1
2 **The relative importance of relative nonlinearity and the storage effect in the**
3 **lottery model**

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Abstract

Although it is likely that many coexistence mechanisms contribute to maintenance of species diversity, most approaches to understanding species coexistence proceed as if only one mechanism would be present. In studies of species coexistence in a temporally fluctuating environment, the storage effect, believed to be the most important coexistence mechanism, has been the focus. Although a different coexistence mechanism—relative nonlinearity—is also predicted to arise frequently with environmental variation, its effect has been overshadowed by the storage effect. The relatively nonlinear growth rates on which the mechanism depends arise simply from differences in life history traits. Many kinds of temporal variation can then interact with these nonlinearity differences to create the relative nonlinearity coexistence mechanism. Much is unknown about when this mechanism is important and its total neglect is not justified. Here, we use the lottery model to provide a much needed quantitative assessment of the relative and combined effects of relative nonlinearity and the storage effect. Our analysis takes advantage of recently developed techniques for quantifying coexistence mechanisms when multiple mechanisms operate in concert. We find that relative nonlinearity is able to contribute substantially to species coexistence in the lottery model when two conditions are satisfied: (1) species must differ greatly in their adult death rates, (2) sensitivity of recruitment to environmental variation must be greater for species with larger adult death rates. In addition, relative nonlinearity has a critical role in compensating for a weakened storage effect when there is high correlation between species in their responses to the varying environment. In some circumstances relative nonlinearity is stronger than the storage effect or is even the sole mechanism of coexistence.

1. Introduction

It has often been remarked that in any diverse natural community, multiple mechanisms of coexistence are likely to operate simultaneously (Amarasekare 2007, 2009, Kuang and Chesson 2010). The diversity present is thus not expected to have a single cause, but many approaches to understanding species coexistence both in nature and in models proceed as if only one mechanism would be present. Methods of analyzing systems to understand the separate contributions of different mechanisms, and the interactions between them, are needed both theoretically and empirically. In particular, theoretical studies have not generally had good means of defining and understanding contributions of different mechanisms to the central question of species coexistence. Here we study the lottery model where two general mechanisms of species coexistence can contribute to diversity maintenance, and show how techniques for quantifying species coexistence (Chesson 1989, 1994, 2003, 2008) can disentangle relative and absolute contributions of the different mechanisms when multiple mechanisms are present. These techniques have been applied previously to understand contributions to species coexistence from jointly acting competition-based and predation-based coexistence mechanisms (Chesson and Kuang 2010, Kuang and Chesson 2010). However, in the lottery model we study the contributions of two competition-based coexistence mechanisms. The lottery model provides a simple theoretical example of how stable species coexistence can occur in a fluctuating environment, but the relative and joint contributions of the separate mechanisms have not previously been elucidated. Fluctuating environments have provided challenges to theoretical and empirical understanding while also being proposed from time to time

as the explanation for high diversity in systems with limited opportunities for traditional coexistence mechanisms, such as resource partitioning, to operate (Hutchinson 1961, Grubb 1977, Sale 1977, Levins 1979, Scheffer et al. 2003, Hiltunen et al. 2008).

A unified theoretical approach to coexistence in temporally varying environments has revealed two broad classes of fluctuation-dependent coexistence mechanism, the storage effect, and relative nonlinearity (Chesson and Warner 1981, Chesson 1994, Chesson 2000, Chesson 2008). The storage effect arises from interactions between fluctuations in the physical environment and fluctuations in the intensity of competition. It provides advantages to a species perturbed to low density by allowing the species to escape competition at times when the environment favors it, but does not favor its competitors. The outcome is recovery from low density and hence species coexistence. The mechanism relative nonlinearity is named from the requirement that different species have different nonlinear responses to competition. If competition fluctuates over time, Jensen's inequality (Needham 1993) means that the long-term growth rates, which are time averages of short-term growth rates, will be affected differently for different species (Armstrong and McGehee 1980, Chesson 2000, Kuang and Chesson 2008). Relative nonlinearity promotes coexistence when species drive fluctuations in competition in directions that favor their competitors. The coexistence mechanism thus involves both the relatively nonlinear growth rates and differences between species in their contributions to fluctuations in competition.

Coexistence by relative nonlinearity can result from endogenous fluctuations in population densities (Armstrong and McGehee 1980, Adler 1990, Abrams and Holt 2002, Kuang and Chesson 2008, Kang and Chesson 2010) and from external environmental fluctuations that drive fluctuations in population densities (Chesson 1994, Chesson 2000, Chesson 2003, 2008). In difference equation models for species with seasonal reproduction, relatively nonlinear growth rates arise simply from differences between species in life-history traits (Chesson 1994, 2003). In such models, fluctuations in competition are often driven by fluctuations in environmental factors (Chesson 1994), although endogenously driven fluctuations have also been considered (Kuang and Chesson 2008). In both cases, coexistence is possible from relative nonlinearity. When fluctuations in competition are driven by environmental fluctuations, as in the lottery model studied here, the storage effect is present too. As the storage effect has been predicted to be the more important coexistence mechanism (Chesson 1994), the role of relative nonlinearity has often been ignored. Moreover, empirical studies of coexistence in a variable environment have focused almost exclusively on the storage effect even though a reasonable expectation is that relative nonlinearity is present too (Chesson 2003).

Both Chesson (1994) and Abrams and Holt (2002) point out that it is difficult for relative nonlinearity alone to maintain coexistence of more than two species competing for single resource whether fluctuations are endogenous in origin or due to temporal environmental variation. However, Abrams and Holt (2002) show that relative nonlinearity can have a coexistence promoting effect comparable to the resource partitioning in the case of two competing species, and Chesson (2003) suggests that relative nonlinearity might still be important in multispecies systems through its interactions with other mechanisms even though alone it is not effective in stabilizing coexistence of more than two species on one fluctuating resource. The case of relative nonlinearity with multiple resources has not been studied extensively, but general considerations in Chesson (1994) suggest that the complex nonlinearities

possible in multiple resource systems have strong potential to promote coexistence. Indeed, one example of relative nonlinearity with multiple resources and endogenous fluctuations was found to strongly promote coexistence of phytoplankton species (Huisman and Weissing 1999, 2002). More study of the potential for coexistence by relative nonlinearity with multiple resources is certainly needed, but no less important is a better understanding the role of relative nonlinearity in the single resource case when other mechanisms are present. As models of recruitment variation that lead to the storage effect coexistence mechanism generally also permit relative nonlinearity, it is essential to understand what the relative contribution of relative nonlinearity to coexistence might be. It is also important to know if relative nonlinearity can make a strong contribution to coexistence in multiple species cases when other mechanisms are present even though alone it is unlikely to permit coexistence of more than two species. Without this understanding, the almost exclusive focus on the storage effect in models of recruitment variation may be seriously misleading.

The lottery model for iteroparous perennials has been an important model for understanding the role of environmental variation in species coexistence. It has been used for perennial plants such as forest trees, and marine space holding organisms such as coral reef fishes or benthic invertebrates (Chesson and Warner 1981, Comins and Noble 1985, Hatfield and Chesson 1997, Hubbell 2001, Kelly and Bowler 2002). The model is in fact closely related to the model commonly used in neutral theory to define dynamics within a forest stand (Hubbell 2001). However, as implemented here, it is far from neutral. Environmental fluctuations cause recruitment to vary from year to year. Persistent adult stages buffer population growth against unfavorable times, permitting the storage effect to be present. At the same time, species differences in adult death rates enable relative nonlinearity to be present. These features mean that these two mechanisms are nearly always present together and their contributions to coexistence are not independent. Indeed, below we show that important factors contributing to the strength of relative nonlinearity also crucially determine the strength of the storage effect. As parameters are changed, relative nonlinearity often changes in a contrasting way to the storage effect, which makes relative nonlinearity more important when the storage effect is weak. We determine the conditions that allow relative nonlinearity to be stronger than the storage effect. These conditions are identified using approximate formulae for mechanism strength, backed up by simulations. Our results show when relative nonlinearity might be important in natural systems providing a guide for empirical studies.

2. Methods

2.1 Relative nonlinearity and the storage effect in the lottery model

The lottery model (Chesson and Warner 1981) describes community dynamics of iteroparous perennial species. Two distinct life stages, juveniles and adults, are considered. Each year, adults reproduce, and the resulting number of juveniles varies stochastically overtime, driven by the varying physical environment. Juveniles require open space to establish and mature as adults. Space is assumed to be limited, becoming available only with adult death. Juveniles compete for this space to recruit as adults. Success of a species in this competition for space is assumed proportional to the total number of juveniles produced during a given recruitment period. After maturation to an adult, the survival of an individual is assumed to be insensitive to

both the varying physical environment and competition.

