When rarity has costs: coexistence under positive frequency-dependence and environmental stochasticity

Sebastian J. Schreiber[1,†], Masato Yamamichi[2,3], and Sharon Y. Strauss[1]

[1]Department of Evolution and Ecology and Center for Population Biology, University of California, Davis

[2]Hakubi Center for Advanced Research, Kyoto University, Sakyo, Kyoto 606-8501, Japan

[3]Center for Ecological Research, Kyoto University, Otsu, Shiga 520-2113, Japan

[†]Corresponding author: sschreiber@ucdavis.edu

July 10, 2017

Abstract

Stable coexistence relies on negative frequency-dependence, in which rarer species invading a patch benefit from a lack of conspecific competition experienced by residents. In nature, however, rarity can have costs, resulting in positive frequency-dependence particularly when species are rare. Many processes can cause positive frequency-dependence, including a lack of mates, mutualist interactions, and reproductive interference. Reproductive interference (RI), fitness reduction due to interspecific matings, is widespread in plants and animals with sexual reproduction. Because species that are rare in the community can be overwhelmed by mating attempts from common species, RI results in positive frequency-dependence and possible extinction of species when they become rare. Understanding the role of RI and positive frequency-dependence is particularly important in systems experiencing environmental fluctuations. These fluctuations can drive species to low frequencies where they are then vulnerable to costs of rarity and positive frequency-dependence. Here we analyze deterministic and stochastic mathematical models of two species interacting through both RI and resource competition. Individual fitness in these models decomposes into two components, mating success and reproductive potential. Mating success always exhibits positive frequency-dependence. Consistent with classical coexistence theory, reproductive potential exhibits negative frequency-dependence when individuals experience greater intraspecific competition than interspecific competition. In the absence of environmental fluctuations, our analysis reveals that (1) a synergistic effect of RI and niche overlap that hastens exclusion, (2) trade-offs between susceptibility to RI and reproductive potential facilitate coexistence, and (3) coexistence, when it occurs, requires that neither species is initially rare. In the presence of environmental fluctuations, our analysis highlights that (1) environmental fluctuations are likely to drive one of the species extinct, and (2) this risk of species loss is marginalized with sufficiently positively correlated demographic responses of the two species to the environmental fluctuations. This dynamic works in opposition to another coexistence mechanism, the storage effect, which gets weaker as species exhibit more similar demographic responses to environmental fluctuations. These results highlight the need to develop a theory of coexistence accounting for positive frequency-dependent interactions and environmental fluctuations.

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Keywords: reproductive interference, coexistence theory, environmental stochasticity, frequency-dependence, Allee effects, heterospecific pollen transfer, competition, density dependence, alternative stable states, invasion success, competitive exclusion, niche overlap

Introduction

Understanding mechanisms of multispecies coexistence is one of the central topics in community ecology. Stabilizing forces of niche differentiation (intraspecific suppression being stronger than interspecific suppression) and fitness differences among species are thought to lie at the heart of stable coexistence by species [Chesson, 2000]. When stabilizing forces are sufficiently strong relative to fitness differences, the fitness functions of competing species exhibit negative frequency-dependence in which the rare species gains a fitness advantage. These properties have been considered primarily in light of resource competition between species, with fitness functions that give fitness advantages to the rarer species through competitive release. The rarer species escapes intense conspecific competition, while the more common species strongly suppresses itself.

On the other hand, a growing body of literature is beginning to appreciate that rarity may have costs that outweigh the fitness gains of competitive release (positive frequency- or density-dependence) [Taylor and Hastings, 2005]. Examples of these costs include a lack of mates when species are rare (Allee effects [Courchamp et al., 1999, Schreiber, 2003, Zhou and Zhang, 2006]), a lack of required mutualists in the environment [Nuñez et al., 2009, Chung and Rudgers, 2016, Lankau and Keymer, 2016] or costs of reproductive interference (RI), in which mating attempts by one species have fitness costs for (reproductively isolated) heterospecifics (reviewed in Gröning and Hochkirch [2008], Burdfield-Steel and Shuker [2011], Kyogoku [2015]). In particular, RI is often most injurious for the rarer species [Field et al., 2008, Gröning and Hochkirch, 2008, Runquist and Stanton, 2013] which gets swamped by matings or attempted matings by the more common species.

RI occurs in both plants and animals. In animals, many mechanisms can cause RI, including heterospecific mating attempts, heterospecific matings, signal jamming, and others (reviewed in Gröning and Hochkirch [2008]). More than 53 cases of field-observed RI have been recorded in animal species spanning three phyla and more than 8 classes [Gröning and Hochkirch, 2008], indicating the ubiquity of RI across diverse animal species. In plants, RI can arise from heterospecific pollen transfer, when heterospecific pollen interferes with the ability of conspecific pollen to fertilize ovules, or when pollen removed from a rare species is lost to the more common species and never reaches a conspecific (reviewed in Arceo-Gómez and Ashman [2016], Weber and Strauss [2016]). While RI is generally sensitive to the frequency of hetero- and conspecifics (e.g., Keränen et al. [2013]), it is almost always also affected by mating or other traits of individual species. In fact, in almost every case of RI, one member of the interacting pair is more strongly affected by the interaction than the other, and the magnitude of effects of RI on fitness is often large (Table 1). This asymmetry may arise from a number of mechanisms including, one species being more likely to mate, or to attempt to mate, with the other, or one species exacting greater fitness costs from heterospecific mating (e.g., Kyogoku and Nishida [2012], Runquist and Stanton [2013], Vági and Hettyey [2016], Arceo-Gómez and Ashman [2016], Weber and Strauss [2016], Bargielowski and Lounibos [2016]). RI has been documented most often in close relatives [Hochkirch et al., 2007, Gröning and Hochkirch, 2008, Arceo-Gómez and Ashman, 2016], likely owing to their shared morphological, niche, phenological, and signal traits. Shared traits might also increase the strength of resource competition between close relatives [Anacker and Strauss, 2016], and

