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Positively and Negatively Autocorrelated Environmental Fluctuations Have Opposing Effects on Species Coexistence

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ABSTRACT: Environmental fluctuations can mediate coexistence between competing species via the storage effect. This fluctuation-dependent coexistence mechanism requires three conditions: (i) there is a positive covariance between species responses to environmental conditions and the strength of competition, (ii) there are species-specific environmental responses, and (iii) species are less sensitive to competition in environmentally unfavorable years. In serially uncorrelated environments, condition (i) occurs only if favorable environmental conditions immediately and directly increase the strength of competition. For many demographic parameters, this direct link between favorable years and competition may not exist. Moreover, many environmental variables are temporal autocorrelated, but theory has largely focused on serially uncorrelated environments. To address this gap, a model of competing species in autocorrelated environments is analyzed. This analysis shows that positive autocorrelations in demographic rates that increase fitness (e.g., maximal fecundity or adult survival) produce the positive environment-competition covariance in condition (i). Hence, when these demographic rates contribute to buffered population growth, positive temporal autocorrelations generate a storage effect; otherwise, they destabilize competitive interactions. For negatively autocorrelated environments, this theory highlights an alternative stabilizing mechanism that requires three conditions: (i′) there is a negative environment-competition covariance, (ii) there are species-specific environmental responses, and (iii′) species are less sensitive to competition in more favorable years. When the conditions for either of these stabilizing mechanisms are violated, temporal autocorrelations can generate stochastic priority effects or hasten competitive exclusion. Collectively, these results highlight that temporal autocorrelations in environmental conditions can play a fundamental role in determining ecological outcomes of competing species.

Keywords: coexistence, autocorrelation, storage effect, competition, environmental stochasticity.

Introduction

Most species compete with other species (Gurevitch et al. 1992; Kaplan and Denno 2007). This mutual antagonism can result in one species driving other species extinct. According to ecological theory, this competitive exclusion is inevitable when there are more species than limiting factors and the community approaches a steady state (Volterra 1928; McGehee and Armstrong 1977). Hutchinson (1961) proposed that fluctuations in environmental conditions may allow species competing for few limiting factors to coexist. In a series of influential articles (Chesson and Warner 1981; Chesson 1983, 1988, 1994), Peter Chesson developed a mathematical theory for when and how environmental fluctuations, via nonlinear averaging and the storage effect, mediate species coexistence. In recent decades, empirical evidence for these coexistence mechanisms has been identified in a diversity of systems, including zooplankton (Cáceres 1997), prairie grasses (Adler et al. 2006), desert annual plants (Angert et al. 2009), tropical trees (Usinowicz et al. 2012), phytoplankton (Ellner et al. 2016), sagebrush (Chu and Adler 2015; Ellner et al. 2016), and nectar yeasts (Letten et al. 2018).

Until recently (Benaïm and Schreiber 2019), mathematical methods for studying coexistence for species experiencing environmental stochasticity assumed that these fluctuations are uncorrelated in time (Chesson 1982; Chesson and Ellner 1989; Ellner 1989; Schreiber et al. 2011; Hening and Nguyen 2018), and ecological theory has mostly focused on this case (Chesson 1994, 2000; Angert et al. 2009; Stump and Chesson 2017; Kortessis and Chesson 2019; but see Li and Chesson 2016). Environmental fluctuations, however, are often autocorrelated (Steele 1985). Minimum and maximal monthly temperatures in both terrestrial and marine systems are typically positively autocorrelated (Vasseur and Yodzis 2004); months with higher temperature maxima tend to be followed by months with higher maxima. Approximately 20% of terrestrial sites on Earth exhibit positively autocorrelated yearly rainfall, while 5% exhibit negatively autocorrelated rainfall (Sun et al.

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2018). Although considered less frequently, negative autocorrelations may be common in other situations (Metcalf and Koons 2007). For example, density-dependent driven oscillations of an herbivore or predator can result in negatively autocorrelated fluctuations in the mortality rates of its prey species.

Theoretical and empirical studies show that autocorrelated environmental fluctuations can have large impacts on population demography (Foley 1994; Petchey et al. 1997; Cuddington and Yodzis 1999; Gonzalez and Holt 2002; Pike et al. 2004; Cuddington and Hastings 2016). Theory predicts that positively autocorrelated fluctuations increase extinction risk when populations exhibit undercompensatory dynamics, but decreases extinction risk when populations exhibit overcompensatory dynamics (Petchey et al. 1997). Consistent with the first theoretical prediction, clonal populations of *Folsomia candida* exhibited shorter times to extinction when fluctuating mortality rates were positively autocorrelated (Pike et al. 2004). For structured populations, temporal autocorrelations can alter long-term population growth rates (Roy et al. 2005; Tuljapurkar and Haridas 2006; Schreiber 2010). For example, laboratory experiments with paramecia and theory predicted that positively autocorrelated fluctuations in the local fitnesses of spatially structured populations can increase long-term population growth rates (Roy et al. 2005; Matthews and Gonzalez 2007; Schreiber 2010).

As autocorrelated fluctuations are common and have demographic impacts, they likely influence ecological outcomes of competing species. As recent mathematical theory (Benaïm and Schreiber 2019) provides the analytical tools to explore this influence, I analyze models of two species competition accounting for autocorrelated fluctuations in environmental conditions. As these models correspond to competition for a single limiting factor and undercompensatory density dependence, stable coexistence does not occur in constant environments; only neutral coexistence is possible. Moreover, uncorrelated environmental fluctuations do not stabilize neutral coexistence in these models. Therefore, using a mixture of analytical and numerical approaches applied to the stochastic models, I tackle the following questions: When do positively or negatively autocorrelated fluctuations mediate coexistence? When do they disrupt neutral coexistence, and if they do, is the identity of the excluded species predictable? What types of shifts in competitive outcomes are possible as temporal autocorrelations shift from negative to positive?

Model and Methods

Consider two competing species with densities n_1 and n_2. The fitness of individuals within species i, $f(C, E_i)$, decreases with the strength of competition C and increases with respect to an environmental response variable E_i. The strength of competition is given by a weighted combination of the species densities, $C = a_1 n_1 + a_2 n_2$, where a_i determines the per capita contribution of species i to the strength of competition. The environmental variable E_i represents the net effect of environmental conditions on species i's fitness. Unlike much of the prior work on the storage effect (e.g., Chesson 1994; Kuang and Chesson 2009; Stump and Chesson 2017), the strength of competition C is not a function of the environmental variables E_i. Therefore, for uncorrelated environmental fluctuations, there is no covariance between the environment and the strength of competition and, consequently, no storage effect (Chesson 1994). Consistent with meteorological models of various weather variables (Wilks and Wilby 1999; Semenov 2008), fluctuations in the environmental response variables follow a multivariate autoregressive process with means $\bar{e}_i$, standard deviations σ_i, cross correlation τ, and temporal autocorrelation ρ. Under these assumptions, the dynamics of the system are

$$\begin{aligned} n_i(t+1) &= n_i(t) f(a_1 n_1(t) + a_2 n_2(t), \bar{e}_i + \Delta e_i(t)) \quad \text{with } i = 1, 2, \\ \Delta e_i(t+1) &= \rho \Delta e_i(t) + \sqrt{1-\rho^2} Z_i(t+1), \end{aligned} \tag{1}$$

where $\Delta e_i(t)$ are the deviations of the environmental variables away from the means $\bar{e}_i$ and $Z_i(t)$ are independent in time with mean 0, standard deviation σ_i, and cross correlation $\mathrm{Corr}[Z_1(t)Z_2(t)] = \tau$. Provided that $|\rho| < 1$ (i.e., the environmental fluctuations are neither perfectly positively nor negatively autocorrelated), the environmental deviations $\Delta e_i(t)$ converge to a unique stationary distribution $\widehat{\Delta e_i}$ with mean 0, variance σ_i^2, and cross correlation τ. The $(1-\rho^2)^{1/2}$ term in equation (1) allows one to independently vary the variance of the stationary distribution and the temporal autocorrelation.