The model is specified by the following difference equation for the dynamics of n perennial species:

$$N_j(t+1) = \left\{ 1 - \delta_j + \left[\sum_{k=1}^n \delta_k N_k(t) \right] \frac{\beta_j(t)}{\sum_{k=1}^n \beta_k(t) N_k(t)} \right\} N_j(t) \quad (1)$$

$j = 1, \dots, n$

Here $N_j(t)$ represents density of species j at time t , δ_j is the adult death rate, which is assumed to be constant over time, and $\beta_j(t)$ is the per capita number of juveniles produced by species j at time t . The recruitment to adults thus depends on per capita reproduction and survival of offspring to the juvenile stage when they compete for space to establish. The vector $\boldsymbol{\beta}(t) = (\beta_1(t), \dots, \beta_n(t))$ is assumed to vary independently over time, but with components correlated between species. In our simulations, $\boldsymbol{\beta}$ follows a multivariate lognormal distribution with parameters that remain constant over time. The variable $\ln(\beta_j)$ has a variance σ_j^2 that we use to measure sensitivity to environment.

Eq. (1) is a population model of the general form

$$N_j(t+1) = \lambda_j(t) N_j(t) \quad (2)$$

where $\lambda_j(t)$ is the finite rate of increase, and is here equal to the term in braces in Eq. (1). Eq. (2) represents population growth multiplicatively. To analyze the model, we need to put it on an additive scale, which is the log scale. The logarithm of the finite rate of increase, $r_j(t) = \ln \lambda_j(t)$,

$$r_j(t) = \ln N_j(t+1) - \ln N_j(t), \quad (3)$$

has the helpful property that its sum over a given period of time gives the change in $\ln N_j(t)$ for that same period of time. Equivalently, the time average, $\bar{r}_j$, of $r_j(t)$ defines the average change in $\ln N_j(t)$.

Log scales for various quantities have also been long found to be the simplest scales for understanding the behavior of the lottery model (Chesson 1982, 1994), and in order to place the model in a generic form for studying relative nonlinearity and the storage effect, we define the environmental response of species j as $E_j(t) = \ln \beta_j(t)$, and the competitive response as

$$C(t) = \ln \left\{ \sum_{j=1}^n \beta_j(t) N_j(t) / \sum_{j=1}^n \delta_j N_j(t) \right\}. \quad (4)$$

Note that in this definition, $\sum_{j=1}^n \delta_j(t) N_j(t)$ represents the amount of space available for juvenile settlement in the year t . It is equal to the total space released by adult death. The quantity $\sum_{j=1}^n \beta_j(t) N_j(t)$ is the demand for this space in terms of the total density of juveniles competing for this space. The ratio of these two quantities is

a measure of the magnitude of competition, which can be understood intuitively as “demand for space” divided by “supply.” Eq. (4) puts this quantity on a log scale as $C(t)$. The model can then be written in the following generic form for iteroparous perennial organisms (Chesson 2003):

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

This formula distinguishes two life-history processes, adult survival, which occurs with probability $1 - \delta_j$, and recruitment to the adult stage, which occurs at the per capita rate $\exp(E_j(t) - C(t))$.

The coexistence mechanism, relative nonlinearity, is present and is able to contribute to stable coexistence when two conditions are satisfied:

(a) Growth rates, $r_j(t)$, need to be relatively nonlinear functions of the common competition.

(b) Each species, when abundant, must drive the magnitude of fluctuations in competition in directions that favor their competitors.

The condition (a) means that different magnitudes of fluctuation in competition will favor different species to different degrees, with some species gaining relative advantages from small fluctuations in competition, and some gaining relative advantages from large fluctuations in competition. This condition is satisfied in lottery model when species differ in adult death rate δ . When δ_j is less than 1, as will always be the case for perennial organisms, $r_j(t)$ is a nonlinear function of the competitive response, $C(t)$. Indeed, it is a convex function of $C(t)$ as can be seen from its positive second derivative in $C(t)$. Because the degree of convexity depends on δ_j , when the δ s differ between species, their growth rates differ in convexity, which means they are relatively nonlinear functions. Note also that $C(t)$ fluctuates over time due to the fluctuating environment and fluctuating species densities. Jensen’s inequality (Needham 1993) says that the average of a convex function, $\overline{f(C)}$ ($= \bar{r}_j$ here), of a varying quantity C , is greater than the function of the average, $f(\bar{C})$. Most important, the difference between $\overline{f(C)}$ and $f(\bar{C})$ depends on the degree of the convexity. Thus, when species differ in their adult death rates, their growth rates (5) will differ in convexity. This outcome means that their time average growth rates (the $\bar{r}_j$) will be affected to different degrees by fluctuations in $C(t)$. In particular, a species with a smaller value of δ , which means a larger degree of convexity, has more to gain from fluctuations in $C(t)$.

For condition (b) to be satisfied, species with large adult death rates, when abundant need to increase fluctuation in C , and species with small adult death rates, when abundant, need to decrease fluctuation in C . The reason is that species with large adult death rates have less convex growth rates as functions of competition than species with small adult death rates and so benefit less from fluctuations in competition. An obvious way in which conditions (b) can be satisfied is for variability in β to positively related to the adult death rates because variability in β of abundant species is a key driver of fluctuations in C as is evident from its formula. However, variability in densities of abundant species also has a role, and these are increased by the magnitude of the adult death because larger adult death rates lead to higher population turnover through time. In these ways species with different values of δ can individually promote conditions that are disadvantageous to themselves but favor their competitors through the mechanism relative nonlinearity.

How the storage effect arises in the lottery model is best appreciated from the generic form Eq. (5) of the growth rate $r_j(t)$, which shows that it depends interactively on the environmental response $E_j(t)$ and $C(t)$ as $\partial r_j / \partial E_j \partial C$ is not zero. This interactive effect, as we shall see, can be separated from the nonlinear effect of $C(t)$ on $r_j(t)$ to reveal the storage effect as a distinct mechanism. The storage effect formalizes the concept of temporal resource partitioning. Because it has been much discussed elsewhere (Chesson and Warner 1981, Chesson 1994, 2003), we will only provide a brief introduction here.

The storage effect also has two key components (Chesson et al 2013):

(c) Density dependence of *covariance between environment and competition*.

(d) Buffered population growth.

This two component statement replaces a previous three component statement (e.g. Chesson 2000), which was not always understood. Requirement (c) combines the first two components from the three component statement for a more precise statement. In the three component statement, (c) is divided into covariance between environment and competition, and species-specific responses to the environment. Species-specific responses to the environment tend to make the covariance density dependent on density, as we now explain.

Covariance between environment and competition measures how much the ability of a species to benefit from favorable environmental conditions is inhibited by competition. It is measured for each species separately. High (positive) covariance means that benefits to a species from favorable environmental conditions are countered by increased competition at those times. In the lottery and similar models, such effects occur when a species is at high density because its strong responses to the physical environment place high demands on resources, as embodied in Eq. (4). However, low covariance means that the competition a species experiences is decoupled from its environmental response. Whether or not a species has high or low covariance of depends on its density, and this dependence is needed for the storage effect, as stated in (c). At low density a species may have times when the environment is favorable, but competition is weak, allowing the species to take full advantage of those environmentally favorable times. In the lottery model, this means that strong recruitment occurs. Low covariance, however, also leads to times the environment is poor and competition is strong, leading to especially poor recruitment. These covariance changes with density occur with species-specific responses to the environment, because as a species density declines the competition it experiences becomes decoupled from its response to the environment.

The requirement (d) is manifested in the lottery model as a persistent adult stage. The adult stage buffers a population against times when recruitment is poor. This means that strong recruitment gains during favorable times are not canceled out by population decline during unfavorable times. Mathematically, this effect is measured by the interaction between environment and competition, $\partial r_j / \partial E_j \partial C$, with a negative value implying buffered population growth, allowing low covariance between environment and competition to be a net advantage. When requirement (c) is

satisfied also, the lower covariance at low density promotes population recovery, leading to coexistence by the storage effect.

In most cases in nature, it can be expected that relatively nonlinear competition and an interaction between environmental responses and competition are both present. Thus, relative nonlinearity and the storage effect are expected often to be found together, as they are in the lottery model whenever adult death rates differ.

2.2 Quantifying coexistence

We use invasion analysis to quantify relative nonlinearity and the storage effect (Turelli 1981, Chesson 1994, 2003). Invasion analysis measures the rate of recovery of each species from low density in the presence of its competitors, which are allowed to approach their stationary state and are termed *residents*. A species perturbed to low density is termed an *invader*. The recovery rate of an invader, $\bar{r}_i$, is long-term average of $r_i(t)$ (equation (3)), which we measure here on the per generation scale, i.e. dividing r_i by δ_i because $1/\delta_i$ is adult longevity (Appendix I). In these units, $\bar{r}_i$ takes the general form

$$\bar{r}_i \approx \eta_i - \bar{\eta}_s^{\{s \neq i\}} + \Delta I_i - \Delta N_i. \quad (6)$$

The formulae for each of these terms is given in table 1. The first term $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$ is a comparison of the average fitness of the invader species i, η_i , relative to the residents, $\bar{\eta}_s^{\{s \neq i\}}$, where the special notation $\bar{\eta}_s^{\{s \neq i\}}$ means the average over the set of residents. In the absence of environmental variation, η_j , reduces to the ln life time reproduction, $\ln(\beta_j/\delta_j)$. In this case, the species with highest η_j will dominate in competition and eventually exclude all others. With environmental variation, the fitness comparison is written in terms of μ differences ($\mu_j = E[\ln(\beta_j/\delta_j)] = E[E_j] - \ln \delta_j$), plus a term δV_i involving variances and adult death rates (Table 1). Thus, η is the variance adjusted average fitness measure.

