j across all species, with little effect. Thus, the main effect of V_j is simply that it rescales α_2 . Therefore, under this new form of competition, the results are qualitatively identical and quantitatively similar. Similarly, we can show that $\Delta I_{P_i} \approx 0$ when P is $O(\sigma^2)$, and can be defined by equation (24) when P is $O(1)$, where the sensitivity of apparent competition to germination is now

$$A'_i = (1 - \tilde{C}'_i) \left(1 - \frac{1 + ha \sum b_r(0)}{1 + ha \sum b_r(1)} \Big|_{G_r(t)=E[G]} \right)^{\{-i\}}. \quad (125)$$

We can similarly show that ΔP_i will not be affected by variation in $G_f(t)$, and that $\Delta N_i \approx 0$. It is possible that the new form of competition may alter the mechanisms through changes in average density; however, this suggests that any differences will be quantitative, rather than qualitative.

In conclusion, we find that our qualitative results do not change when we introduce a different form of competition. This is in accordance with the general theory (Chesson 1994, 2003). There is no reason think that the analyses in here are overly dependent on the form of competition.

Appendix F. Computer simulations

We ran computer simulations to back up the following claims that we could not prove analytically:

- 1) More than three species can coexist in a stable environment.
- 2) Our approximations hold, even under moderate σ^2 and $E[A_r(t) - A_i(t)]$, large P , and between-year changes in diet range.

F.1 Multi-species coexistence in a stable environment

To determine whether more than three species could coexist in a stable environment, we ran computer simulations that successively added species to the community. We seeded our community with two coexisting species. We then added an additional species with yield $Y_3 = 0.8Y_2$, and determined the range of e_3 values that would allow it coexist with species 1 and 2. e_3 was set to the midpoint of those possible values. Then, this process was repeated with $Y_4 = 0.8Y_3$, then again with $Y_5 = 0.8Y_4$, and so on.

We have been able to construct communities in which many species are able to coexist. For example, Fig. F.1 shows a community with four coexisting species. We have been able to construct a community with nine coexisting species, and conjecture that optimal foragers can allow an arbitrary number of species to coexist. However, we found that when the number of species was high, there was an extremely narrow band of Y_j and e_j values that would allow species j to persist without outcompeting other species.

Unfortunately, in many cases, the loss of one member of the community causes other species to go extinct. This occurs because the risk of predation, A_j^* , is a complicated function of N_j and e_j values. As a result, $A_j^{*\{-k\}} \neq A_j^{*\{-l\}}$. To see an example of this, consider Fig. F.1A. When species 1 is removed from the system, species 3's population crashes, and cannot reestablish itself until species 1 has become established.

F.2 Moderate variation in $E_j(t)$ and $E[A_r(t) - A_i(t)]$

We ran a large number of simulations to test how well our approximations held up at moderate to large values of σ^2 and $E[A_r(t) - A_i(t)]$. For each simulation, we calculated $E[r_i]$ using the last 250 years of a 500 year simulation, and then using our approximations

for ΔI_i and ΔP_i . Our simulations were done in a community with two prey species. Each simulation was repeated 3 times, and the mean was recorded. Additionally, we estimated Y_2^* , the value of Y_2 that would allow $E[r_i]$ to equal 0, both according to simulations and according to our approximations.

For our analysis, we varied parameters as listed in Table F.1. Parameters were chosen using Latin hypercube sampling (McKay et al., 1979). In some cases, the predators were so numerous and effective that a viable resident population could not be maintained; in these cases, the simulation results were discarded. Overall, we used 150 parameter sets (74 after discarding resident extinctions).