I study the dynamics of equation (1) using a mixture of analytical and numerical methods. The analysis is based on the per capita growth rates $\log f$ averaged over fluctuations in the environmental variables and the strength of competition (Chesson 1994). The analysis assumes that the maximal per capita growth rates, $\mathbb{E}[\log f(0, \bar{e}_i + \Delta e_i(t))]$, of each species in the absence of competition are positive and that the fitness function f exhibits compensating density dependence. These assumptions ensure there exists a unique stationary distribution for the subsystem consisting of species i and the two environmental variables $E_1 = \bar{e}_1 + \Delta e_1$ and $E_2 = \bar{e}_2 + \Delta e_2$ (Benaïm and Schreiber 2009). Let $(\hat{n}_i, \hat{E}_1, \hat{E}_2)$ be random variables with this stationary distribution. Here, the stationary distribution of the competitive strengths equals $\hat{C}_i = a_i \hat{n}_i$. Conditions for coexistence or exclusion depend on the invasion growth rate of species $j \neq i$

$$r_j = \mathbb{E}[\log f(\hat{C}_i, \hat{E}_j)] \quad j \neq i, \tag{2}$$

which corresponds to the average per capita growth rate of species j when it is rare and species i is common. If both invasion growth rates are positive ($r_1 > 0$, $r_2 > 0$), then the species coexist in the sense of stochastic persistence (see theorem 1 in Benaïm and Schreiber 2019), that is, a statistical tendency to stay away from the extinction set (fig. 1*A*). If $r_1 < 0 < r_2$ (respectively, $r_2 < 0 < r_1$), then species 2 excludes species 1 (respectively, species 1 excludes species 2; see corollary 2 in Benaïm and Schreiber 2019; fig. 1*B*). Finally, if both invasion growth rates are negative, then the system exhibits a stochastic bistability: whenever both species are initially present, there is a positive probability ($p > 0$ depending on the initial densities) that species 1 is excluded and a complementary positive probability ($1 - p > 0$) that species 2 is excluded (see theorem 3 and corollary 2 in Benaïm and Schreiber 2019).

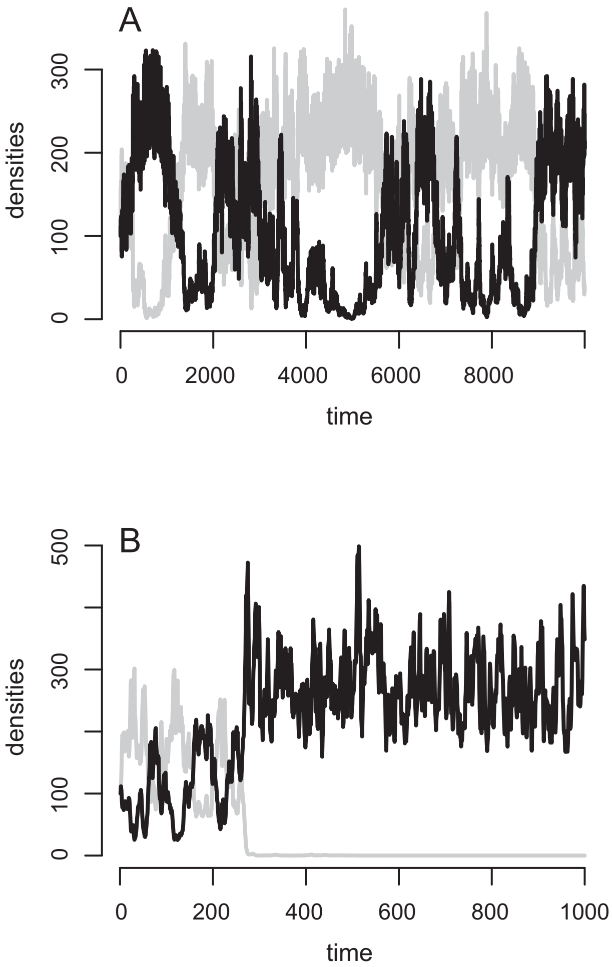

Figure 1: Stochastic coexistence (*A*) or exclusion (*B*) for competition in a fluctuating environment. Parameters: Fitness function (4) with fluctuations in survival, with $\lambda = 2$ and $a_1 = a_2 = 0.01$. $Z_i(t)$ are normally distributed with means 0, standard deviations $\sigma_i = 0.5$, cross correlation $\tau = -1$, and autocorrelations $\rho = -0.5$ in *A* and $\rho = 0.5$ in *B*.

To derive analytic approximations for the invasion growth rates r_j, I use a diffusion-type scaling in which $\bar{e}_1 - \bar{e}_2$, σ_1^2, and σ_2^2 are small and of the same order (Turelli 1977; Karlin and Taylor 1981). To illustrate the analytic results for general model (1), I numerically compute the invasion growth rates for fitness functions f with a density-dependent component $\lambda/(1 + C)$ and a density-independent component s. In the theoretical and empirical literature (e.g., Adler et al. 2007; Godoy et al. 2014), the density-dependent term is usually interpreted as a maximal per capita fecundity λ that is reduced by competition C, while the density-independent term $0 < s < 1$ corresponds to survivorship. I examine environmentally driven fluctuations in both terms. For fluctuations in the density-dependent term, the fitness function equals

$$f(C, E_i) = \frac{\exp(E_i)}{1 + C} + s, \tag{3}$$

while for fluctuations in the density-independent terms it equals

$$f(C, E_i) = \frac{\lambda}{1 + C} + \frac{\exp(E_i)}{1 + \exp(E_i)}. \tag{4}$$

In both cases, the variables $Z_i(t)$ are drawn from bivariate normals with mean 0, variances σ_i^2, and cross correlation τ. Thus, with their traditional interpretation, the fluctuations in equation (3) correspond to lognormally distributed fluctuations in maximal fecundities, and the fluctuations in equation (4) correspond to logit-normally distributed fluctuations in survival. While I focus on this traditional interpretation of equations (3) and (4), one can reverse their interpretation for species where density dependence acts more strongly on survivorship than reproduction, for example, in salmonids (Grossman and Simon 2020).

Results

I first present results for the deterministic model, which show that stable coexistence does not occur without environmental fluctuations. Next, I present results for environmental fluctuations, where species only differ to the degree the environmental responses are cross correlated, that is, to the extent $\rho < 1$. In this special case, the deterministic dynamics are neutrally stable, and environmental fluctuations lead to coexistence, to fluctuating neutral coexistence, or to a stochastic priority effect. Finally, I present results in which the species differ in their mean environmental response ($\bar{e}_1 \neq \bar{e}_2$), the variation in their environmental responses ($\sigma_1 \neq \sigma_2$), and the correlation in their environmental responses. These results highlight when environmental stochasticity reverses competitive outcomes as well as stabilizes competitive interactions.