Relative nonlinearity depends multiplicatively on the variance in competition and the difference in adult death rates (Table 1). In models with a single competitive factor (here C), ΔN_i has different signs for different species. Note that for historical reasons associated with its derivation (Chesson 1994), relative nonlinearity is entered with a negative sign, and therefore a negative value of ΔN_i promotes recovery of species i . As shown in the formulae for relative nonlinearity in Table 1, ΔN_i will always promote recovery of species with above average adult survival, and undermine recovery of species with below average adult survival. The formula for the storage effect is resident-invader difference in the product of the adult survival rate (which provides buffered population growth) and covEC. The storage effect, ΔI_i , is often positive for all species, although we shall see some cases later when it is not

A species with a fitness disadvantage (negative value of $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$) can invade if

$$\eta_i - \bar{\eta}_s^{\{s \neq i\}} > \Delta N_i - \Delta I_i. \quad (7)$$

Notation Ψ_i is used for total contribution of storage effect and relative nonlinearity:

$$\Psi_i = \Delta I_i - \Delta N_i. \quad (8)$$

Coexistence by its very nature is a community property, not a property of

individual species. When the species level mechanism magnitudes, ΔI_i and ΔN_i , differ between species, as they necessarily do with relative nonlinearity, they must be considered jointly to understand the overall effect of the mechanism on species coexistence. Fortunately, the simple averages of the species-level mechanism magnitudes across species provide robust measures of their contributions at the community level, i.e. to species coexistence (Chesson 2003), as summarized below. We begin with a joint measure of mechanism contributions to coexistence,

$$\frac{1}{n} \sum_{i=1}^n \bar{r}_i = \bar{\Psi} = \overline{\Delta I} - \overline{\Delta N} \quad (9)$$

which is just the average of the Ψ_i over species because the fitness comparisons, $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$, necessarily average to zero. The quantity $\bar{\Psi}$ measures the overall stabilization of coexistence in the community in two senses. Most obviously, if the species can coexist, it measures the average rate at which they recover from low density, but also it measures the size of the coexistence region in parameter space, as we now explain.

If $\bar{\Psi}$ is not positive, the species cannot coexist—at least one must have negative growth from low density. On the other hand a positive value of $\bar{\Psi}$ means that there is a nonempty parameter region allowing coexistence and $\bar{\Psi}$ measures the size of this region (Chesson 2003). To see this, we can rewrite the recovery rate as

$$\bar{r}_i = \xi_i + \bar{\Psi}, \quad (10)$$

where ξ_i is a modification of the average fitness-difference $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$ accounting for the asymmetries in species level coexistence mechanisms. The quantity ξ_i takes the form

$$\begin{aligned} \xi_i &= \eta_i - \bar{\eta}_s^{\{s \neq i\}} + (\Delta I_i - \overline{\Delta I}) - (\Delta N_i - \overline{\Delta N}) \\ &= \eta_i - \bar{\eta}_s^{\{s \neq i\}} + \delta I_i - \delta N_i \end{aligned} \quad (11)$$

Thus, ξ_i not only includes the comparison of mean life time reproduction $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$, adjusted for environmental variation, but also the deviations of the species level storage effect and relative nonlinearity from their community averages, denoted δI_i and δN_i . From Eq. (10), we see that the species coexist if

$$\min_i \xi_i > -\bar{\Psi}. \quad (13)$$

Hence, if the ξ can be varied independently of $\bar{\Psi}$ then we see that $\bar{\Psi}$ determines the size of the coexistence region in terms of the average fitness inequalities, ξ . A larger value of $\bar{\Psi}$ gives a larger region of ξ values permitting coexistence. In Appendix I and Table 2, we show that the ξ values can be varied by varying the μ values in the two species case with no effect on $\bar{\Psi}$. Beyond the two species coexistence $\bar{\Psi}$ does depend on the μ values too, but the effects are relatively small, and so the magnitude of the coexistence region is still largely determined by $\bar{\Psi}$ (Appendix III).

Together, stabilizing mechanisms of relative nonlinearity ($\overline{\Delta N}$) and the storage effect ($\overline{\Delta I}$) contribute to $\bar{\Psi}$ (Eq. 9). The community average measures have instructive general formulae in essence defining how these mechanisms work (Chesson 2003, 2008). Community average relative nonlinearity, $\overline{\Delta N}$, is proportional to a covariance (Table 1 and Appendix II) between the variance in competition that residents generate $V(C^{\{-i\}})$ and the average death rate $\bar{\delta}_s^{\{s \neq i\}}$ of the resident species. Because $\overline{\Delta N}$ contributes to the long term growth rate with a negative sign, as shown in

Eq. 9, positive covariance between the adult death rate and variance in competition leads to a stabilizing effect. Thus this formula embodies quantitatively the understanding given above that for relative nonlinearity to stabilize coexistence: species with larger death rates must generate larger variation in competitive factors when they are resident species.

The community average storage effect is similarly a precise mathematical expression for understanding the mechanism. It is given as an average over species of a within-species comparison of resident and invader state covariances between environment and competition ($\chi_j^{\{-j\}}$ for species j in the invader state, and $\overline{\chi_j^{\{-i\}}^{(i \neq j)}}$ for species j in resident state). The average over species is weighted by the adult survival rate of each species specifying the degree of buffering of population growth (Table 1). If species, on weighted average, have higher resident-state covariance than invader-state covariance, the community average storage effect is positive, and therefore stabilizing.

We study both two-species and three-species communities. Analytical approximations of sufficient accuracy are available for the two-species lottery model (Table 2), but in the three species case we use simulations to derive the resident competition variance. Studies of two-species communities dominate the theoretical literature on competition, but such studies are inadequate when the efficacy of a mechanism can depend greatly on the number of species. As relative nonlinearity was regarded as ineffective in promoting coexistence beyond the two species case, it is critical that we study it in situations with three species as well. However, because these simulations are stochastic, high replication is needed and this need increases dramatically with the number of species. For this reason, we do not go beyond the three species case where ten replicates were generally adequate. In general, we chose enough replicates to make the graphs smooth without evident error. Thus, the standard errors are small compared to the trends that the graphs show.

In our investigation, we kept the average variance in the environmental response fixed, and varied only the relative variances (σ_1/σ_2) for the different species. In the two species case, the storage effect and relative nonlinearity are linear functions of variances and covariances (Table 2), and so the relative magnitudes of these mechanisms depend on the relative magnitudes of the variances, not their absolute values. In the three species case, our simulations showed negligible effects of the absolute values of the variances, σ_j^2 , on relative mechanism magnitude if species averages of these variances are 0.5 or less, and no individual variance is greater than 1 (Fig. A.1). With fixed relative variances, the absolute magnitudes of the storage effect and relative nonlinearity are approximately proportional to the average variance, which is fixed at 0.5 in the remainder of this study.

2.3. Focal questions

In the classic deterministic models where relative nonlinearity emerges as a coexistence mechanism, the nonlinearities in a species growth rate automatically generate the changes in variance with abundances needed for a stabilizing role of relative nonlinearity. To study that possibility here, we consider cases where all species are equally sensitive to the environment (i.e. have the same environmental response variances σ_j^2), but differ in adult death rates. We then compare these outcomes with cases where environmental sensitivities differ between species so that

competition fluctuations are not just driven by nonlinearity differences but also by intrinsic biological differences in response to the environment. In all cases, the relative contributions of relative nonlinearity and the storage effect are of interest, but in addition, of interest are cases where the storage effect might be weak, leaving relative nonlinearity to be the sole mechanism. To find such situations we vary the correlation between species in their environmental responses expecting that high correlation will lead to a weak storage effect because it will make the responses of the species to the environment more similar, and thereby reduce the density dependence of covEC. However, such correlations need not weaken relative nonlinearity. Indeed, there is a possibility that relative nonlinearity will be strengthened in the three species case due to stronger fluctuations in competition when resident species respond to the environment in the same way.