The value Y_2^* acts as a bifurcation point, since coexistence will occur when $Y_2 > Y_2^*$, and competitive exclusion will occur when $Y_2 < Y_2^*$. To calculate Y_2^* , we reran simulations with varying Y_2 values until $|E[r_i]| < 0.01$. To estimate Y_2^* using our approximations, we used the formula

$$\ln Y_2^* = \ln Y_1 - \frac{1}{\beta} (\Delta I_C + \Delta I_P + \Delta P) ; \quad (126)$$

When predators consume the invader during some or all years, we approximate this using,

$$\ln Y_2^* = \ln Y_1 - s\sigma^2(1-\rho)(C' + A') - (A_r(t) - A_i(t)) \Big|_{E_r(t)=\ln E[G], N_r(t)=E[N_r]} , \quad (127)$$

and when the predators consume only the resident, we approximate this as

$$\ln Y_2^* = \ln Y_1 - s\sigma^2(1-\rho)(C') - (A_r(t)) \Big|_{E_r(t)=\ln E[G], N_r(t)=E[N_r]} . \quad (128)$$

Overall, we found that our approximations worked extremely well over a wide range of parameters (Fig. F.2). Both of our estimates had a correlation of greater than 0.99 with their simulated values. Our estimate value of $E[r_i]$, based on approximations,

was on average within 0.01 of the value of $E[r_i]$ estimated from simulations (Fig. F.2A). Similarly, our estimated values of Y_2^* based on approximations were on average within 1% of the value estimated from simulations (Fig. F.2B). Thus, we conclude that our approximations held under a wide range of parameters.

Additionally, using computer simulations, we investigated whether our approximations held when predators changed their host-range between years (i.e., sometimes they did not consume the invader, sometimes they consumed the invader for part of the year, and sometimes they consumed the invader throughout the year).

We chose several parameter sets, and calculated ΔI_i and ΔP_i when species 2 was an invader. For each parameter set, we varied e_2 over a large range. Large e_2 tended to cause the predators to consume both species, and small e_2 tended to cause the predators to act as specialist on the resident. The storage effect from predation was calculated as

$$\Delta I_{P_i} = s \text{cov}\left(A_r(t)^{\{-i\}}, E_r(t)\right) - s \text{cov}\left(A_i(t)^{\{-i\}}, E_i(t)\right), \quad (129)$$

and the mean difference in predation was calculated as

$$\Delta P_i = E\left[A_r(t)^{\{-i\}}\right] - E\left[A_i(t)^{\{-i\}}\right], \quad (130)$$

using the actual values of $A_j(t)^{\{-i\}}$ and $E_j(t)$ during the last 300 years in a 500 year simulation.

Overall, we found that ΔI_{P_i} and ΔP_i varied fairly continuously with e_2 . Figure F.3 represents a typical result. In all of our simulations, ΔI_{P_i} was relatively unaffected by e_2 , and was dwarfed by ΔP_i when the consumed species at different levels.

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Table 1.
Variables used.

Symbol	Definition
$G_j(t)$	Germination rate of species j in year t .
$E_j(t)$	The environmental response of species j in year t , $E_j(t) = \ln G_j(t)$.
s	Seed survival of ungerminated seeds.
Y_j	The seed yield of species j .
$C(t)$	The effect of resource competition in year t , $C(t) = \ln \left(\alpha_1 + \alpha_2 \sum_{j=1}^n G_j(t) N_j(t) \right).$
A_1, α_2	Competition parameters for determining $C(t)$.
$N_j(t)$	The number of seeds of species j at time t .
$A_j(t)$	The effect of apparent competition on species j in year t , $A_j(t) = \ln(b_j(0)/b_j(1))$.
$b_j(u)$	The number of seeds of species j at time u of the vulnerable period (e.g., $b_j(0)$ is the number of seeds produced, $b_j(1)$ is the number entering the seed bank).
u	Within-year time, i.e., the time during which seeds are exposed to predators.
a	The predator's attack rate.
P	The number of predators.
h	The handling time of each seed.
$p_j(u)$	The probability that a predator will consume a species j seed if it encounters it. Under optimal foraging theory, this will be 0 or 1.
e_j	The caloric content of a seed of species j .
$\tilde{b}_j$	The critical switching density. If there are $\tilde{b}_j$ or fewer seeds of species 1 through $j - 1$, the predator will consume species j .
$\tilde{u}_j$	The time of the year when the predator begins consuming species j .
$\overline{e_{j \square}}$	The density-weighted mean caloric content for species 1 through $j - 1$.
$\lambda_j(t)$	The population level finite rate of increase of species j at time t .
$r_j(t)$	The population level growth rate of species j , $r_j(t) = \ln \lambda_j(t)$.
σ^2	The variance of $E_j(t)$.
ρ	The correlation between $E_j(t)$ and $E_k(t)$ for $j \neq k$.
β	The fraction of seeds lost from the seed bank each year, $\beta = 1 - s(1 - E[G])$.
μ_j	The contribution of competitive ability to species j 's fitness, $\mu_j = \ln Y_j$.
C_i'	The amount that a change in resident germination changes the level of resource competition when species I is an invader.
$E[X]$	The average of X across time.
r_i^i $\{-i\}$	Subscripts to indicate resident and invader species, respectively. Superscript to indicate that species i has been removed from the community.