Neutrality or Exclusion in Constant Environments

When the mean environmental responses are equal ($\bar{e}_1 = \bar{e}_2$) and there are no environmental fluctuations ($\sigma_1 = \sigma_2 = 0$), the species exhibit neutral coexistence (proof is provided in the appendix, available online). Specifically, there exists a line of equilibria connecting the single-species equilibria. Community trajectories always converge to one of these equilibria, but different initial conditions can converge to different equilibria. This coexistence is not stable in that small pulse perturbations typically shift the community to a different equilibrium state (Schreiber 2006). In contrast, if one species has a higher mean environmental response than the other ($\bar{e}_1 \neq \bar{e}_2$), then this species competitively excludes the other species (proof is provided in the appendix). These conclusions are consistent with general theory on limiting similarity (see, e.g., Meszéna et al. 2006; Pásztor et al. 2016).

From Neutrality to Coexistence or Alternative Stable States

The simplest case in which environmental fluctuations alter ecological outcomes is when both species have the same mean environmental response ($\bar{e}_1 = \bar{e}_2$) and experience the same degree of variation in their environmental response ($\sigma_1 = \sigma_2$). Without environmental fluctuations, this leads to neutral coexistence in which $r_j = 0$ for both species. With environmental fluctuations, our diffusion approximation for model (1) yields (derivation is provided in the appendix)

$$r_j \approx \frac{\partial^2 \log f}{\partial C \partial E} \times \mathrm{Cov}[\hat{C}_{\mathrm{i}}, \hat{E}_{\mathrm{j}} - \hat{E}_{\mathrm{i}}], \qquad (5)$$

where the mixed partial derivative, $(\partial^2 \log f)/(\partial C \partial E)$, is evaluated at $E = \bar{e}_j$ and the equilibrium value $C = a_i n_i^*$, where $f(a_i n_i^*, \bar{e}_i) = 1$. The sign of this mixed partial derivative determines whether the log fitness function is superadditive (positive sign) or subadditive (negative sign) with respect to the interactive effects of competition and environmental fluctuations (see, e.g., Puterman 2014). Subadditivity means that the log fitness function, $\log f$, is less sensitive to the effects of competition when environmental conditions are poor. This corresponds to population buffering, a necessary component of the storage effect (Chesson 1994; Ellner et al. 2016). Superadditivity, in contrast, means that the log fitness function is more sensitive to the effects of competition when environmental conditions are poor, but also that it is less sensitive to the effects of competition when environmental conditions are good. For example, for fitness function (3) with fluctuations in fecundity and positive survival $0 < s < 1$, the log fitness function is subadditive and population buffering occurs. In contrast, for fitness function (4) with fluctuations in survival, the log fitness function is superadditive and populations are less sensitive to competition in years with high survival.

The final term in equation (5) corresponds to the covariance between the strength of competition due to the common species (C_i) and the difference ($E_j - E_i$) between the environmental responses of the rare and common species. This term is positive when years with high and low densities, respectively, of the common species also correspond to years where the rare species has a higher and a lower environmental response, respectively. This covariance for model (1) is proportional to a product of three terms (derivation is provided in the appendix):

$$\mathrm{Cov}\left[\hat{C}_i, \hat{E}_j - \hat{E}_i\right] = -\mathrm{k} \times \rho \times (1 - \tau) \times \sigma^2, \qquad (6)$$

where the proportionality term $k = k(\rho)$ is positive for all ρ and $k(\rho) \times \rho$ is an increasing function of ρ. When the environmental fluctuations are serially uncorrelated ($\rho = 0$) or the species have identical responses to the environment ($\tau = 1$), this covariance is zero; consequently, the invasion growth rates equal zero, and the species exhibit a fluctuating form of neutral coexistence. In contrast, when there are species-specific response to the environment ($\tau < 1$) and environmental fluctuations are autocorrelated ($\rho \neq 0$), equation (6) implies that the sign of $\mathrm{Cov}[\hat{C}_{\mathrm{i}}, \hat{E}_{\mathrm{j}} - \hat{E}_{\mathrm{i}}]$ is opposite of the sign of the autocorrelation. Hence, in positively autocorrelated environments, years with greater densities of the common species tend to be years where the environmental conditions are less favorable to the rare species. Moreover, the magnitude of the covariance is greater for positive autocorrelations than negative autocorrelations—that is, $|\mathrm{Cov}[\hat{C}_{\mathrm{i}}, \hat{E}_{\mathrm{j}} - \hat{E}_{\mathrm{i}}]|$ is greater for a given $\rho > 0$ than for the corresponding $-\rho < 0$ (derivation is provided in the appendix). Intuitively, positive autocorrelations generate greater variance in the strength of competition than negative autocorrelations and, thereby, yield a greater covariance.

Collectively, equations (5) and (6) imply that environmental fluctuations promote coexistence (i.e., $r_j > 0$) in two situations: (i) the log fitness is superadditive and environmental fluctuations are negatively autocorrelated or (ii) the log fitness is subadditive and environmental fluctuations are positively autocorrelated (i.e., the storage effect). In contrast, if (iii) the log fitness function is superadditive and environmental functions are positive autocorrelated or (iv) the log fitness function is subadditive and the fluctuations are negatively autocorrelated, then the system is stochastically bistable: with complementary, positive probabilities species 1 or 2 is excluded.

Figure 2 illustrates these analytical conclusions for the specific fitness functions with fluctuating fecundity (eq. [3]) or with fluctuating survival (eq. [4]). As the log fitness for equation (3) is subadditive with respect to fecundity, positively autocorrelated fluctuations in fecundity mediate coexistence, while negative autocorrelations lead to stochastic bistability (fig. 2*A*). In contrast, as the log fitness for equation (4) is superadditive with respect to survival, positively autocorrelated fluctuations in survival lead to stochastic bistability, while negative autocorrelations promote coexistence (fig. 2*B*).