3. RESULTS

3.1. The effect of adult death rate differences alone

Adult death rate differences are necessary for the species growth rates to be relatively nonlinear (condition (a)), but do they also lead to changes in the variance of competition as the identity of the invader changes (i.e. does $V(C^{(-i)})$ depend on i , condition (b)) when species are equally sensitive to the environment? If they do, as has been found in deterministic models (Armstrong and McGehee 1980, Kuang and Chesson 2009), then they can generate a stabilizing effect of relative nonlinearity given by a negative value for $\overline{\Delta N}$. In the two-species lottery model the answer is no, because the resident population size does not fluctuate over time. The resident fills all space and has constant density. Thus, $V(C^{(-i)})$ is simply equal to the variance in the resident environmental response, and if both species have equal sensitivity (measured by σ^2) to the environment ($\sigma_1^2 = \sigma_2^2$), $V(C^{(-i)})$ will not change with the identity of the invader, giving a zero community average relative nonlinearity, $\overline{\Delta N}$ (Table 2).

By way of contrast, in the three species case, lower resident survival rates lead to more fluctuation in competition even though species are equally sensitive to the environment. The strength of this effect increases with the differences in death rates as expected (Fig. 1a). However, the magnitude of the resulting community average relative nonlinearity is minor compared with the storage effect ($\overline{\Delta I}$). Thus, we conclude that adult death rate differences alone do not generate enough changes in the variance of competition with the identity of the invader (and hence the identities of the residents) for much effect on stabilizing coexistence in comparison with the storage effect.

3.2. Adding sensitivity differences

For stronger stabilizing effects of relative nonlinearity, sensitivity to the environment must be positively related to the magnitude of the adult death rate. When this is done, positive contributions to stabilizing coexistence arise in the two-species case ($(\delta_1 - \delta_2)(\sigma_2^2 - \sigma_1^2) < 0$, Table 2), and in the three species case (Fig 1b), with the effect increasing linearly as the spacing of adult death rates is increased. In concert with the increasing contribution from relative nonlinearity, Fig 1b shows the contribution of the storage effect declining, and at the extremes of adult death rate spacing, the contributions of the storage effect and relative nonlinearity to stabilizing

coexistence are similar. However, the opposite trends in these two mechanisms mean that the overall stabilizing effect ($\overline{\Delta I} - \overline{\Delta N}$) hardly changes with adult death rate spacing.

These trends for the three-species case are consistent with analytical findings for the two species case (Table 2), which show that although the stabilizing effect of relative nonlinearity increases with adult death rates differences, the overall stabilizing effect is in fact constant, and depends only on the average of the adult death rates for the species, not their spacing. Although the overall stabilizing effect of the combined mechanisms may be insensitive to adult death rate spacing, the relative contributions of the two mechanisms can change dramatically in these cases of sensitivity differences aligned with adult death rate differences. For example, Fig 1b shows an almost 50% contribution to stabilizing coexistence from relative nonlinearity at the extremes of death rate spacing compared with no contribution when adult death rates are equal.

A rather different outcome is seen in Fig 1c where sensitivity to the environment is negatively associated with adult death rates. In that case relative nonlinearity has a small destabilizing effect on coexistence ($-\overline{\Delta N} < 0$), with a slight generally increasing trend in this effect as the death rate spacing increases. Interestingly, the magnitude of storage effect increases substantially with death rate spacing, more than counteracting the destabilizing effect of relative nonlinearity. Fig. 2 shows all these factors varying together in the two-species case, illustrating in addition that these various effects are generally increasing functions of the difference in environmental sensitivities ($\sigma_2^2 - \sigma_1^2$) of the species.

3.3. Correlated environmental responses.

Correlations between the environmental responses of the species weaken the storage effect in both the two-species (Fig 2b vs 2c) and three-species cases (Fig 3). This effect gives the potential that relative nonlinearity can increase in relative importance in stabilizing coexistence. This outcome is automatic in the two-species case, because the correlations between the environmental responses do not affect resident competition and thus have no effect on relative nonlinearity (Table 2). In the three-species case, the effects of correlation depend on environmental sensitivity differences. With equal sensitivity, increasing correlation further reduces the weak relative nonlinearity (Fig. 3a). With different sensitivities, increasing correlation increases the magnitude of the relative nonlinearity: it either leads to a stronger stabilizing effect of relative nonlinearity if species with higher adult death rates are more sensitive (Fig. 3b) or a stronger destabilizing effect if species with lower adult death rates are more sensitive (Fig. 3c). The net effect is that the relative magnitude of relative nonlinearity always increases with correlation, in large part due to the rapid decline of the storage effect (Fig. 4). When the species with higher adult death rates are more sensitive, the storage effect can become weaker than relative nonlinearity as correlation increases (Fig. 3b, 4). Moreover, in the two-species case, high correlation can lead to a negative contribution from the storage effect (Fig 2c). This outcome is consistent with substantial stabilizing effects from relative nonlinearity as seen in the upper right corner of Fig 2a, which then constitutes the sole positive contribution to species coexistence.

4. Discussion

In nature, it is a reasonable expectation that multiple coexistence mechanisms contribute to diversity maintenance in any system (Amarasekare 2007, 2009, Kuang and Chesson 2010). Yet very few studies distinguish conditions required for different coexistence mechanisms to be important. Even less is known about the relative importances of different mechanisms and how they interact. In this study, we present a comprehensive comparison of two coexistence mechanisms functioning together in a single mathematical model of community dynamics. Our model is the lottery model, and we use it to investigate the joint action of the storage effect and relative nonlinearity coexistence mechanisms. The lottery model is the simplest model where species coexist through recruitment variation driven by a fluctuating environment. Previous studies have focused almost exclusively on the storage effect, neglecting the potential important role of relative nonlinearity. Our work is the first to identify when relative nonlinearity can be important in the stabilization of species coexistence in such a model both absolutely, and in comparison to the storage effect.

Our ability to compare the contributions of these two mechanisms to stabilizing coexistence depends on our technique of quantifying coexistence so that their separate contributions can be assessed when they are acting together. Coexistence analyses are more commonly qualitative, distinguishing coexistence and exclusion, and have difficulty separating the effects of mechanisms acting simultaneously. In some cases, with our technique, we see no change in the combined effects of the mechanisms as parameters change coincident with major shifts in which mechanism is contributing most, with important implications as to how the system should be studied. Such findings are not possible without quantification. An added virtue is that the formulae for the mechanism magnitudes define precisely how the mechanism functions, facilitating its understanding and study.

The community average measures, which we justify below as most appropriate for the community scale of analysis, show that a coexistence stabilizing effect of relative nonlinearity in the lottery model requires adult death rates to covary across species with the variance in competition they generate as resident species. Large differences in adult death rates generate large differences in the nonlinearities of growth rates as functions of competition. Where relative nonlinearity has been studied in a constant environment (Armstrong and McGehee 1980, Abrams and Holt 2002, Kuang and Chesson 2008), relatively nonlinear growth rates also drive covarying differences in the variance of competition that stabilize coexistence. We asked whether this effect might also occur in the lottery model by examining the mechanism in the case where the species are equally sensitive to the environment. We do find that death rate differences do indeed lead to variance differences that contribute to stable coexistence by relative nonlinearity, but the effect is relatively weak, and negligible compared with the storage effect.

To obtain large effects of relative nonlinearity on stabilization of coexistence in the lottery model, the species must differ substantially in their sensitivities to environmental variation. These sensitivity differences then drive large differences in the variance of competition. When sensitivities and death rates covary positively across species—in other words, shorter-lived species are more sensitive to environmental variation—relative nonlinearity can be a strong stabilizing mechanism. However, if the opposite pattern prevails, namely longer-lived species are more sensitive to the environment, relative nonlinearity has a negative effect on stabilizing coexistence.

The contributions of relative nonlinearity to coexistence become especially

important when the different species have highly correlated responses to the environment even though they are differentially sensitive to it. While the storage effect decreases linearly with this correlation, the contribution of relative nonlinearity to coexistence stays constant or even increases with the correlation. At high correlation, relative nonlinearity can be the dominant or even the sole coexistence stabilizing mechanism in the system. It is not uncommon to see the role of the environmental questioned when species have are highly correlated in their responses (Clark 2010), but this exactly where relative nonlinearity might be making substantial contributions to species coexistence.

Though in specific circumstances relative nonlinearity can be very important, the storage effect can be a strong stabilizing mechanism in more general situations. The storage effect arises naturally when strong resource consumption, due to favorable environmental conditions for a species, leads to strong competition. Relative nonlinearity, on the other hand, has more restrictive conditions requiring a species to drive resource variation in a direction that favors its competitors. The key driver of differential resource variation in the lottery model, viz differential sensitivities to environmental variation, is commonly observed in nature (Wright et al. 2005). But do sensitivities covary positively with death rates in natural communities? Life-history theory as developed in single-species models, mostly predicts that long life and sensitivity to environmental variation should go hand in hand (Bulmer 1985, Real and Ellner 1992) contrary to the requirements for a strong stabilizing effect of relative nonlinearity. It would be good to have life-history theory for multispecies contexts to be confident of the relevance of this prediction, but as it stands, it implies that a strong destabilizing effect of relative nonlinearity is more likely in nature than a strong stabilizing effect.