Table F.1.

Values used for randomization tests.

Variable	Minimum	Maximum	Distribution
seed survival, s	0.1	0.8	uniform
resident yield, Y_1	30	150	uniform
yield difference, Y_2/Y_1	0.6	1.0	uniform
competition parameter, α_1	10^{-4}	1	exponential
competition parameter, α_2	10^{-1}	$10^{1.5}$	exponential
correlation for germination	-0.8	0.8	uniform
variance for germination	0.01	0.6	uniform
mean for calculating germination	-1	1.5	uniform
encounter rate, a	0.1	0.7	uniform
predator density, P	3	30	uniform
handling time, h	0.05	0.4	uniform
relative energy in seeds, e_2/e_1	0.01	1	uniform

Our analysis of variation in $N_r(t)$ did not consider difference in yield (Y_2/Y_1), because this would not affect the results. Germination rates, $G_j(t)$, were calculated using a Johnson's distribution (i.e., $e^X/(1+e^X)$, where X is a normal random variable); values for the mean, variance and correlation in germination listed below are for X , rather than the mean or variance of $E_j(t)$ or the correlation between $E_1(t)$ and $E_2(t)$.

Fig. 1. *Strength of competition and predation in a community with three species at equilibrium.* Here we show the results of an invasion analysis, to show that three species are coexisting stably. We display the combined effect of resource competition, C^* , and apparent competition, A_j^* , that each species experiences for each resident-invader combination. In each case, A_j^* is reduced relative to its competitors when species j is an invader, and the amount it is reduced is equal to species j 's invader growth rate. Each species has a lower total amount of density-dependence ($A_j^* + C^*$) as an invader, and this drop allows them to have a positive growth rate as an invader. The grey region is labeled “growth” because the invader’s growth rate will be that value times the scaling factor β . Because each species has a positive invader growth rate, the species coexist. In all simulations, $s = 0.5$, $Y_1 = 150$, $Y_2 = 120$, $Y_3 = 60$, $e_1 = 1$, $e_2 = 0.55$, $e_3 = 0.45$, $h = 0.1$, $\alpha_1 = 0$, $\alpha_2 = 0.1$, $a = 0.1$, $P = 110$, $G_j = 0.5$, and $\sigma^2 = 0$.

Fig. 2. *Coexistence region without environmental variation.* (A) We determine what combination of yield (Y_2) and seed energy (e_2) values for species 2 will allow two species to coexist. ΔP_2 (the amount that species 2 is consumed less than species 1) is an increasing function of e_2 ; thus, species 2 can invader under a wider range of Y_2 values when e_2 is small. In this simulation, $s = 0.5$, $Y_1 = 100$, $e_1 = 1$, $h = 0.05$, $\alpha_1 = 0$, $\alpha_2 = 0.3$, $a = 0.25$, $P = 12$, $G_j = 0.5$, and $\sigma^2 = 0$. (B) We determine what combination of Y_3 and e_3 values allow three species to coexist. In this simulation, $s = 0.5$, $Y_1 = 100$, $Y_2 = 85$, $e_1 = 1$, $e_2 = 0.7$, $h = 0.05$, $\alpha_1 = 0$, $\alpha_2 = 0.3$, $a = 0.25$, $P = 12$, $G_j = 0.5$, and $\sigma^2 = 0$.