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both RI and competition have been shown to impede coexistence [Kishi and Nakazawa, 2013, Drury et al., 2015]. In sum, RI has been documented in large number of diverse taxa, almost always has asymmetric effects on the fitnesses of interacting species, and its direction and magnitude of effects on fitness are highly frequency- and density-dependent. Thus, RI, along with other processes that exhibit positive frequency-dependence when species are rare, has the potential to affect the conditions of long-term ecological coexistence.

Environmental stochasticity may magnify the importance of frequency-dependent processes. If environmental fluctuations reduce population sizes of a species to the point where positive density- or frequency-dependence kicks in, then such stochasticity may result in the loss of that species from the system. This phenomena has been demonstrated in single species models with an Allee effect [Dennis, 2002, Liebhold and Bascompte, 2003, Roth and Schreiber, 2014]. For example, using models coupled with historical data, Liebhold and Bascompte [2003] found that environmental stochasticity could cause extinction of local gypsy moth populations (*Lymantria dispar*) in North America even when their densities were well above the Allee threshold – the density at which the per-capita growth rate, on average, equals zero. In sharp contrast, environmental fluctuations can, via the storage effect, mediate coexistence between competing species [Chesson and Warner, 1981, Chesson, 1994]. This positive effect of environmental fluctuations on maintaining species diversity is greater when the competing species exhibit negatively correlated responses to the environmental fluctuations. However, the simultaneous effects of positive frequency-dependence and environmental stochasticity on species coexistence is not understood.

Here, we use models to explore how positive frequency-dependence, environmental stochasticity, and asymmetry in RI interact to influence the coexistence of species. Previous theoretical studies have considered species coexistence with resource competition and RI by numerical simulations [Waser, 1978, Ribeiro and Spielman, 1986, Feng et al., 1997, Ruokolainen and Hanski, 2016] as well as with graphical approaches [Levin and Anderson, 1970, Kuno, 1992, Yoshimura and Clark, 1994, Kishi and Nakazawa, 2013]. Although these studies revealed positive frequency-dependence and alternative stable states arising due to RI, they are not well integrated into the framework of modern coexistence theory [Chesson, 2000]. To facilitate this integration, we formulated a new discrete-time model accounting for the interactive effects of competition and RI of individual fitness. This model builds on a model that has been used extensively to empirically test and further develop coexistence theory [Adler et al., 2007, Levine and HilleRisLambers, 2009, Godoy et al., 2014, Hart et al., 2016, Godoy et al., 2017]. We present an analysis of the deterministic and stochastic versions of the model to address the following questions: How strong does niche differentiation have to be in the face of RI to generate negative frequency-dependence and allow for coexistence? How do asymmetries in RI and reproductive potential between species influence whether coexistence occurs? How robust is species coexistence to environmental fluctuations and how does this robustness depend on the degree of correlation between the species demographic responses to these fluctuations?

[Table 1 about here.]

Model and Methods

To integrate the dynamics of competition and reproductive interference (RI), we build on the Leslie-Gower model of competing species [Leslie and Gower, 1958] which has been used extensively for describing the dynamics of competing annual plants and insects [Leslie and Gower, 1958, Chesson, 1994,

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Adler et al., 2007, Godoy and Levine, 2014, Godoy et al., 2014]. The dynamics of these models are fully characterized and serve as discrete-time analogs of the classical, continuous-time Lotka-Volterra competition models [Cushing et al., 2004]. Unlike earlier models of RI [Kuno, 1992, Yoshimura and Clark, 1994, Kishi and Nakazawa, 2013], this model choice allows us to directly account for the interactive effects of RI and competition on reproductive output.

The model

The model has two competing species with densities N_1 and N_2. The maximal number of offspring produced by a mated individual of species i is λ_i. Due to competition, this intrinsic fitness of mated individuals is only achieved at low densities of both species. Intra- and inter-specific competition reduce this fitness by a linear function of the species densities. That is, let α_i and β_i be the strengths of intra- and inter-specific competition, respectively. Then the expected number of offspring produced by an individual of species i experiencing no RI is

$$\frac{\lambda_i}{1 + \alpha_i N_i + \beta_i N_j} \text{ with } j \neq i.$$

Due to RI with heterospecific individuals, this potential reproductive output decreases with the frequency of these heterospecific individuals. Specifically, we assume the realized fraction of the potential reproductive output equals

$$\frac{N_i}{N_i + b_i N_j} \tag{1}$$

where b_i measures the strength of RI of species j on species i. One mechanistic interpretation of expression (1) is that it equals the probability of a conspecific mating.