We measure these stabilizing and destabilizing effects using the community average measure, which is obtained by averaging species-level measures of the mechanism. Species-level measures relate to the contributions of each species to recovery from low density. For relative nonlinearity, even when the community average is weak, the species-level measures can in fact be very strong, but with opposite effects on different species. Indeed, relative nonlinearity is a mechanism that necessarily contributes asymmetrically to the recovery of the different species from low density. At the species level, it makes negative contributions (positive values of ΔN_i) for species with larger than average adult death rates, and positive contributions (negative values of ΔN_i) for other species. Inequality is the nature of relative nonlinearity: longer-lived species will benefit more than the shorter-lived species from variations in resources due to Jensen's inequality.

The asymmetric effects of relative nonlinearity at the species level mean that it can act as an equalizing mechanism (Chesson 2000). Equalizing mechanisms cannot alone lead to stable coexistence, but strong equalizing mechanisms mean that even weak stabilizing mechanisms permit stable coexistence. Equalizing mechanisms favor species with average fitness disadvantages, as measured by the μ values (ln mean life-time fecundity in the absence of competition). Thus, relative nonlinearity will tend to equalize average fitness differences when species with small μ values also have small adult death rates. Life-history studies (Charnov 1991, 1993, 1997) show limited variation in the ratio of annual fecundity to annual mortality across different species, suggesting that life-time fitness, measured here by μ , should not vary too greatly between species. However, the variation that is present in μ values could be equalized by relative nonlinear when it arises from a greater than proportional tradeoff between

annual fecundity and annual adult survival.

Asymmetries in relative nonlinearity also have the potential to equalize asymmetries in the storage effect. In the two-species case, this outcome is clear: the combined mechanisms always have a positive effect on growth from low density even when one of the contributing mechanisms has a negative effect (Table 2). Inspection of Table 1 suggests that this result is more general than the two-species case. A positive contribution of relative nonlinearity to a longer-lived and less sensitive species can make up for a weaker storage effect. Similarly, a negative contribution of relative nonlinearity to a shorter-lived and more sensitive species reduces the advantage of a strong storage effect (Tables 1&2).

Our focus in this work has been on the community average mechanism measures because we wish to understand how coexistence is stabilized, and coexistence by its very nature is a community-level property. A positive value for the combined community average measures means that there is a range of fitness differences between species compatible with coexistence, but this range does not necessarily include the equal fitness cases, before accounted for mechanism effects, i.e. the equal μ values assumed in the figures in the text above. Importantly, we find in Appendix III that these community average measures are relatively insensitive to μ differences. A strong community average measure of coexistence means that on average species recover strongly from low density, and that the range of μ differences compatible with coexistence is large. However, is it possible that although the community average measure is positive, the community is destabilized by species that do not have strong recovery? To answer this question, we investigated fluctuational stability, which measures the average tendency of the coexisting species to remain away from zero density (Appendix IV).

We find that whenever the community average measure of coexistence is strong, it is always possible to find strong fluctuational stability for some μ values. However, these need not be equal μ values, especially if relative nonlinearity is a major contributor to coexistence. In fact in this case, the community average measures of coexistence might imply strong stability, but fluctuational stability is weak at equal μ values. However, this case highlights the advantage of community average measures. The low fluctuational stability is due to strong asymmetries in the species-level measures, especially due to relative nonlinearity. Adjusting the μ values to equalize average fitnesses in the presence of relative nonlinearity allows strong fluctuational stability when the community average measure is strong. These results illustrate how the community average measures give the best measure of the potential for coexistence by the various mechanisms, while the focus on species-level mechanism measures, and therefore individual species, can be misleading.

Mechanisms such as relative nonlinearity emphasize the need to go beyond the two-species case when studying species coexistence mechanisms because in many cases, relative nonlinearity alone has difficulty allowing multiple-species coexistence. Study of just two-species cases gives limited understanding of the mechanism. Simple tradeoffs, for example, competition-predation tradeoffs, provide a general example of where coexistence of two species occurs relatively easily, but often alone are unable to explain multispecies coexistence (Holt et al. 1994, Kuang and Chesson 2008). Here we have seen how a mechanism that alone would at best permit weak coexistence beyond the two-species case can still have important effects on coexistence when more than two species are present. It can do this through its effects on fitness inequalities, either positively or negatively, and also by adding to or subtracting from

the overall stability of coexistence. Multispecies cases also can importantly involve features that have no effect in two-species cases because in those cases, the resident community is a single species. For example, we found important effects on coexistence from differences between resident species in their life-history traits and their environmental responses. Such issues simply do not arise in two-species cases.

Throughout our investigation, we have focused on iteroparous species such as perennial plants, but the same phenomena can be expected in species with seasonal recruitment, as long as these species have a persistent stage in the life history (Kuang and Chesson 2008). The presence of the persistent stage provides the buffered population growth that can lead to the storage effect (Chesson 1994). Differences between species in the longevity of the persistent stage can lead to relatively nonlinear growth rates, and potentially the relative nonlinearity coexistence mechanism, as demonstrated here. An extraordinary diversity of organisms has persistent life stages. In annual plants, the persistent stage is the seed in the common case where between-year dormancy is present with a seed bank (Adonakis and Venable 2004, Facelli et al. 2005). Relative nonlinearity based on both fluctuations in competition and apparent competition have been shown theoretically for annual plants systems (Kuang and Chesson 2008), as has the storage effect (Chesson and Kuang 2010). Similarly arthropods may have between-year diapause, both zooplankton and phytoplankton can have long-lived stages in the form of resting eggs or cysts (Nehring 1995, Cáceres 1997).

Our findings have much relevance to empirical studies of the role of recruitment variation in species coexistence. Empirical work on this topic has focused on the storage effect alone (Cáceres 1997, Kelly and Bowler 2002, Descamps-Julien and Gonzalez 2005, Facelli et al. 2005, Adler et al. 2006, Angert et al. 2009, Chesson et al. 2011). This study emphasizes paying attention to relative nonlinearity, especially in systems where short-lived species and long-lived species occur together, for example, native perennials and exotic annuals in California coastal grassland (Hamilton et al. 1999, Corbin and D'Antonio 2004). It is also common to have a mixture of perennial and ephemerals coexisting in communities of marine benthic invertebrates (Giangrande et al. 1994). While high diversity in survival of a persistent stage is the key for relative nonlinearity in the lottery model and related models of recruitment variation (Chesson 2003), only limited study of selection for life-history differences exists (Ellner 1987). Unfortunately, empirical studies of species coexistence have not often focused on life-history traits, leading a limited understanding of their potential roles.

Our study calls for serious life-history based approaches to studying species coexistence. The first discussion of relative nonlinearity as a coexistence mechanism in the literature (Armstrong and McGehee 1980) did not examine life-history differences. Instead relatively nonlinear growth rates arose from different nonlinear functional responses of two consumer species to a common resource, but as we have shown here, differences in life-history traits also lead to relatively nonlinear growth rates. Although studies of relative nonlinearity as a coexistence mechanism have tended to focus on endogenous population fluctuations, we show here a potentially larger role for fluctuations driven by a variable environment. Recent work has highlighted the potential role of environmentally driven fluctuations in Lotka-Volterra models where relative nonlinearity is absent (Ripa and Ives 2003, Ruokolainen and Ripa 2012). Our work implies that broadening such studies to combine the traditionally studied nonlinear functional responses, environmental variation and life-history differences, could potentially reveal much stronger roles of relative

nonlinearity in species coexistence.

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Appendix I Component of invasion rate and analytical solutions in two-species cases

Chesson (1989, 1994, 2003) provides the basic analysis of the lottery model, which is elaborated here to provide formulae needed for our analyses. While Chesson (1989) provides a complete analysis of the lottery model for the two species case, Chesson (1994) provides the general theory for multispecies competition in a variable environment for models of the form

$$r_j(t) = g_j(E_j(t), C_j(t)) \quad (\text{A.1})$$

where g_j is an arbitrary continuously differentiable function. Chesson (2003) focuses on models given by Eq. (5), which are general models for recruitment variation, with the lottery model as a special case. However, the emphasis in Chesson (1994 and 2003) is on the case where the variances of environmental responses are the same for all species. Quadratic approximation of Eq. (A.1) results in expressions for the invasion rates, $\bar{r}_i$, and their division in contributions from different mechanisms have errors no more than $o(\sigma^2)$. Here σ^2 can be interpreted here as the maximum value of the σ_j^2 (the sensitivities) across species. For the lottery model, the only assumption needed for the quadratic approximations to apply is that the μ_j differ between species by no more than $O(\sigma^2)$. The formulae for species coexistence in the lottery model show that this assumption is valid in both the interior and boundary of the coexistence region. Our simulations, and the approximations in Hatfield and Chesson (1989), show that high numerical accuracy is achieved by the parameter range considered here with σ^2 no more than 1. In addition, our results on the relative importances of the two mechanisms are not changed by the absolute magnitude of σ^2 (Fig A.1).