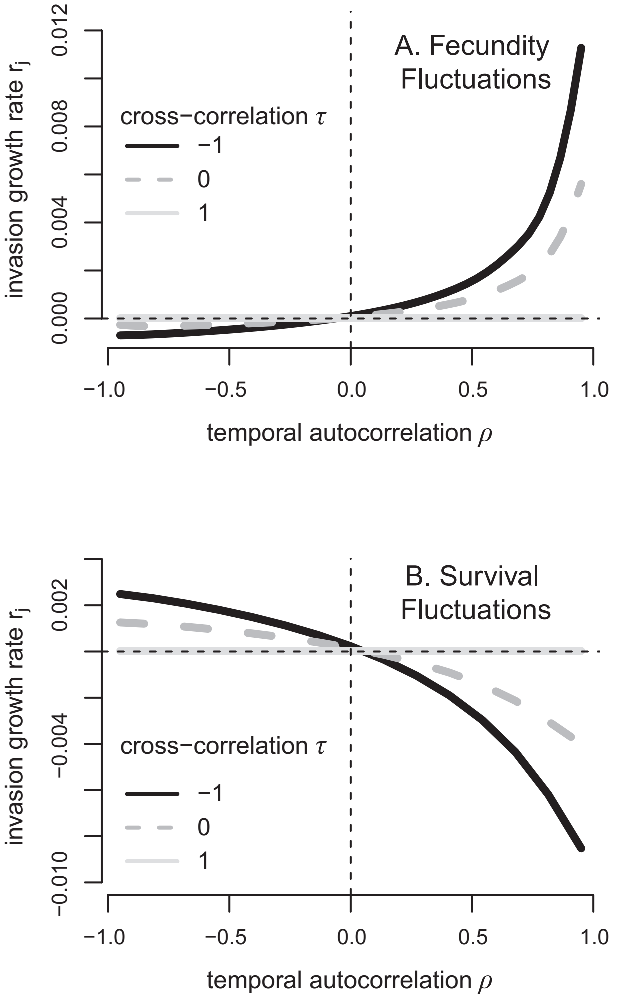

Figure 2: Positively autocorrelated fluctuations in fecundity (*A*) and negative autocorrelated fluctuations in survival (*B*) mediate coexistence. Shown are numerically computed invasion growth rates r_j as a function of the temporal autocorrelation ρ for competing species. In *A*, the fitness function *f* is given by equation (3), and there are fluctuations in fecundity. In *B*, the fitness function is given by equation (4) with fluctuations in survival. Different curves correspond to different levels of cross correlation τ, where competitors only differ demographically if $\tau < 1$. For positive invasion growth rates, the competitors coexist (stochastic persistence). For negative invasion growth rates, each competitor is excluded with positive complementary positive probabilities (stochastic bistability). Parameters: $a_1 = a_2 = 1$ and $(Z_1(t), Z_2(t))$ is normally distributed with standard deviation 0.3 for both panels. For *A*, $s = 0.9$ and $\bar{e} = \ln 2$. For *B*, $\bar{e} = 0$ and $\lambda = 2$.

The Effects of Fitness Differences and Nonlinear Averaging

Asymmetries in the mean response ($\bar{e}_1 \neq \bar{e}_2$) and the variability of these responses ($\sigma_1 \neq \sigma_2$) lead to two additional terms in the invasion growth rate for model (1) (derivation is provided in the appendix):

$$r_j \approx \frac{\partial \log f}{\partial E}(\bar{e}_j - \bar{e}_i) + \frac{1}{2}\frac{\partial^2 \log f}{\partial E^2}(\sigma_j^2 - \sigma_i^2) + \frac{\partial^2 \log f}{\partial C \partial E} \times \mathrm{Cov}[\hat{C}_i, \hat{E}_j - \hat{E}_i]. \tag{7}$$

As the log fitness increases with the environmental response variable (*E*), the first term in equation (7) is proportional to the difference, $\bar{e}_j - \bar{e}_i$, in the mean environmental response between the rare and common species. Intuitively, when the rare species benefits more, on average, from the environmental conditions ($\bar{e}_j > \bar{e}_i$), its invasion growth rate is larger. The sign of the second term in equation (7) depends on the concavity of log fitness with respect to the environmental response variable. When the log fitness function is concave at this point, the second term contributes positively to the invasion growth if the rare species exhibits less variation in its environmental response ($\sigma_i^2 < \sigma_j^2$). This second term corresponds to the effect of nonlinear averaging (Chesson 1994). Namely, there is a reduction (respectively, increase) in the invasion growth rate due to the concavity (respectively, convexity) of the log fitness function.

Differences in the variation of the environmental responses also impact the covariance between the density of common species and difference in the environmental responses, that is, the third term of equation (7). Specifically, a refinement of expression (6) shows that (derivation is provided in the appendix)

$$\mathrm{Cov}[\hat{C}_i, \hat{E}_j - \hat{E}_i] = -k \times \rho \times \sigma_i(\sigma_i - \tau\sigma_j), \tag{8}$$

where *k* is a positive constant. To better understand this expression, I partition it into the sum of two terms: a community average term and a species-specific term (Chesson 2018). The community average term equals the average of the covariances $\mathrm{Cov}[\hat{C}_1, \hat{E}_2 - \hat{E}_1]$ and $\mathrm{Cov}[\hat{C}_2, \hat{E}_1 - \hat{E}_2]$ and contributes equally to both species invasion growth rates. This community average equals

$$-k \times \rho \times \left[\frac{\sigma_1^2 + \sigma_2^2}{2} - \tau\sqrt{\sigma_1^2\sigma_2^2}\right].$$

As the arithmetic mean $(\sigma_1^2 + \sigma_2^2)/2$ is greater than the geometric mean $(\sigma_1^2\sigma_2^2)^{1/2}$, the community average term has the opposite sign of the sign of the autocorrelation ρ. On the other hand, the species-specific term equals

$$\frac{k \times \rho(\sigma_j^2 - \sigma_i^2)}{2}.$$

Thus, the species-specific contribution to $\mathrm{Cov}[\hat{C}_i, \hat{E}_j - \hat{E}_i]$ has the same sign as the autocorrelation ρ for the species with larger variance and the opposite sign for the species with smaller variance. This asymmetry may benefit or harm the species with the smaller variance. For example, if there is population buffering and positively autocorrelated fluctuations, then the species with the smaller variance benefits more from the storage effect than the species with the larger variance. Alternatively, if there is negative population buffering and negative autocorrelated fluctuations, then the species with the larger variance benefits more from the environment-competition covariance.

To illustrate these analytical results, figure 3 shows invasion growth rates r_j with fitness function (3) with fluctuations in fecundity. In figure 3*A*, the species exhibit only differences in their mean environmental response and have negatively correlated environmental responses. With small differences in the mean environmental response, sufficiently negative autocorrelations result in bistability, intermediate autocorrelations result in the species with the larger mean environmental response excluding the other species, and sufficiently positive autocorrelations mediate coexistence. When the difference in mean environmental response is large, sufficiently positive autocorrelations mediate coexistence; otherwise, the species with the lower mean environmental response is excluded. In figure 3*B*, one species has a higher mean environmental response ($\bar{e}_1 > \bar{e}_2$) but also experiences greater variability in its environmental response ($\sigma_1 > \sigma_2$). When the difference in variation is sufficiently low, species 1 excludes species 2 unless temporal autocorrelation is sufficiently high. In contrast, when the difference in variation is sufficiently high, species 2 excludes species 1 unless temporal autocorrelation is sufficiently high. This reversal in fates stems from the reduction of r_1 as a result of greater environmental variation simultaneously increasing the negative effect of nonlinear averaging and reducing the strength of the storage effect.

Discussion

Hutchinson (1961, p. 138) wrote that “the diversity of the plankton was explicable primarily by a permanent failure to achieve equilibrium as the relevant external factors changes.” It was not until 30 years later that Peter Chesson