Multiplying these components of individual fitness together yields the following deterministic model:

$$N_{1,t+1} = N_{1,t} \overbrace{\frac{N_{1,t}}{N_{1,t} + b_1 N_{2,t}}}^{\text{mating success}} \underbrace{\frac{\lambda_1}{1 + \alpha_1 N_{1,t} + \beta_1 N_{2,t}}}_{\text{reproductive potential}} =: N_{1,t} f_1(N_{1,t}, N_{t,2}) \tag{2}$$

$$N_{2,t+1} = N_{2,t} \frac{N_{2,t}}{N_{2,t} + b_2 N_{1,t}} \frac{\lambda_2}{1 + \alpha_2 N_{2,t} + \beta_2 N_{1,t}} =: N_{2,t} f_2(N_{1,t}, N_{t,2}) \tag{3}$$

where $N_{i,t}$ denotes the density of species i in year t.

To account for environmental stochasticity, we replace the intrinsic fitnesses λ_i with random terms $\lambda_{i,t}$ that are log-normally distributed with log means μ_i, log variances σ_i^2, and log correlation r. The correlation r determines to what extent the intrinsic fitnesses of the two species respond in a similar manner to the environmental fluctuations. For $r = 1$, the species respond identically to the fluctuations. For $r = 0$, their responses are uncorrelated, while for $r = -1$, good years from one species are bad years for the other species.

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Methods

To analyze the deterministic model, we use the theory of monotone maps [Smith, 1986, 1998, Hirsch and Smith, 2005] to show that the dynamics always converge to a one-dimensional curve in the two species state space. The dynamics on this one-dimensional set are governed by a finite number of equilibria. We analytically and numerically explore the structure of these equilibria to determine how niche overlap, fitness differences, and RI interact to determine species coexistence and exclusion. Our presentation focuses on the case of highly fecund species (i.e., $\lambda_i \gg 1$) for which analysis is substantially simpler yet still captures the full dynamical complexity of the model. Analytical details for both the special and general case are presented in Appendix S1.

To analyze the stochastic model, we use theory of stochastic difference equations [Chesson and Ellner, 1989, Schreiber, 2012, Roth and Schreiber, 2014] to identify when stochastic fluctuations do or do not ultimately result in species loss. When species loss occurs, it occurs at a super-exponential rate and rapidly produces numerical zeros for a species' density (i.e., density lower than 10^{-16}). We use these numerical zeros as a proxy for extinction. We numerically explore how the probability of species loss over finite time intervals depends on RI, the standard deviations σ_i of the environmental fluctuations, and the interspecific correlation r in these fluctuations. Analytical results are provided in Appendix S2.

Results

[Figure 1 about here.]

Frequency-dependence, coexistence, and exclusion

Our analysis begins with the deterministic model. To ensure each species i can persist in isolation, we assume that the intrinsic fitness λ_i of mated individuals is greater than one for each species. Under this assumption, species i in isolation converges to the positive equilibrium at which $K_i \equiv N_i = \frac{\lambda_i - 1}{\alpha_i}$. When there is RI ($b_j > 0$), the low density fitness of species $j \neq i$ is zero at this equilibrium as individuals fail to mate with conspecifics due to their low frequency. Consequently, species j is excluded whenever it reaches such low frequencies, and the equilibria $(N_1, N_2) = (K_1, 0)$ and $(0, K_2)$ are locally stable.

Despite these stable, single-species equilibria, coexistence may occur at another stable equilibrium. To see when this contingent coexistence occurs, we focus on the case of highly fecund species (i.e., $\lambda_i \gg 1$) for which competition is more likely to be severe, and present analysis of the general case in Appendix S1. In this case, competitive outcomes depend on the relative fitness ($R_1 = f_1/f_2$) of species 1 as a function of its frequency $x = \frac{N_1}{N_1 + N_2}$. The relative fitness of species 1 is a product of two terms:

$$R_1(x) = \underbrace{\frac{x}{1-x} \frac{(1-x+b_2x)}{x+b_1(1-x)}}_{\text{relative mating success}} \times \overbrace{\frac{\lambda_1}{\lambda_2} \frac{\alpha_2(1-x)+\beta_2 x}{\alpha_1 x + \beta_1(1-x)}}^{\text{relative reproductive potential}} .$$

The first term, the relative mating success of species 1, exhibits positive frequency-dependence whenever species 1 experiences RI (dotted curves in Fig. 1A,C; Appendix S1). Intuitively, as species 1 becomes more frequent, it is less likely to experience RI while species 2 is more likely to experience RI.

Frequency-dependence in the second term, the relative reproductive potential, can be positive or negative. The sign of this frequency-dependence depends on the niche overlap of these two species:

$$\rho = \sqrt{\frac{\beta_1}{\alpha_1}\frac{\beta_2}{\alpha_2}}$$

[Chesson, 2013, Godoy and Levine, 2014]. If there is partial niche overlap ($\rho < 1$), the relative reproductive potential exhibits negative frequency-dependence (dashed curves in Fig. 1A,C; Appendix S1). Intuitively, as a species becomes more frequent in the community, it experiences more intraspecific competition than interspecific competition; as intraspecific competition is stronger than interspecific competition, the relative reproductive potential decreases. When there is perfect niche overlap ($\rho = 1$) or excessive niche overlap ($\rho > 1$), the relative reproductive potential is frequency independent or exhibits positive frequency-dependence, respectively. In either of these latter two cases, the relative fitness only exhibits positive frequency-dependence and coexistence is not possible. Consequently, from now on, we assume $\rho < 1$.