Chesson (2003), Table 1, gives the formulae for the components of the invasion rate $\bar{r}_i$ ($\eta_i - \bar{\eta}_s^{\{s \neq i\}}$, ΔN_i and ΔI_i) for general models obeying Eq. (5), which include the lottery model. We express these results here on the natural timescale of a generation (Chesson 2008). A generation here is $1/\delta$ ($1/d$ in Chesson 2003), which means dividing $r_j(t)$ by δ_j before taking the average. The variance-adjusted average fitness comparison ($\eta_i - \bar{\eta}_s^{\{s \neq i\}}$) is denoted as $\bar{r}_i'$ in Chesson (2003), and is given by the formula

$$\begin{aligned} \eta_i - \bar{\eta}_s^{\{s \neq i\}} &= \mu_i - \overline{\mu_s^{\{s \neq i\}}} + \frac{1}{2}(1 - \delta_i)\sigma_i^2 - \frac{1}{2}(1 - \delta_s)\overline{\sigma_s^2}^{\{s \neq i\}} \\ &= \delta\mu_i + \delta V_i \end{aligned} \quad (\text{A.2})$$

where $\delta\mu_i = \mu_i - \overline{\mu_s^{\{s \neq i\}}}$ is comparison of mean ln life time fecundity (average fitness without variance adjustment) and $\delta V_i = (1 - \delta_i)\sigma_i^2 - (1 - \delta_s)\overline{\sigma_s^2}^{\{s \neq i\}}$ is the variance adjustment. We now develop the particular forms of ΔN_i and ΔI_i for the two-species lottery model, and Appendix II does the same for the general multispecies case.

In the two species lottery model, the formulae for the mechanisms from the

quadratic approximation, which have been derived in Chesson (1989), do not require simulation for evaluation. These formulae show that the species-level relative nonlinearity is

$$\Delta N_i = -\left[\frac{1}{2}(1-\delta_i) - \frac{1}{2}(1-\delta_r)\right]V(C^{(-i)}) = \frac{1}{2}(\delta_i - \delta_r)\sigma_r^2 \quad (\text{A.3})$$

(Eq. 39, Chesson 1989), where i the invader species and r is the resident species. Averaging over species, this formula gives the community average

$$\overline{\Delta N} = \frac{1}{4}(\delta_1 - \delta_2)(\sigma_2^2 - \sigma_1^2). \quad (\text{A.4})$$

Subtracting (A.4) from (A.3) gives the fitness modifying component of relative nonlinearity, which defines its equalizing effect:

$$\delta N_i = \Delta N_i - \overline{\Delta N} = \frac{1}{4}(\delta_i - \delta_r)(\sigma_1^2 + \sigma_2^2). \quad (\text{A.5})$$

The species level storage effect is given as

$$\Delta I_i = (1-\delta_s)\chi_s^{\{-i\}\{s \neq i\}} - (1-\delta_i)\chi_i^{\{-i\}} = (1-\delta_r)\sigma_{ir} - (1-\delta_i)\sigma_{ir}^2 \quad (\text{A.6})$$

(Eq. 40, Chesson 1989). Averaging over species gives the community average storage effect as:

$$\overline{\Delta I} = \frac{1}{2}[(\sigma_1^2 - \sigma_{12})(1-\delta_1) + (\sigma_2^2 - \sigma_{21})(1-\delta_2)]. \quad (\text{A.7})$$

The fitness modifying component of the storage effect is thus

$$\delta I_i = \frac{1}{2}[(1-\delta_r)\sigma_r^2 - (1-\delta_i)\sigma_i^2] + \frac{1}{2}(\delta_i - \delta_r)\sigma_{12}. \quad (\text{A.8})$$

The stabilizing effect in two species case can be written as the following expression and is always positive:

$$\bar{\Psi} = \overline{\Delta I} - \overline{\Delta N} = \frac{1}{2}(1-\bar{\delta})(\sigma_1^2 + \sigma_2^2 - 2\sigma_{12}) = \frac{1}{2}(1-\bar{\delta})V(E_1 - E_2). \quad (\text{A.9})$$

Fitness inequality accounting for the coexistence mechanisms becomes

$$\xi_i = \eta_i - \bar{\eta}_s^{\{s \neq i\}} + \delta I_i - \delta N_i = \mu_i - \mu_r - \frac{1}{4}(d_i - d_r)V(E_i - E_r). \quad (\text{A.10})$$

Note that combining A.9 and A.10 we obtain a very simple formula for the recovery rate,

$$\bar{r}_i = \xi_i + \bar{\Psi} = \mu_i - \mu_r + \frac{1}{2}(1-\delta_i)V(E_1 - E_2), \quad (\text{A.11})$$

(Eq. 41, Chesson 1989), which shows that the species will always coexistence in the two species case if the μ 's are the same for both species.

Appendix II General formulae for the storage effect and relative nonlinearity

Table 1 lists the general formulae that can be used to quantify relative nonlinearity and the storage effect. As explained in the previous appendix, the two-species case is the special situation where all mechanism magnitudes can be derived analytically. For three or more species, quantifications of the mechanisms rely at least partially on simulations. The covariance between environment and competition (CovEC) needed for calculating the storage effect in Table 1 can be obtained completely using the simulated time series values for the environmental and competitive responses. However, following the calculations in Chesson (1994) section 5.3, without applying the symmetry assumptions used there, and dividing by δ_i to obtain results on the per-generation timescale, the species level storage effect becomes

$$\Delta I_i = \gamma_i \delta_i \sum_{s \neq i} \delta_s a_s \sigma_{is} - \frac{1}{n-1} \sum_{r \neq i} \sum_{s \neq i} \gamma_r \delta_r \delta_s a_s \sigma_{rs}, \quad (\text{A.12})$$

where $\gamma_i = 1 - \delta_i^{-1}$, and $a_s = E\left[N_s / \sum_r \delta_r N_r\right]$. In Eq. (A.12). evaluation of a_s relies on simulation. This formula was found to give almost identical values to evaluation of

the formula for ΔI_i in Table 1 by calculating CovEC directly from simulations.

Relative nonlinearity was calculated using Eq. (18), where the variance in competitive responses, $V(C^{(-i)})$, was obtained from simulation. The formula for community average relative nonlinearity is given in Chesson (2003) as

$$\overline{\Delta N} = \frac{n}{2(n-1)} \text{Cov}(\delta_i, V(C^{(-i)})) \quad (\text{A.15})$$

This formula can be rearranged as follows to give community average relative nonlinearity (Table 1) used here:

$$\overline{\Delta N} = \frac{1}{2(n-1)} \sum_{i=1}^n (\delta_i - \bar{\delta}) V(C^{(-i)})$$

But, $\delta_i - \bar{\delta} = -(n-1)(\bar{\delta}_s^{(s \neq i)} - \bar{\delta})$. Thus,

$$\begin{aligned} \overline{\Delta N} &= \frac{1}{2(n-1)} \sum_{i=1}^n -(n-1)(\bar{\delta}_s^{(s \neq i)} - \bar{\delta}) V(C^{(-i)}) \\ &= -\frac{n}{2} \text{cov}_i(\bar{\delta}_s^{(s \neq i)}, V(C^{(-i)})) \end{aligned} \quad (\text{A.16})$$

Eq. (18), identical with A.16, has the advantage that it directly associates the resident death rates with the variance in competition that the residents create.

Appendix III The effect of fitness inequality on species coexistence

The effect of mean fitness differences

Although results in the main text were investigated with species having equal mean ln life-time fecundity (equal μ values), the conclusions are robust to μ differences. First note that in the two-species case, relative nonlinearity and the storage effect are both independent of μ differences, which is the ideal condition for the stabilizing effect $\bar{\Psi}$ to be a direct measure of the coexistence region in terms of range of ζ values that allows species to coexist (Eq. 13). In three species cases, the overall stabilizing effect changes with μ differences; and the direction of the changes depends on which species in the community is at a disadvantage (Table A.1). Nevertheless, the subtle difference in the overall stabilizing effect between the invasion boundary and the interior of the coexistence region is too small to change our conclusions based on the case of equal μ values (Table A.1). This result is reassuring that in the three species case, the overall stabilizing effect is a satisfactory measure of the coexistence region given the minimal impact of μ differences on the stabilizing effect.

The small effects of μ differences on the overall stabilizing effect are partially due to the opposite responses of relative nonlinearity and the storage effect as μ differences vary (Fig. A.2). Both mechanisms change essentially linearly with μ differences: when μ of either the least sensitive species (also the longest-lived species) or the most sensitive species (also the shortest-lived species) is reduced, relative nonlinearity is reduced and the storage effect is increased (Fig. A.2 a&c); the opposite is found when the μ of the median sensitive species (also the species with median longevity) is reduced (Fig. A.2b). Nevertheless, the effects of μ differences on the community average storage effect and relative nonlinearity are still small, as we can tell from the slopes of the lines in Fig. A. 2 and Table A.1.