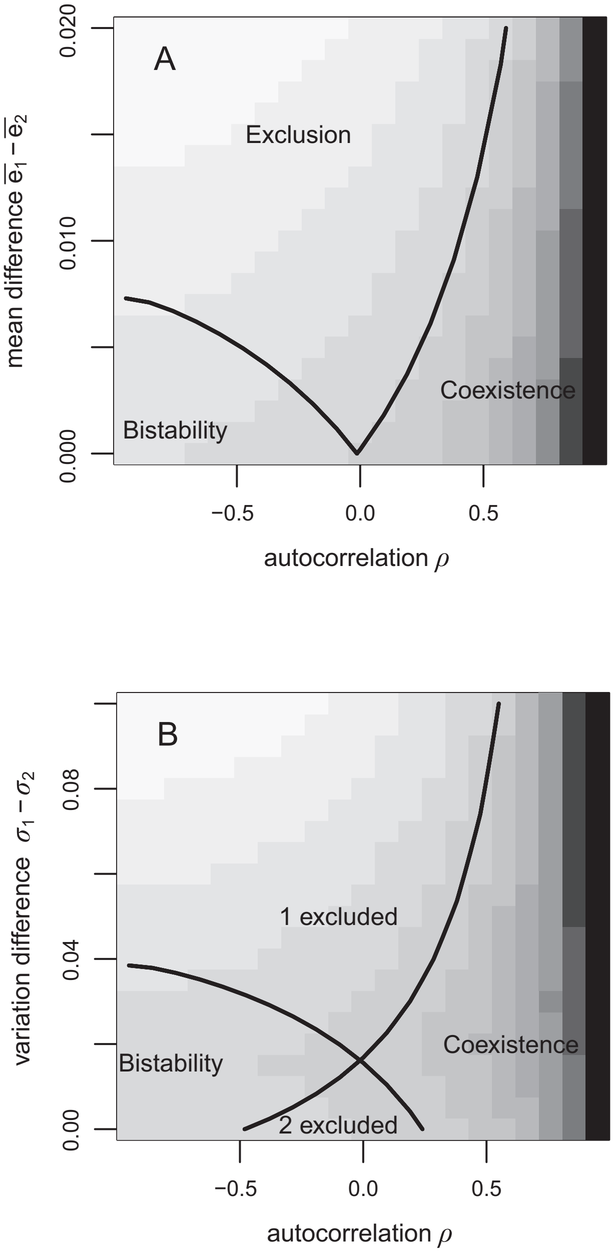

Figure 3: Interactive effects of fitness differences and autocorrelation on ecological outcomes. In *A*, species 1 has a larger mean environmental response ($\bar{e}_1 - \bar{e}_2 > 0$) over species 2. In *B*, species 1 has a slightly stronger mean environmental response than species 2 but experiences greater environmental variation ($\sigma_1 - \sigma_2 \geq 0$) than species 2. Regions of coexistence, competitive exclusion, and bistability are shown. Solid contour lines correspond to $r_1 = 0$ and $r_2 = 0$. Shading is determined by the minimum of the invasion growth rates, $\min\{r_1, r_2\}$, from light gray for the most negative values to black for the most positive values. Parameters: fitness function f is given by equation (3) with $s = 0.9$, $\bar{e}_2 = \ln 2$, and $\bar{e}_1 = \ln 2.01$ in *B* and with $\bar{e}_1$ determined by the mean difference in the environmental response $\bar{e}_1 - \bar{e}_2$ in *A*; $Z_i(t)$ are normally distributed with $\tau = -1$ and $\sigma_1 = \sigma_2 = 0.3$ in *A* and with $\sigma_2 = 0.3$ and σ_1 as shown in *B*.

developed a theoretical framework for precisely identifying fluctuation-dependent mechanisms for coexistence (see, e.g., Chesson 1983, 1988, 1994; Chesson and Warner 1981), including the storage effect. The storage effect stabilizes coexistence when (i) there is a positive correlation between the environmental response of each species and the competition experienced by that species, (ii) there are species-specific environmental responses, and (iii) there is buffered population growth in which species are less sensitive to competition in years of poor environmental conditions. In serially uncorrelated environments, the first condition requires that there is a direct and immediate impact of the environmental response on the strength of competition. This occurs, for example, in annual populations with year to year variation in germination rates: when more seeds germinate, more plants compete for limiting resources. This direct and immediate impact, however, does not occur when maximal yield or adult survival varies, as in the models considered here. However, when the temporal fluctuations in these demographic rates are autocorrelated, the analysis presented here reveals that the environment-competition covariance can still occur in these fundamental demographic parameters. Furthermore, these autocorrelated fluctuations highlight how another, underappreciated stabilizing mechanisms arises when conditions (i) and (iii) simultaneously do not hold.

Hutchinson (1961) hinted at temporal autocorrelations as a stabilizing mechanism when he wrote, “equilibrium would never be expected in nature whenever complete competitive replacement of one species by another occurred in a time (t_c), of the same order, as the time (t_e) taken for a significant seasonal change in the environment.” As competitive exclusion typically takes several generations, Hutchinson’s quote implies that coexistence requires the shifts in environmental conditions favoring differing species to take several generations. Thus, the environmental conditions must be positively autocorrelated over several generations. Consistent with this suggestion, I show that when there is population buffering (i.e., log fitness is subadditive) and there are species-specific environmental responses, positively autocorrelated fluctuations in environmental conditions yield a storage effect. Namely, condition (i) is satisfied as better years for one species tend to be preceded by better years for this species and, therefore, tends to lead to higher densities (greater competition) in the focal year. The strength of this environment-competition covariance depends on the degree that competitive communities are biotically saturated with individuals. For saturated communities, such as those modeled by Chesson’s lottery model (Chesson and Warner 1981) and Hubbell’s neutral model (Hubbell 2001), autocorrelated fluctuations cannot generate this covariance when one competitor is rare; the abundance of the common species remains relatively constant. In contrast, for less saturated communities, which are common (Houlahan et al. 2007), fluctuations in environmental conditions can lead to fluctuations in the abundance of the common species and, when positively autocorrelated, lead to a positive environment-competition covariance. Our findings about positive autocorrelations generating a storage effect are consistent with three prior studies (Jiang and Morin 2007; Li and Chesson 2016; Schreiber et al. 2019). Jiang and Morin (2007) manipulated temporal fluctuations experienced by two species of ciliated protists competing for bacterial resources. These temperature fluctuations had large effects on the intrinsic growth rates of the two species, consistent with the fluctuating fecundity model considered here. When the temperature fluctuations were temporally uncorrelated, their experimental results suggested that resource partitioning and temperature-dependent competitive effects lead to coexistence, not a storage effect. In contrast, when temperature fluctuations were positively autocorrelated, their experimental results suggested that resource partitioning and the storage effect lead to coexistence. Alternatively, for continuous-time models of competing consumers whose attack rates are driven by environmental fluctuations, Li and Chesson (2016) found that fast resource depletion generates a positive environment-competition covariance and, thereby, can promote coexistence. Although not explicitly stated by Li and Chesson (2016), this positive environment-competition covariance arises from attack rates being positively autocorrelated at the timescale of the resource depletion. Finally, using models with a symmetric version of fitness function (3), Schreiber et al. (2019) demonstrated numerically that the invasion growth rates r_j increase with positive autocorrelations. However, they did not analyze this numerical trend.

Autocorrelated fluctuations also can lead to an alternative stabilizing mechanism when (i′) there is a negative covariance between environment and competition, (ii) there are species-specific environmental responses, and (iii′) species are less sensitive to competition in years of good environmental conditions. Condition (iii′) can arise when adult survival fluctuates. Condition (i′) occurs when fluctuations in survival are negatively autocorrelated, as populations densities are higher in years following higher survival but survival in the following year tend to be lower. My analytical and numerical results show, however, that the strength of this stabilizing effect is weaker for a given magnitude of negative autocorrelation than the strength of the storage effect for the same magnitude of positive autocorrelation. Negatively autocorrelated environments can arise in a variety of ways (Metcalf and Koons 2007). For example, approximately 5% of sites analyzed by Sun et al. (2018) exhibit negatively autocorrelated rainfall. Adler and Levine (2007) found that species richness in central

North American grasslands increased most in wet years that followed dry years. Alternatively, models and empirical studies show that overcompensatory or delayed density-dependent feedbacks can generate negatively autocorrelated fluctuations in densities (May 1976; Tilman and Wedin 1991; Crone and Taylor 1996; Gilg et al. 2003). If these fluctuations in densities occur in an herbivore, pathogen, or predator, then they can generate negatively autocorrelated fluctuations in survival of competing plants, hosts, or prey. Finally, competing species that exhibit two to three generations per year may experience negative autocorrelations in seasonal environments (Metcalf and Koons 2007).