Provided there is sufficiently low niche overlap, the relative fitness R_1 of species 1 exhibits negative frequency-dependence at intermediate species frequencies (Fig. 1A,B). When this occurs, there are two critical frequencies, $x_* < x^*$ of species 1 such that (i) the fitness of species 1 is greater than the fitness of species 2 when its frequency is slightly above x_*, and (ii) the fitness of species 2 is greater than the fitness of species 1 when species 1's frequency is slightly below x^*. When species 1's frequency lies between x_* and x^*, negative frequency-dependent feedbacks dominate and the species approach a unique stable coexistence equilibrium. In contrast, when species 1's frequency falls below x_* or exceeds x^*, positive frequency-dependent feedbacks dominate and either species 1 gets excluded by species 2 or excludes species 2, respectively.

When niche overlap is too great, positive frequency-dependence dominates at all species frequencies and coexistence is not possible (Fig. 1C,D). Consequently, there is a critical frequency x_* of species 1 below which species 1 is excluded and above which species 2 is excluded.

[Figure 2 about here.]

Niche overlap, fitness differences, and contingent coexistence

To better understand when coexistence or exclusion occurs, we focus on the case where the species are demographically similar with respect to competition ($\alpha_1 = \alpha_2$ and $\beta_1 = \beta_2$) but potentially differ in their intrinsic fitnesses (λ_i) or their susceptibility to RI (b_i). The general case is presented in Appendix S1. If there is no RI ($b_1 = b_2 = 0$), coexistence occurs if the niche overlap is less than the intrinsic fitness ratios λ_i/λ_j:

$$\rho < \frac{\lambda_1}{\lambda_2} \text{ and } \rho < \frac{\lambda_2}{\lambda_1}.$$

In this case, coexistence is not contingent upon initial conditions. Alternatively, if the species experience RI but no interspecific competition ($\beta_1 = \beta_2 = 0$), then coexistence occurs if the RI experienced by each species is less than the associated intrinsic fitness ratio

$$b_1 < \frac{\lambda_1}{\lambda_2} \text{ and } b_2 < \frac{\lambda_2}{\lambda_1}.$$

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In this case, coexistence is contingent upon initial conditions. These coexistence conditions are sharp: if they are satisfied, the species coexist, else they do not (Fig. 2A).

When species experience both RI and interspecific competition, coexistence requires that the additive effects of niche overlap and RI are less than intrinsic fitness ratios:

$$\rho + b_1 < \frac{\lambda_1}{\lambda_2} \text{ and } \rho + b_2 < \frac{\lambda_2}{\lambda_1}. \tag{4}$$

If (4) is not satisfied, negative frequency-dependent feedbacks are too weak to promote coexistence. Satisfying (4), however, need not ensure coexistence due to nonlinear, interactive effects between RI and niche overlap (the distance between the dashed lines and the coexistence region in Fig. 2). For species that exhibit no fitness differences ($\lambda_1 = \lambda_2$) and are equally susceptible to RI ($b_1 = b_2$), this interactive effect equals $3\rho\, b_i$ and coexistence occurs if

$$\rho + b_i + 3\rho b_i < 1.$$

As niche overlap and RI contribute equally to this nonlinear interactive effect, coexistence is least likely when RI and niche overlap are equally strong (Fig. 2B).

Intrinsic fitness differences or asymmetries in RI lead to larger, nonlinear effects on coexistence (the greater distance between the dashed line and the coexistence region in Figs. 2C,D than B). When RI is symmetric, intrinsic fitness differences (e.g., larger values of λ_1/λ_2) always inhibit coexistence (Fig. 2C). Numerical simulations suggest that interactive effects of RI and niche overlap continue to be symmetric in this case. When intrinsic fitness differences are too large to permit coexistence, the species with the fitness disadvantage can be excluded despite being at an initially higher frequency.

When there are sufficiently strong asymmetries in RI ($b_1/b_2 > 3.5$ in Fig. 2D), coexistence occurs at intermediate intrinsic fitness differences. If the intrinsic fitness advantage of the species 1 is not sufficiently high, coexistence is not possible and this species can be excluded even when it is initially at the higher frequency (the bottom-right dark gray region in Fig. 2D). Alternatively, if the intrinsic fitness advantage of species 1 is too large, coexistence is not possible and species 2 has a lower threshold frequency below which it is excluded (the top-left light gray region of Fig. 2D).