Fig. 3. *Effect of variation in germination on the difference in predation, ΔP_i .* We simulated coexistence in communities using randomly generated parameters (Appendix F). We calculated the average difference in predation risk, $E[A_r(t) - A_i(t)]$, using the last 250 years in a 500 year simulation (ΔP - with variation), and compared this to $A_r(t) - A_i(t)$ calculated when species density, $N_r(t)$, and seed germination, $G_r(t)$, were fixed at there average value (ΔP - no variation). Each dot represents a simulation, and the one-to-one line shows where the no-variation approximation is exactly correct. Because most dots are very close to the one-to-one line, this shows that variation in germination has little effect on ΔP_i , at least for the parameter values considered.

Fig. 4. *The storage effect from competition promotes coexistence.* We determine what combination of seed yield (Y_2) and seed energy (e_2) values for species 2 will allow two species to coexist, with (solid line) and without (dashed line) variation in germination. Here, a competition-predation trade-off will not occur if $e_2 > 0.86$ (since the predator will consume both species) or if $Y_2 > 100$ (since then species 2 is the stronger competitor). In this simulation, $s = 0.5$, $Y_1 = 100$, $e_1 = 1$, $h = 0.05$, $\alpha_1 = 1$, $\alpha_2 = 0.2$, $a = 0.25$, $P = 3$. Germination rates were generated from a Johnson's distribution using $N(-0.1, 0.2)$ random variables with correlation of 0, such that $E[G] \approx 0.48$, $\sigma^2 \approx 0.06$, and $\rho \approx 0$. In the constant environment, coexistence regions could be calculated exactly. In the variable environment, invader growth rates varied due to the stochastic nature of the simulation, and the coexistence regions were determined by taking the average of multiple simulations.

Fig. F.1. *Mutual invasibility in a four species community.* Each community was seeded with 10 individuals of each resident, and no invaders. At time $t = 200$, the invader's density, N_i , was set to 10^{-5} , and allowed to grow naturally from there. Any resident populations that had fallen below 10^{-5} were also set to 10^{-5} at $t = 200$. Simulations were run with the following parameters: $s = 0.5$, $Y_1 = 150$, $Y_2 = 90$, $Y_3 = 45$, $Y_4 = 21$, $e_1 = 1$, $e_2 = 0.6$, $e_3 = 0.5$, $e_4 = 0.4$, $\alpha_1 = 0$, $\alpha_2 = 0.1$, $a = 0.1$, $h = 0.1$, $P = 100$, $G = 0.5$, $\sigma^2 = 0$.

Fig. F.2. *Simulation results for the quality of approximations when effect sizes are large.* We simulated coexistence in 74 communities with randomly generated parameters (Table F.1). Each point is the mean value of three simulations, and the dotted line is when the approximations were exactly correct. (A) We calculated the invader growth rate, $E[r_i]$, based on the mean of $r_i(t)$ over 250 years of simulation, and compared this to $E[r_i]$ calculated using our approximations. (B) We estimated Y_2^* , the value of Y_2 needed to make $E[r_i] = 0$, using computer simulations, and compared this to Y_2^* estimated using our approximations.

Fig. F.3. *Simulation results when predator diet range could change between years.* In this simulation, the predator consumed only species 1 when $e_2 \leq 0.325$ (where e_2 is species 2's seed energy content), and consumed both every year when $e_2 \geq 0.575$. Simulations were run with the following parameters: $s = 0.5$, $Y_1 = 40$, $Y_2 = 40$, $e_1 = 1$, $\alpha_1 = 1$, $\alpha_2 = 0.1$, $a = 0.1$, $h = 0.1$, $P = 7$, $E[G] = 0.41$, $\sigma^2 = 0.14$, $\rho = -0.5$. Germination rates were generated from a Johnson's distribution using $N(-0.4, 0.4)$ random variables, with correlation -0.5. This figure represents a typical result.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. F.1

Sp. 3 invades

Sp. 4 invades

Fig. F.2

Fig. F.3