Autocorrelated fluctuations in survival or fecundity can generate alternative stable states and drive complex shifts in ecological outcomes. Alternative stable states arise as a stochastic priority effect: either species has a nonzero probability of being excluded, but the species at initially lower frequencies is more likely to be excluded. For small differences in mean fitness, stochastic induced alternative states arise whenever buffered populations experience a negative environment-competition covariance or whenever unbuffered populations experience a positive environment-competition covariance. Chesson (1988) highlights this possibility for annual plants with fluctuating seed survival, but his observation appears to be underappreciated in the priority effects literature (Fukami 2015; Fukami et al. 2016). Shifts in temporal autocorrelations also generate complex shifts in ecological outcomes when one species has an inherent competitive advantage over the other, such as a higher mean environmental response or less variability in their environmental response. Under these circumstances, shifts from negative to positive temporal autocorrelations can result in shifts from a stochastic priority effect to competitive exclusion to coexistence (fig. 3).

In conclusion, temporally autocorrelated environmental fluctuations indirectly generate a covariance between environmental conditions and the strength of competition. When this covariance is positive and there is population buffering, this leads to a storage effect (Chesson 1994, 1988). As positive autocorrelations are seen in many climatic variables, accounting for these autocorrelations in data-driven models (Chu and Adler 2015; Ellner et al. 2016, 2018) likely will lead to more empirically based examples of the storage effect. In contrast, when there is a negative environment-competition covariance, an alternative stabilizing mechanism to the storage effect arises provided species are less sensitive to competition in years where environmental conditions are favorable. As there are simple, ecologically plausible conditions that generate this alternative stabilizing mechanism, it will be exciting to see whether empirically based demonstrations will be found.

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Data and Code Availability

R code for this article is available on Zenodo (Schreiber 2020).

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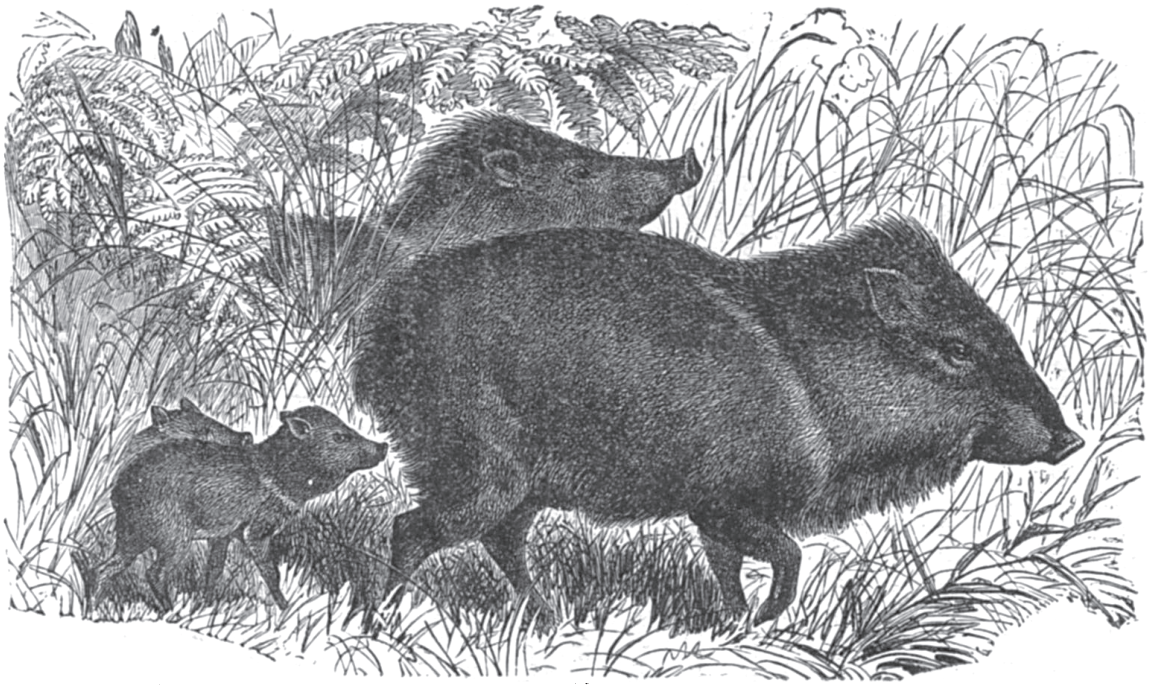

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Appendix from S. J. Schreiber, "Positively and Negatively Autocorrelated Environmental Fluctuations Have Opposing Effects on Species Coexistence"
(Am. Nat., vol. 197, no. 4, p. 405)

In this appendix, I provide the mathematical details of the analysis of the deterministic and stochastic versions of model (1). Define the new coordinate system $x_i = a_i n_i$, in which model (1) becomes

$$x_i(t+1) \quad = x_i(t) f(x_1(t) + x_2(t), \bar{e}_i + \Delta e_i(t)), \Delta e_i(t+1) = \rho \Delta e_i(t) + \sqrt{1-\rho^2}\ Z_i(t+1), \tag{A1}$$

where $Z_i(1), Z_i(2), \ldots$ are a sequence of independently and identically distributed (i.i.d.) random variables with mean 0, variance σ_i^2, and cross correlation τ. Throughout this analysis, I assume that f is a continuous positive function, that $C \mapsto f(C,e)$ is a decreasing function for all e, that $e \mapsto f(C,e)$ is an increasing function for all C, and that $C \mapsto Cf(C,e)$ is an increasing bounded function. The first two assumptions ensure that fitness depends continuously on competition and environment, decreases with competition, and increases with the environmental variable. The third assumption corresponds to compensating density dependence and populations remaining bounded. A classic example of such a fitness function is the Beverton-Holt function with survival; that is, $f(C,e) = \lambda/(1+C) + s$, where the maximal fitnesses λ or the survivorships s are functions of e. Finally, I assume that $Z_i(t)$ take values in a compact set and that $|\rho| < 1$. Collectively, these assumptions imply that the dynamics of equation (A1) are dissipative; that is, there is a compact set in $K \subset [0,\infty)^2 \times \mathbb{R}^2$ such that nonnegative solutions of equation (A1) eventually enter and remain in K for sufficiently large t.

Below, I first analyze the deterministic dynamics of equation (A1), that is, when $\Delta e_i(t) = 0$ for all t. This analysis shows that there are three possible competitive outcomes: species 1 excludes species 2, species 2 excludes species 1, or neutral coexistence, in which the dynamics converge to a line of equilibria. Next, I analyze the stochastic dynamics of equation (A1) in three steps. First, using results from Benaïm and Schreiber (2009), I provide a condition that ensures that each species can persist in isolation. When this condition holds, the dynamics of the environmental variables and each species converges to a unique stationary distribution; let $(\widehat{x}_i, \widehat{\Delta e}_1, \widehat{\Delta e}_2)$ be random variables with this stationary distribution. When this condition does not hold, the species asymptotically converges to extinction with probability 1. For the remainder of the stochastic analysis, I assume that the condition for each species persisting holds. Under this assumption, I use results from Benaïm and Schreiber (2019) to characterize coexistence and exclusion using the invasion growth rates r_j. Finally, I use a diffusion type of approximation to derive the approximations for the invasion growth rates r_j presented in the main text.