Stochastic environments

When the intrinsic fitnesses $\lambda_{i,t}$ fluctuate stochastically, the fluctuations in the frequency dynamics are determined by the fluctuations in the intrinsic fitness ratio $\lambda_{1,t}/\lambda_{2,t}$. As the intrinsic fitnesses $\lambda_{i,t}$ are log-normally distributed with log-mean μ_i, log-variance σ_i^2 and correlation r, the intrinsic fitness ratio $\lambda_{1,t}/\lambda_{2,t}$ is log-normally distributed with

$$\text{log-mean: } \mu_1 - \mu_2 \text{ and log-variance: } \sigma_1^2 - 2r\sigma_1\sigma_2 + \sigma_2^2. \tag{5}$$

Equation 5 implies that positively correlated responses ($r > 0$) of the two species to the environmental fluctuations decrease the log-variance in the frequency dynamics. Intuitively, environmental fluctuations cause the intrinsic fitness of each species to change by the same factor and, thereby, reduces their effect of these fluctuations on the intrinsic fitness ratios (Fig. 3B). Indeed, when the responses to environmental fluctuations are of the same magnitude and perfectly correlated ($\sigma_1^2 = \sigma_2^2$ and $r = 1$), there are no fluctuations in the intrinsic fitness ratios and species may coexist indefinitely.

In contrast, when species exhibit opposing responses to environmental fluctuations ($r < 0$), environmental fluctuations that drive one species to higher densities simultaneously drives the other species to low densities. This results in larger fluctuations in the intrinsic fitness ratios (Fig. 3A). In the extreme case where the responses to the environmental fluctuations are of the same magnitude and are perfectly negatively correlated ($\sigma_1^2 = \sigma_2^2$ and $r = -1$), the fluctuations in the log intrinsic fitness ratios are twice as large than as for uncorrelated fluctuations (i.e., $4\sigma_1^2$ versus $2\sigma_1^2$).

[Figure 3 about here.]

When species exhibit some differentiated responses to environmental fluctuations ($r < 1$ or $\sigma_1^2 \neq \sigma_2^2$), environmental fluctuations ultimately will drive one of the species extinct, whether or not deterministic coexistence is possible (Appendix S2, Fig. 4). Intuitively, environmental fluctuations can push one of the species to a sufficiently low frequency that the deterministic effects of RI rapidly drive the species to extinction. Larger environmental fluctuations increase the likelihood of these events and, thereby, increase the probability of species loss. As negative correlations increase fluctuations in frequencies, they also increase the likelihood that one species falls below its critical frequency and rapidly goes extinct. Consequently, the probability of extinction decreases with positive correlations. In fact, when species responses to the environmental fluctuations are identical (i.e., $\sigma_1^2 = \sigma_2^2$ and $r = 1$), environmental stochasticity does not drive any species extinct provided they are initially near a stable, coexistence equilibrium of the deterministic model (Appendix S2).

[Figure 4 about here.]

The effects of asymmetries in intrinsic fitnesses and RI on extinction risk largely follow patterns suggested by the deterministic model: when a species is at low frequency at the stable, coexistence equilibrium, extinction risk is greater (compare Fig. 2D to Fig. 5). In particular, for a given level of asymmetry in RI, persistence of both species is most likely at an intermediate intrinsic fitness advantage of the species more susceptible to RI. For smaller intrinsic fitness differences, the species with the intrinsic fitness advantage is more likely to go extinct. For larger intrinsic fitness differences, the species less susceptible to RI is more likely to go extinct. As larger intrinsic fitness differences (i.e., μ_1 larger than μ_2) result in larger fluctuations in the intrinsic fitness differences (i.e., variance $\lambda_{1,t}/\lambda_{2,t}$ equals $\exp(2(\mu_1 - \mu_2) + \sigma_1^2 + \sigma_2^2)(\exp(\sigma_1^2 + \sigma_2^2) - 1)$ when $r = 0$), extinction risk is generally greater due to larger intrinsic fitness differences rather than smaller intrinsic fitness differences (blue region larger in Fig. 5B than in Fig. 5A).

[Figure 5 about here.]

Discussion

Many competing species are likely to experience both negative and positive frequency-dependence. Positive frequency-dependence, in and of itself, does not allow for coexistence and leads to alternative stable states supporting only a single species [Amarasekare, 2002]. In contrast, negative frequency-dependence allows for stable coexistence [Adler et al., 2007] but does not allow for alternative stable states. For competing species experiencing both positive and negative frequency-dependent feedbacks, a new dynamic emerges supporting alternative stable states that allow for coexistence (Fig. 1). This

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dynamic occurs when positive frequency-dependence occurs at low species frequencies, and negative frequency-dependence dominates at intermediate species frequencies. When this occurs, coexistence is no longer determined by the celebrated "mutual invasability criterion" of modern coexistence theory [Turelli, 1978, Chesson, 2000] or, more generally, by species growth rates when rare [Hofbauer and Sigmund, 1998, Schreiber, 2000, Schreiber et al., 2011].

In our models, negative frequency-dependence arises through resource competition while positive frequency-dependence stems from reproductive interference (RI). For these models, we can decompose the relative fitness of each species into two demographic components: mating success and reproductive potential–the number of offspring produced by an individual not experiencing RI (Fig. 1). Mating success always exhibits positive frequency-dependence and dominates at low frequencies of either species. Consistent with modern coexistence theory [Chesson, 2000, Adler et al., 2007, Godoy and Levine, 2014], reproductive potential exhibits negative frequency-dependence only if there is partial niche overlap ($\rho < 1$, Appendix S1).