Mechanism asymmetries and coexistence regions

So far our conclusions have focused simply on the community average components of the coexistence mechanisms, but in general both the storage effect and relative nonlinearity make unequal contributions to the recovery rates of different species. These unequal contributions can be examined through the mean fitness adjustment, δI_i and δN_i . In the two species case, these mean fitness adjustments are available analytically, and the fitness comparison ξ , reduces to the following form

$$\xi_i = \delta\mu_i + \underbrace{\frac{1}{2}(\delta_i - \delta_r)\sigma_{ir}}_{\delta V_i + \delta I_i} - \underbrace{\frac{1}{2}(\delta_i - \delta_r)\overline{\sigma^2}}_{\delta N_i}, \quad (\text{A.17})$$

where σ_{ir} is the covariance between E_i and E_r , and $\overline{\sigma^2}$ is the average of the variances in the environmental responses (E) across species. Relative nonlinearity is only present when the δ 's of the two species are different. Of necessity δN_i is non-zero. If δN_i has the same sign as the combination $\delta\mu_i + \delta V_i + \delta I_i$, it will have a net equalizing effect provided it is not too large. Moreover, as δN_i is always larger in magnitude than $\overline{\Delta N}$, the fitness equalizing effect of relative nonlinearity is likely often to be more important than its stabilizing effect. However, as μ can be changed independently of the mechanisms, these fitness comparison components do not affect the size of the coexistence region in terms of the range of μ values compatible with coexistence. With three species, there is some sensitivity of the mechanism to μ but the sensitivity is low (Table A.1), and so for general considerations of the extent to which these mechanisms promote coexistence, focus on community average measures is sufficient. However, this result likely does not generalize to models where relative nonlinearity is present alone because in those cases, up to quadratic level of approximation, the strong asymmetries between species with relative nonlinearity preclude the coexistence of more than two species (Chesson 1994).

Appendix IV Fluctuational stability

Except in Table A.1, all results in the text are given for the case of equal μ values (ln mean life time fecundity). With equal μ values, both species in any two species community coexist stably according to the lottery model provided there is any variance in the difference between their environmental responses, as can be seen from Eq. (A.11). This means that the two species studies above with equal μ values are studies where the species do stably coexist. This also means that all two-species resident communities exist for the three species studies with equal μ 's (i.e. the two resident species coexist). However, stable coexistence is not necessarily guaranteed for any three-species assemblage at equal μ values, as one or more may not be able to invade the two-species resident community despite equality in μ value. This outcome is understandable given that the contributions of the coexistence mechanisms can be highly asymmetric in the cases studied in this investigation.

Our calculations presented in Table A.1 show that the community average measures $\bar{\Psi}$ are not greatly sensitive to fitness inequality, justifying the focus on the equal μ case for our calculations. The combined community average mechanisms $\bar{\Psi}$ gives the average invader recovery rate, and indicates coexistence strength in terms of the fitness differences compatible with coexistence. Our question here is whether patterns observed for how $\bar{\Psi}$ changes with the circumstances can be related to patterns of community stability defined in terms of joint population fluctuations. To consider this question, we develop here a measure of fluctuational stability,

$$n \left(E \left[\prod_{j=1}^n N_j \right] \right)^{\frac{1}{n}}. \quad (\text{A.17})$$

Taking the n^{th} root of the expectation in (A.17) and then multiplying it by n scales the stability measure between 0 and 1. Fluctuational stability measures the degree of fluctuation in the community in terms of how much the densities keep away from 0. If there are no fluctuations over time, and species stay at the equal constant density of $1/n$, the fluctuational stability reaches the maximum value 1. If instead, the community has large fluctuations, with some species often near zero, the measure approaches the minimum value of 0.

The two species stationary distribution, as derived by diffusion approximation (Hatfield and Chesson 1989), depends on $(\mu_1 - \mu_2)/V(E_1 - E_2)$, δ_1 and δ_2 only. As $\bar{\Psi}$ is proportional to $V(E_1 - E_2)$, but does not involve $\mu_1 - \mu_2$ in this case, fluctuational stability should depend on $\bar{\Psi}$ when average fitnesses are different, but not otherwise. Thus, fluctuational stability should provide new insight into the effects of the coexistence mechanisms. In three-species cases, individual level coexistence mechanisms can have strong effects on average fitness differences between species as well as on community average stabilizing mechanisms, summarized by $\bar{\Psi}$. Patterns of fluctuational stability for equal μ values should give very different results from $\bar{\Psi}$, especially when such average fitness differences arising from the mechanisms would predict extinctions in the three-species case with equal μ values. For a comparison, we measure both the fluctuational stability with equal μ values and the maximum fluctuational stability possible inside the entire coexistence region.

Our results show that maximum fluctuational stability is not sensitive to the spacing of adult death rates (Fig. A.3a, A.4), sensitivity differences (Fig. A.3, A.4, A.5), or correlations in the environmental responses between species (Fig. A.3b, A.5), in the range of situations that we have studied. Surprisingly, these results imply that, provided the conditions for coexistence are actually satisfied, maximum fluctuational stability is dependent primarily on the number of species. However, we have not studied the effects of mean sensitivity across species or mean adult death rates across species. These quantities are fixed in our analysis. Nevertheless, it is clear that maximum fluctuational stability is indeed giving different information than $\bar{\Psi}$, which measures the species average invasion rate and the size of the coexistence region. Despite these various differences, in all cases with positive $\bar{\Psi} > 0$, we were always able to find strong fluctuational stability for some μ values (compare Figs 1 and 3 with A.4 and A.5).

Consistent with our predictions, fluctuational stability measured at equal μ values shows a very different pattern from its maximum value (Fig. A.3, A.4, A.5). At equal μ values, fluctuational stability declines rapidly with death rate spacing (Fig. A.3a, A.4). This is likely to be the result of increasing average fitness differences between species introduced by relative nonlinearity. In contrast $\bar{\Psi}$ can increase with death rate spacing (Fig. 1 a&c), or at least stay at high values (Fig. 1b) at fixed μ values, not greatly different from maximum fluctuational stability. Correlation between environmental responses has a negligible effect on fluctuational stability with equal μ 's. Indeed, this is predicted by the stationary distribution in the two species case because then $(\mu_1 - \mu_2)/V(E_1 - E_2) = 0$, nullifying any effect of correlation on the form of this distribution. Naturally, in this case also, sensitivity differences are unimportant, as seen in Supp. Fig. 4. However, in the three species case, sensitivity differences affect the fluctuation stability measured at equal μ values. Among all three

cases, the strongest fluctuational stability as equal μ values occurs when the shorter-lived species is more sensitive to the environment. This is also the case when relative nonlinearity can potentially equalize fitness differences between species due to the effects of δV_i , i.e. fitness inequality introduced by variance differences despite equal μ values (Fig A.4, A.5).

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Table 1 : Components of the invasion rate

	Species Level	Community Level
Variance adjusted average Fitness Difference	$\eta_i - \bar{\eta}_s^{\{s \neq i\}} = \delta\mu_i + \delta V_i$	n.a.
Relative Nonlinearity	$\Delta N_i = \frac{1}{2} V(C^{\{-i\}}) \left(\delta_i - \bar{\delta}_s^{\{s \neq i\}} \right)$	$\overline{\Delta N} = -\frac{n}{2} \text{cov}_i \left(\bar{\delta}_i^{\{s \neq i\}}, V(C^{\{-i\}}) \right)$
The Storage Effect	$\Delta I_i = \overline{(1 - \delta_s) \chi_s^{\{-i\}}}_{\{s \neq i\}} - (1 - \delta_i) \chi_i^{\{-i\}}$	$\overline{\Delta I} = (1 - \delta_s) \left(\overline{\chi_s^{\{-i\}}}_{\{s \neq i\}} - \chi_s^{\{-s\}} \right)^s$

1094 Notation: $\mu_j = E[E_j] - \ln \delta_j$, the mean ln life-time fecundity for species j where $E[]$ means expected
1095 value; $\delta\mu_i = \mu_i - \bar{\mu}_s^{\{s \neq i\}}$, the mean ln life-time fecundity comparison between species; $\sigma_j^2 = V(E_j)$,
1096 the variance of the environmental response for species j (species j 's sensitivity to environment);
1097 $\delta V_i = \frac{1}{2} (1 - \delta_i) \sigma_i^2 - \frac{1}{2} (1 - \delta_s) \sigma_s^2$ the contribution to average fitness differences from variance
1098 differences in ln fecundity; $C^{\{-i\}}$ is the competitive response of all species in the community when
1099 species i is the invader; and $\chi_j^{\{-i\}} = \text{cov}(E_j, C^{\{-i\}})$ is the covariance between environment and
1100 competition for species j when i is the invader. Measurements of the coexistence mechanism are in the
1101 natural scale of a generation.