Deterministic Analysis

The model assumptions imply that equation (A1) is a strictly monotone, planar map with respect to the competitive ordering (see, e.g., Smith 1998). Each species persists individually if $f(0,\bar{e}_i) > 1$ for $i = 1,2$. Assume that this condition holds for each species. Then there are three cases to consider. First, assume that $\bar{e}_1 > \bar{e}_2$. Define $\lambda = \max_{(x_1,x_2)\in K} f(x_1+x_2,\bar{e}_2)/f(x_1+x_2,\bar{e}_1)$, which is strictly less than 1 as $\bar{e}_1 > \bar{e}_2$, $e \mapsto f(C,e)$ is a strictly increasing continuous function, and K is compact. Given any solution $(x_1(t), x_2(t))$ to equation (A1) with $x_1(0) > 0$, we get $x_2(t)/x_1(t) \leq \lambda^t (x_2(0)/x_1(0))$. As $x_1(t)$ is uniformly bounded (i.e., $(x_1(t),x_2(t)) \in K$), $x_2(t)$ converges to zero as $t \to \infty$. Similarly, if $\bar{e}_2 > \bar{e}_1$, species 2 excludes species 1. Finally, consider the case that $\bar{e}_1 = \bar{e}_2$. Then $x_1(t)/x_2(t) = x_1(0)/x_2(0)$ for all time whenever $x_2(0) > 0$. Namely, the relative frequency of either species does not change over time. Moreover, as $y(t) = x_1(t) + x_2(t)$ satisfies $y(t+1) = y(t) f(y(t), \bar{e}_1)$, which a strictly monotone map with a unique positive equilibrium $y^* > 0$, $x_1(t) + x_2(t)$ converges to the y^* as $t \to \infty$. Hence, $x_i(t)$ converges to $x_i(0) y^*/(x_1(0) + x_2(0))$ as $t \to \infty$ for $i = 1,2$. Thus, there is a globally stable line of equilibria given by $\{(y^* p, y^*(1-p)) : 0 \leq p \leq 1\}$.

General Stochastic Analysis

Define $g(x,e) = \log f(x,e)$ and assume $|\rho| < 1$. As the dynamics of Δe_i are given by a multivariate autoregressive process where the linear term is contracting (i.e., $|\rho| < 1$) and $Z(t)$ are uniformly bounded, $\Delta e_i(t)$ converge to a unique stationary distribution (see, e.g., Schreiber and Moore 2018). For each species i in isolation of the other species, their per capita growth rate at low densities is $\mathbb{E}[g(0, \bar{e}_i + \widehat{\Delta e_i})] > 0$. When this invasion growth rate is positive and $x_i(0) > 0$, theorem 1 in Benaïm and Schreiber (2009) implies that solutions $((x_i(t), \Delta e_1(t), \Delta e_2(t))$ for the species i subsystem with $x_i(0) > 0$ converge to a unique stationary distribution. Let $(\widehat{x}_i, \widehat{\Delta e_1}, \widehat{\Delta e_2})$ be random variables with this stationary distribution. In contrast, if $\mathbb{E}[g(0, \bar{e}_i + \widehat{\Delta e_i})] < 0$, proposition 1 in Benaïm and Schreiber (2009) implies that $x_i(t)$ converges to zero with probability 1. From the rest of the stochastic analysis, assume that $\mathbb{E}[g(0, \bar{e}_i + \widehat{\Delta e_i})] > 0$ for both species $i = 1, 2$.

The invasion growth rate of species $j \neq i$ when species i is at its stationary distribution equals

$$r_j = \mathbb{E}[g(\widehat{x}_i, \bar{e}_j + \widehat{\Delta e_j})].$$

Theorem 1 from Benaïm and Schreiber (2019) implies that the two species coexist (in the sense of stochastic persistence) whenever $r_1 > 0$ and $r_2 > 0$. In contrast, if $r_j < 0$, then theorem 3 from Benaïm and Schreiber (2019) implies that species j becomes extinct with high probability whenever its initial density is sufficiently low. Under suitable accessibility assumptions (for definitions, see Benaïm and Schreiber 2019), stronger conclusions hold when $r_j < 0$. In particular, if $r_1 > 0 > r_2$ (respectively, $r_2 > 0 > r_1$), then species 1 excludes species 2 with probability 1 (respectively, species 2 excludes species 1) whenever $x_1(0) > 0$ (respectively, $x_2(0) > 0$). Alternatively, if $r_1 < 0$ and $r_2 < 0$, then either species, with complementary positive probabilities, becomes extinct whenever both are initially present (i.e., a stochastic priority effect).

Diffusion Scaling to Approximate r_j

For any $\varepsilon > 0$, assume that (i) $Z_i(t) = \varepsilon \eta_i(t)$ where $\eta_i(t)$ are i.i.d. with mean 0, variance v_i, and $\mathbb{E}[\eta_1(t)\eta_2(t)] = \tau$ and that (ii) $\bar{e}_i = \bar{e} + \varepsilon^2 a_i$. To ensure each species persists in the absence of the other, assume that the invasion growth rate $g(0, \bar{e})$ is positive. Then there exists $x^* > 0$ such that $g(x^*, \bar{e}) = 0$. The term x^* corresponds to the single-species equilibrium density in the absence of fitness differences and environmental fluctuations. Assume that $g(x, e)$ is three times continuously differentiable, and let g_x, g_e, g_{xe}, and so on denote the partial derivatives $(\partial g/\partial x)(x^*, \bar{e})$, $(\partial g/\partial e)(x^*, \bar{e})$, $(\partial^2 g/\partial x \partial e)(x^*, \bar{e})$, and so on evaluated at $(x^*, \bar{e})$.

Consider species i as the common or resident species and $j \neq i$ as the rare or invading species. Proposition 1(iii) from Benaïm and Schreiber (2019) implies that the invasion growth of i, $\mathbb{E}[g(\widehat{x}_i, \bar{e}_i + \widehat{\Delta e_i})]$, at its stationary distribution equals zero. Thus, taking a Taylor expansion and defining $\widehat{\Delta x_i} = \widehat{x}_i - x^*$ yields

$$\begin{aligned} 0 &= \mathbb{E}[g(\widehat{x}_i, \bar{e}_i + \widehat{\Delta e_i})] = g(x^*, \bar{e}) + g_x \mathbb{E}[\widehat{\Delta x_i}] + g_e \mathbb{E}[\varepsilon^2 a_i + \widehat{\Delta e_i}] + \frac{g_{xx}}{2}\mathbb{E}[(\widehat{\Delta x_i})^2] + \frac{g_{ee}}{2}\mathbb{E}[(\varepsilon^2 a_i + \widehat{\Delta e_i})^2] \\ &\quad + g_{xe}\mathbb{E}[(\widehat{\Delta x_i})(\varepsilon^2 a_i + \widehat{\Delta e_i})] + \mathrm{O}(\varepsilon^3) = g_x \mathbb{E}[\widehat{\Delta x_i}] + \varepsilon^2 \left(g_e a_i + \frac{g_{ee}}{2} v_i \right) + \frac{g_{xx}}{2}\mathbb{E}[(\widehat{\Delta x_i})^2] + g_{xe}\mathbb{E}[\widehat{\Delta x_i}\widehat{\Delta e_i}] + \mathrm{O}(\varepsilon^3), \end{aligned} \tag{A2}$$

as $g(x^*, \bar{e}) = 0$ due to the definition of x^*, $\mathbb{E}[\widehat{\Delta e_i}] = 0$, $\mathbb{E}[(\widehat{\Delta e_i})^2] = v_i$ and $\mathbb{E}[\widehat{\Delta x_i}\varepsilon^2 a_i] = \mathrm{O}(\varepsilon^3)$.