Our deterministic model is similar to that of Kishi and Nakazawa [2013] (originally from Kuno [1992]), focusing on population dynamics of two competing species experiencing RI. Our model, however, accounts for the simultaneous reduction of birth rates due to competition and RI, while Kishi and Nakazawa [2013] assume that competition increases mortality rates whereas RI reduces birth rates. Thus, our model is more easily integrated into the framework of modern coexistence theory [Chesson, 2000, Adler et al., 2007]. Furthermore, as our model is in discrete-time (i.e. difference equations) and Kishi and Nakazawa [2013] is in continuous-time (i.e. differential equations), our model is readily applicable to RI in annual plants [Levine and HilleRisLambers, 2009, Godoy and Levine, 2014, Hart et al., 2016] and insects (see also Ribeiro and Spielman [1986]). Assuming high fecundity also allowed us to obtain explicit analytical results missing from earlier models (e.g. Kishi and Nakazawa [2013]). We show that the additive effects of niche overlap and RI need to be smaller than intrinsic fitness differences to allow for coexistence (Fig. 2), an analytical finding extending results of Kishi and Nakazawa [2013]. In particular, this result implies there is always a synergistic effect of RI and niche overlap on inhibiting coexistence. Also, we found that asymmetries in RI result in intermediate intrinsic fitness differences promoting coexistence (Fig. 2D). This is consistent with Kishi and Nakazawa [2013], although they focused on the trade-off between RI and niche overlap (Fig. 4 of Kishi and Nakazawa [2013]), whereas we focused on the trade-off between RI and intrinsic fitness difference (Fig. 2D).

Systems with positive frequency-dependence are particularly vulnerable to fluctuations in environmental conditions, or taken more broadly, any process that rapidly alters the relative frequencies of species, such as invasions [Bargielowski and Lounibos, 2016]. Indeed, extinction is expected when populations are repeatedly pushed over the critical threshold where positive frequency-dependence kicks in. The effects of such positive frequency-dependence are most severe for interacting species exhibiting opposing demographic responses to environmental fluctuations. For species with highly positively correlated responses to environmental fluctuations, fluctuations in species frequencies are minimal and extinction risk is small. These results are in direct contrast with the theory of the storage effect [Chesson and Warner, 1981, Chesson, 1994], in which the competitively inferior species sometimes has a "good" year relative to the dominant species, and is able to capitalize on that year by through long term storage of offspring until the next "good" year. For the storage effect, uncorrelated and negative environmental correlations in fitnesses across years promote coexistence. However, in the presence of RI, our results demonstrate that such negative correlations may actually promote extinction. As the classical formulation of the storage effect requires overlapping generations, a feature not included in our model, it will be interesting to extend our model by adding overlapping generations and analyze

how the storage effect and RI interact.

While our theory provides a first step in developing community ecology theory accounting for positive frequency-dependence and environmental fluctuations, there are many additional complexities that need to be explored in future studies. These complexities include interactions between RI and spatial population structure [Ruokolainen and Hanski, 2016], interference competition [Amarasekare, 2002], evolution toward avoiding RI (i.e., reproductive character displacement or RI-driven niche partitioning [Liou and Price, 1994, Goldberg and Lande, 2006]), and conservation of rare species by considering the interaction between genetic and demographic swamping [Todesco et al., 2016]. For example, aggregative behavior of species may allow species at low frequency in the larger community to be partially buffered from RI and other positive frequency-dependent processes by creating tiny local patches of higher density [Molofsky et al., 2001, Ruokolainen and Hanski, 2016]. Going beyond RI, positively frequency-dependent phenomena include a large range of ecological and evolutionary interactions contributing to biodiversity. These phenomena include below-ground mutualisms between plants and microbes that facilitate increases of plant species at low densities, the basis of selection on intricate warning coloration in mimicry complexes [Chouteau et al., 2016], in which rare morphs rapidly increase to converge on a common model, and processes favoring patchiness that contributes to spatial heterogeneity, which, in turn, generates opportunities for local diversity [Ruokolainen and Hanski, 2016]. Developing a theory to understand how these many forms of positive frequency-dependence interact with environmental fluctuations to determine community structure is a major challenge that will likely require a paradigm shift in coexistence theory.

References

P.B. Adler, J. HilleRisLambers, and J.M. Levine. A niche for neutrality. *Ecology Letters*, 10:95–104, 2007.

P. Amarasekare. Interference competition and species coexistence. *Proceedings of the Royal Society of London B: Biological Sciences*, 269:2541–2550, 2002.

B. L. Anacker and S. Y. Strauss. Ecological similarity is related to phylogenetic distance between species in a cross-niche field transplant experiment. *Ecology*, 97:1807–1818, 2016.

G. Arceo-Gómez and T. L. Ashman. Invasion status and phylogenetic relatedness predict cost of heterospecific pollen receipt: implications for native biodiversity decline. *Journal of Ecology*, 104: 1003–1008, 2016.

G. Arceo-Gómez, R. A. Raguso, and M. A. Geber. Can plants evolve tolerance mechanisms to heterospecific pollen effects? An experimental test of the adaptive potential in *Clarkia species*. *Oikos*, 125:718–725, 2016.

I. E. Bargielowski and L. P. Lounibos. Satyrization and satyrization-resistance in competitive displacements of invasive mosquito species. *Insect Science*, 23:162–174, 2016.

D. Bruckman and D. R. Campbell. Timing of invasive pollen deposition influences pollen tube growth and seed set in a native plant. *Biological Invasions*, 18:1701–1711, 2016.