Table 2 Mechanism magnitudes in the two-species case

Mechanism	Species Level	Community Level
Relative Nonlinearity	$\Delta N_i = \frac{1}{2}(\delta_i - \delta_r)\sigma_r^2$	$\overline{\Delta N} = \frac{1}{4}(\delta_1 - \delta_2)(\sigma_2^2 - \sigma_1^2)$
The Storage Effect	$\Delta I_i = -(1 - \delta_i)\sigma_{ir} + (1 - \delta_r)\sigma_r^2$	$\overline{\Delta I} = \frac{1}{2}\{(\sigma_1^2 - \sigma_{12})(1 - \delta_1) + (\sigma_2^2 - \sigma_{12})(1 - \delta_2)\}$
Combined mechanisms	$\Psi_i = \frac{1}{2}(1 - \delta_i)\sigma_{\text{diff}}^2$	$\overline{\Psi} = \frac{1}{2}(1 - \bar{\delta})\sigma_{\text{diff}}^2$

Legend δ_j : adult death rate for species j ; σ_j^2 : variance in environmental response for species j ; σ_{ir} : covariance between the environmental responses, E_i and E_r , of species i and species r ; $\sigma_{ir} = \rho_{ir}\sigma_i\sigma_r$ with ρ_{ir} the correlation between environmental responses; σ_{diff}^2 : $\text{var}(E_1 - E_2) = \sigma_1^2 + \sigma_2^2 - 2\sigma_{12}$
 For derivation see Appendix I.

Figure 1. *The effects of death-rate spacing on mechanism magnitudes in the three-species case.* In (a), (b), and (c) the stabilizing effects of relative nonlinearity ($-\overline{\Delta N}$, solid line), the storage effect ($\overline{\Delta I}$, dashed line), and the overall stabilizing effect ($-\overline{\Delta N} + \overline{\Delta I}$, dotted line) are plotted against death rate spacing. The three panels are: species have common sensitivities to environmental fluctuations (a), shorter-lived species more sensitive (b), and longer-lived species more sensitive (c). *Parameters:* $\mu_1 = \mu_2 = \mu_3$; $\rho = 1/3$; $\overline{\delta} = 0.5$, with δ_1 and δ_3 spaced equally about the mean; $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$ for (b) or $= 11:6:1$ for (c).

(a) Relative nonlinearity

(b) The storage effect, $\rho = 0$

(c) The storage effect, $\rho = 0.9$

Fig. 2. Heat maps for mechanism magnitudes in the two-species case. Community averages effect of relative nonlinearity $-\overline{\Delta N}$ (a) and storage effect $\overline{\Delta I}$ (b,c) plotted against differences in sensitivity ($\sigma_2^2 - \sigma_1^2$) and differences in adult death rates in two-species cases. Relative nonlinearity is insensitive to correlation between species. The storage effects are compared between zero correlation ($\rho = 0$) in (b) and high correlation ($\rho = 0.9$) in (c). Parameters: $\overline{\sigma^2} = 0.5, \overline{\delta} = 0.5$.

Figure 3. *Effects of correlation on mechanism magnitudes in the three species case.* In (a), (b), (c) stabilizing effect of relative nonlinearity (solid line), the storage effect (long dashes), and the overall stabilizing effect (short dashes) are plotted against increasing correlation in environmental responses. Comparisons are made between three situations: species have the same sensitivity (a), shorter-lived species are more sensitive (b) and longer-lived species are more sensitive (c). *Parameters:* $\mu_1 = \mu_2 = \mu_3$, $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$ for (b) or , 11:6:1 for (c).

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Figure A.1. *Insensitivity of mechanism relative importance to the magnitude of environmental variation.* The relative contribution of relative nonlinearity ($-\overline{\Delta N} / (-\overline{\Delta N} + \overline{\Delta I})$) for different average variances in the environmental responses (lines for different $\overline{\sigma^2}$ can be seen to be essentially coincident) are plotted in two panels. a) $-\overline{\Delta N} / (-\overline{\Delta N} + \overline{\Delta I})$ against differences in death rate. b) $-\overline{\Delta N} / (-\overline{\Delta N} + \overline{\Delta I})$ against correlation in environmental responses (ρ). Parameters: $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$. For (a) $\rho = 1/3$; $\overline{\delta} = 0.5$, with $\delta_1 < \delta_2 < \delta_3$ following an arithmetic sequence and for (b) $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$. The average variances ($\overline{\sigma^2}$) for these lines are 0.1 (solid line), 0.2 (dashed line), 0.3 (dotted line), 0.4 (dashed dot line), 0.5 (dashed dot dot line).

1161 Table A.1. Sensitivities of coexistence mechanisms to mean ln life time fecundity

Correlation ρ	Species i	Sensitivity of equalizing effect $\frac{\partial(\delta I_i - \delta N_i)}{\partial \mu_i}$	Sensitivity of stabilizing effect $\frac{\partial(\Delta I - \Delta N)}{\partial \mu_i}$	Mean fecundity differences $\frac{\partial(\Delta I - \Delta N)}{\partial \mu_i}$
$\rho = 0$	$i = 1$	-0.032	0.031	-0.112
	$i = 2$	0.013	-0.013	-0.088
	$i = 3$	-0.046	0.046	-0.048
$\rho = 0.3$	$i = 1$	-0.024	0.023	-0.102
	$i = 2$	0.038	-0.038	-0.061
	$i = 3$	-0.037	0.037	-0.035
$\rho = 0.6$	$i = 1$	-0.104	0.108	-0.093
	$i = 2$	0.143	-0.144	-0.033
	$i = 3$	-0.148	0.054	-0.023

1162 Notes: The quantity δI_i and δN_i are deviations between the species-level and community average
1163 storage effect and relative nonlinearity: $\delta I_i = \Delta I_i - \overline{\Delta I}$ and $\delta N_i = \Delta N_i - \overline{\Delta N}$. Columns 3 and 4 are
1164 average slopes of $\delta I_i - \delta N_i$ and $\Delta I - \Delta N$ as functions of μ_i , as μ_i is varied from the invasion boundary
1165 to equality with the other μ values. The change in μ_i is given by $\partial \mu_i$ in the last column. The
1166 correlations between species in environmental responses are listed in column 1. Column 2 defines the
1167 species whose μ is varied. *Parameters:* $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$.

Figure A.2. *The effect of individual species' average fecundities on the stabilizing effects.* The stabilizing effects of relative nonlinearity (solid line), storage effect (dashed line) and the overall stabilizing mechanism (dotted line) are plotted against mean $\ln$ fecundity (μ) for each species separately, keeping other species' mean $\ln$ fecundity constant. In each panel, the μ value for a species is varied from its invasion boundary to coexistence central ($\mu = 0$ for all species), while the μ values for the rest are kept 0. (a) species 1: the least sensitive and longest-lived species; (b), species 2: the species with median sensitivity and median longevity; In (c), species 3: the most sensitive and shortest-lived species. *Parameters:* $\rho = 0.6$; $\overline{\sigma^2} = 0.5$; $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1 : 6 : 11$; $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$.

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Figure A.3. *Fluctuational stability in two species cases under different life history scenarios.* Comparisons between the fluctuational stability with equal μ values (solid line) and the maximum fluctuational stability with different μ values (dashed line) in the two species case. In (a) fluctuational stability is plotted against death rate spacing. In (b) the fluctuational stability is plotted against ρ (the pairwise correlation between environmental responses). The result is insensitive to which species is more sensitive to the environment. *Parameters:* $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 = 1 : 2$ (black lines) or $2 : 1$ (grey lines), for (a) $\rho = 0.3$, $\overline{\delta} = 0.5$, and for (b) $\delta_1 = 0.2$, $\delta_2 = 0.8$.

Figure A.4. *Fluctuational stability as a function of death rate spacing in three species cases.* In each figure, comparisons are made between fluctuational stability with equal μ values (solid line) and the maximum fluctuational stability with different μ values (dashed line). (a) Species have equal sensitivities to the environment, (b) shorter-lived species are more sensitive, and (c) longer-lived species are more sensitive. *Parameters:* $\rho = 1/3$, $\bar{\delta} = 0.5$, $\bar{\sigma}^2 = 0.5$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$ for (b) or $11:6:1$ for (c).

Figure A.5. *Fluctuational stability as a function of correlation (ρ) between species in environmental responses.* In each figure, comparisons are made between fluctuational stability with equal μ values (solid lines) and the maximum fluctuational stability with different μ values (dashed lines). (a) species have equal sensitivity to environmental variation, (b) shorter-lived species are more sensitive, and (c) longer-lived species more sensitive. *Parameters:* $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$. $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$ for (b) or $11:6:1$ for (c).