Similarly, we get

$$\begin{aligned} r_j &= \mathbb{E}[g(\widehat{x}_i, \bar{e}_j + \widehat{\Delta e_j})] = g(x^*, \bar{e}) + g_x \mathbb{E}[\widehat{\Delta x_i}] + g_e \mathbb{E}[\varepsilon^2 a_j + \widehat{\Delta e_j}] + \frac{g_{xx}}{2}\mathbb{E}[(\widehat{\Delta x_i})^2] + \frac{g_{ee}}{2}\mathbb{E}[(\varepsilon^2 a_j + \widehat{\Delta e_j})^2] \\ &\quad + g_{xe}\mathbb{E}[(\widehat{\Delta x_i})(\varepsilon^2 a_j + \widehat{\Delta e_j})] + \mathrm{O}(\varepsilon^3) = g_x \mathbb{E}[\widehat{\Delta x_i}] + \varepsilon^2 \left(g_e a_j + \frac{g_{ee}}{2} v_j \right) + \frac{g_{xx}}{2}\mathbb{E}[(\widehat{\Delta x_i})^2] + g_{xe}\mathbb{E}[\widehat{\Delta x_i}\widehat{\Delta e_j}] + \mathrm{O}(\varepsilon^3). \end{aligned} \tag{A3}$$

Subtracting equation (A2) from equation (A3) yields

$$r_j = \varepsilon^2 \left(g_e(a_j - a_i) + \frac{g_{ee}}{2}(v_j - v_i) \right) + g_{xe}\mathbb{E}[\widehat{\Delta x_i}(\widehat{\Delta e_j} - \widehat{\Delta e_i})] + \mathrm{O}(\varepsilon^3). \tag{A4}$$

To get an explicit expression for $\mathbb{E}[\widehat{\Delta x_i}(\widehat{\Delta e_j} - \widehat{\Delta e_i})]$, one can approximate the dynamics of x_i as a first-order autoregressive process by linearizing equation (A1) at $(x_i, e_1, e_2) = (x^*, \bar{e}, \bar{e})$. To this end, define $F(x, e) = xf(x, e)$ and F_x, F_e as the partial derivatives $(\partial F/\partial x)(x^*, \bar{e})$, $(\partial F/\partial e)(x^*, \bar{e})$. Then, the first-order autoregressive approximation of equation (A1) is

$$\begin{aligned} \Delta x_i(t+1) &= F_x \Delta x_i(t) + F_e(\varepsilon^2 a_i + \Delta e_i), \\ \Delta e_i(t+1) &= \rho \Delta e_i(t) + \sqrt{1 - \rho^2} Z_i(t), \\ \Delta e_j(t+1) &= \rho \Delta e_j(t) + \sqrt{1 - \rho^2} Z_j(t). \end{aligned} \tag{A5}$$

Equivalently, defining $z = (\Delta x_i, \Delta e_i, \Delta e_j)$,

$$z(t+1) = \underbrace{\begin{bmatrix} F_x & F_e & 0 \\ 0 & \rho & 0 \\ 0 & 0 & \rho \end{bmatrix}}_{=:A} z(t) + \underbrace{\begin{bmatrix} F_e \varepsilon^2 a_i \\ \sqrt{1-\rho^2} Z_i(t) \\ \sqrt{1-\rho^2} Z_j(t) \end{bmatrix}}_{=:b(t)}.$$

The covariance matrix of $z(t)$, $\mathrm{Cov}[\hat{z}]$, at stationarity (see, e.g., Schreiber and Moore 2018) satisfies

$$\mathrm{vec}(\mathrm{Cov}[\hat{z}]) = (\mathrm{Id} - \mathrm{A} \otimes \mathrm{A})^{-1} \mathrm{vec}(\mathrm{Cov}[\mathrm{b(t)}]),$$

where $\mathrm{vec}(*)$ is a column vector given by concatenating the columns of its argument $*$ and $\otimes$ denotes the Kronecker product. Carrying out this calculation yields the approximations

$$\mathbb{E}[\widehat{\Delta x_i}\widehat{\Delta e_i}] = \frac{F_e \rho \sigma_1^2}{F_x \rho^3 - \rho^2 - F_x \rho + 1} \quad \text{and} \quad \mathbb{E}[\widehat{\Delta x_i}\widehat{\Delta e_j}] = \frac{F_e \rho \tau \sigma_1 \sigma_2}{F_x \rho^3 - \rho^2 - F_x \rho + 1}.$$

To see that the denominator of these expressions is positive for $|\rho| < 1$, define $h(y) = y\rho(\rho^2 - 1) - \rho^2 + 1$. As $F_x \in (0, 1)$ (i.e., the equilibrium is stable as the dynamics are compensatory), one needs to only consider $h(y)$ for $y \in (0, 1)$. The minimum of $h(y)$ occurs either at $y = 1$ or at $y = -1$ or at $0 < y < 1$, where $h'(y) = 0$. For $|\rho| < 1$, $h'(y) = \rho(\rho^2 - 1) = 0$ only when $\rho = 0$, in which case $h(y) = 1 > 0$. As $h(0) = 1 - \rho^2 > 0$ for $|\rho| < 1$ and $h(1) = \rho^3 - \rho^2 - \rho + 1 > 0$ for $|\rho| < 1$, it follows that $h(y) > 0$ for $y \in (0, 1)$ whenever $|\rho| < 1$.

Define

$$k(\rho) = \frac{F_e}{F_x \rho^3 - \rho^2 - F_x \rho + 1} > 0.$$

Then

$$r_j = g_e(\bar{e}_j - \bar{e}_i) + \frac{g_{ee}}{2}(\sigma_j^2 - \sigma_i^2) + k(\rho) g_{xe} \rho (\tau \sigma_j - \sigma_i) \sigma_i + \mathrm{O}(\varepsilon^3), \tag{A6}$$

as claimed in the main text. Let $H(\rho) = \rho k(\rho)$. Then

$$H'(\rho) = F_e \frac{\rho^2(1 - 2F_x \rho) + 1}{(F_x \rho^3 - \rho^2 - F_x \rho + 1)^2}.$$

As $0 < F_x < 1$, the numerator of $H'(\rho)$ is positive for all $\rho \in (-1, 1)$. Therefore, as claimed in the main text, $H(\rho)$ is an increasing function of ρ. Finally, consider $\rho > 0$. Then $k(-\rho) < k(\rho)$ if and only if $F_x \rho^3 - \rho^2 - F_x \rho + 1 < -F_x \rho^3 - \rho^2 + F_x \rho + 1$. This occurs if and only if $\rho^3 < \rho$, which is true whenever $\rho \in (0, 1)$. Thus, $|\rho k(\rho)| > |-\rho k(-\rho)|$ for any $\rho \in (0, 1)$, as claimed in the main text.