E. R. Burdfield-Steel and D. M. Shuker. Reproductive interference. *Current Biology*, 21:R450–R451, 2011.

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

P. Chesson. Species competition and predation. In Rik Leemans, editor, *Ecological Systems*, pages 223–256. Springer, 2013.

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

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

P.L. Chesson and R.R. Warner. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, 117:923, 1981.

M. Chouteau, M. Arias, and M. Joron. Warning signals are under positive frequency-dependent selection in nature. *Proceedings of the National Academy of Sciences*, 113:2164–2169, 2016.

Y. A. Chung and J.A. Rudgers. Plant–soil feedbacks promote negative frequency dependence in the coexistence of two aridland grasses. *Proceedings of the Royal Society B*, 283:20160608, 2016.

F. Courchamp, T. Clutton-Brock, and B. Grenfell. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, 14:405–410, 1999.

J.M. Cushing, S. Levarge, N. Chitnis, and S.M. Henson. Some discrete competition models and the competitive exclusion principle. *Journal of Difference Equations and Applications*, 10:1139–1151, 2004.

P. J. N. de Bruyn, C. A. Tosh, and M. N. Bester. Sexual harassment of a king penguin by an antarctic fur seal. *Journal of Ethology*, 26:295–297, 2008.

B. Dennis. Allee effects in stochastic populations. *Oikos*, 96:389–401, 2002.

J. P. Drury, K. W. Okamoto, C. N. Anderson, and G. F. Grether. Reproductive interference explains persistence of aggression between species. *Proceedings of the Royal Society B: Biological Sciences*, 282:20142256, 2015.

W. Feng, X. Lu, and W. Liu. Comparison and numerical simulations for diffusive models of resource and sexual competition. *Nonlinear Analysis: Theory, Methods & Applications*, 30:2765–2774, 1997.

D. L. Field, D. J. Ayre, R. J. Whelan, and A. G. Young. Relative frequency of sympatric species influences rates of interspecific hybridization, seed production and seedling performance in the uncommon *Eucalyptus aggregata*. *Journal of Ecology*, 96:1198–1210, 2008.

M. Friberg, O. Leimar, and C. Wiklund. Heterospecific courtship, minority effects and niche separation between cryptic butterfly species. *Journal of Evolutionary Biology*, 26:971–979, 2013.

O. Godoy and J.M. Levine. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, 95:726–736, 2014.

O. Godoy, N.J.B. Kraft, and J.M. Levine. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17:836–844, 2014.

O. Godoy, D.B. Stouffer, N.J.B. Kraft, and J.M. Levine. Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology*, 98:1193–1200, 2017.

E. E. Goldberg and R. Lande. Ecological and reproductive character displacement on an environmental gradient. *Evolution*, 60:1344–1357, 2006.

J. Gröning and A. Hochkirch. Reproductive interference between animal species. *The Quarterly Review of Biology*, 83:257–282, 2008.

D. L. Grossenbacher and M. L. Stanton. Pollinator-mediated competition influences selection for flower-color displacement in sympatric monkeyflowers. *American Journal of Botany*, 101:1915–1924, 2014.

W. A. Haddad, R. R. Reisinger, T. Scott, M. N. Bester, and P. J. N. de Bruyn. Multiple occurrences of king penguin (*Aptenodytes patagonicus*) sexual harassment by Antarctic fur seals (*Arctocephalus gazella*). *Polar Biology*, 38:741–746, 2015.

S.P. Hart, S.J. Schreiber, and J.M. Levine. How variation between individuals affects species coexistence. *Ecology Letters*, 19:825–838, 2016.

M. W. Hirsch and H. L. Smith. Monotone maps: A review. *Journal of Difference Equations and Applications*, 11:379–398, 2005.

A. Hochkirch, J. Gröning, and A. Bücker. Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology*, 76:633–642, 2007.

J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, 1998.

I. Keränen, A. Kahilainen, K. E. Knott, J. S. Kotiaho, and K. Kuitunen. High maternal species density mediates unidirectional heterospecific matings in *Calopteryx* damselflies. *Biological Journal of the Linnean Society*, 108:534–545, 2013.

S. Kishi and T. Nakazawa. Analysis of species coexistence co-mediated by resource competition and reproductive interference. *Population ecology*, 55:305–313, 2013.

E. Kuno. Competitive exclusion through reproductive interference. *Researches on Population Ecology*, 34:275–284, 1992.

D. Kyogoku. Reproductive interference: ecological and evolutionary consequences of interspecific promiscuity. *Population Ecology*, 57:253–260, 2015.

D. Kyogoku and T. Nishida. The presence of heterospecific males causes an Allee effect. *Population Ecology*, 54:391–395, 2012.

R. A. Lankau and D. P. Keymer. Ectomycorrhizal fungal richness declines towards the host species' range edge. *Molecular Ecology*, 25:3224–3241, 2016.

P. H. Leslie and J. C. Gower. The properties of a stochastic model for two competing species. *Biometrika*, 45:316–330, 1958.

D.A. Levin and W.W. Anderson. Competition for pollinators between simultaneously flowering species. *The American Naturalist*, 104(939):455–467, 1970.

J.M. Levine and J. HilleRisLambers. The importance of niches for the maintenance of species diversity. *Nature*, 461:254–257, 2009.

A. Liebhold and J. Bascompte. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, pages 133–140, 2003.

L. W. Liou and T. D. Price. Speciation by reinforcement of premating isolation. *Evolution*, 48:1451–1459, 1994.

J. Molofsky, J.D. Bever, and J. Antonovics. Coexistence under positive frequency dependence. *Proceedings of the Royal Society of London B: Biological Sciences*, 268:273–277, 2001.

S. Noriyuki, N. Osawa, and T. Nishida. Asymmetric reproductive interference between specialist and generalist predatory ladybirds. *Journal of Animal Ecology*, 81:1077–1085, 2012.

M. A. Nuñez, T. R. Horton, and D. Simberloff. Lack of belowground mutualisms hinders *Pinaceae* invasions. *Ecology*, 90:2352–2359, 2009.

J. M. C. Ribeiro and A. Spielman. The satyr effect: a model predicting parapatry and species extinction. *The American Naturalist*, 128:513–528, 1986.

K. Rohde, Y. Hau, J. Weyer, and A. Hochkirch. Wide prevalence of hybridization in two sympatric grasshopper species may be shaped by their relative abundances. *BMC Evolutionary Biology*, 15:14, 2015.

G. Roth and S.J. Schreiber. Pushed to brink: Allee effects, environmental stochasticity, and extinction. *Journal of Biological Dynamics*, 8:187–205, 2014.

R. B. Runquist and M. L. Stanton. Asymmetric and frequency-dependent pollinator-mediated interactions may influence competitive displacement in two vernal pool plants. *Ecology Letters*, 16:183–190, 2013.

L. Ruokolainen and I. Hanski. Stable coexistence of ecologically identical species: conspecific aggregation via reproductive interference. *Journal of Animal Ecology*, 85:638–647, 2016.

Y. Sato, J. M. Alba, and M. W. Sabelis. Testing for reproductive interference in the population dynamics of two congeneric species of herbivorous mites. *Heredity*, 113:495–502, 2014.

S. J. Schreiber. Criteria for C^r robust permanence. *Journal of Differential Equations*, 162:400–426, 2000.

S. J. Schreiber. Allee effects, chaotic transients, and unexpected extinctions. *Theoretical Population Biology*, 2003.

S. J. Schreiber. Persistence for stochastic difference equations: a mini-review. *Journal of Difference Equations and Applications*, 18:1381–1403, 2012.

S. J. Schreiber, M. Benaïm, and K. A. S. Atchadé. Persistence in fluctuating environments. *Journal of Mathematical Biology*, 62:655–683, 2011.

H.L. Smith. Periodic competitive differential equations and the discrete dynamics of competitive maps. *Journal of Differential Equations*, 64:165–194, 1986.

H.L. Smith. Planar competitive and cooperative difference equations. *Journal of Difference Equations and Applications*, 3:335–357, 1998.

C.M. Taylor and A. Hastings. Allee effects in biological invasions. *Ecology Letters*, 8:895–908, 2005.

M. Todesco, M. A. Pascual, G. L. Owens, K. L. Ostevik, B. T. Moyers, S. Hübner, S. M. Heredia, M. A. Hahn, C. Caseys, D. G. Bock, and L. H. Rieseberg. Hybridization and extinction. *Evolutionary Applications*, 9:892–908, 2016.

M. Turelli. Random environments and stochastic calculus. *Theoretical Population Biology*, 12:140–178, 1978.

B. Vági and A. Hettyey. Intraspecific and interspecific competition for mates: *Rana temporaria* males are effective satyrs of *Rana dalmatina* females. *Behavioral Ecology and Sociobiology*, 70:1477–1484, 2016.

Nickolas M. Waser. Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia*, 36:223–236, 1978.

M. G. Weber and S. Y. Strauss. Coexistence in close relatives: beyond competition and reproductive isolation in sister taxa. *Annual Review of Ecology, Evolution, and Systematics*, 47:359–381, 2016.

J. Yoshimura and C.W. Clark. Population dynamics of sexual and resource competition. *Theoretical Population Biology*, 45:121–131, 1994.

S.R. Zhou and D.Y. Zhang. Allee effects and the neutral theory of biodiversity. *Functional Ecology*, 20:509–513, 2006.

Study	Species	Mechanism	FD or DD[†]	Fitness-related trait	Nature of Reproductive Interference
Plants					
Bruckman and Campbell [2016]	*Phacelia parryi, Brassica nigra*	heterospecific pollen deposition	yes	seed set	At low densities, *B. nigra* facilitates *P. parryi*; at high densities *B. nigra*, reduces *P. parryi* seed set via heterospecific pollen.
Arceo-Gómez et al. [2016]	*Clarkia speciosa, C. xantiana*	heterospecific pollen deposition/conspecific pollen loss	na	# of pollen tubes reaching base of style	Heterospecific pollen deposition reduces conspecific pollen tubes reaching styles by 20% (*speciosa*) and 32% (*xantiana*).
Runquist and Stanton [2013]	*Limnanthes douglasii rosea, L. alba*	heterospecific pollen deposition	yes	seed set	30-65% reduction in seed set in *L. d. rosea* with 8:8 *rosea:alba* plants relative to all *L. d. rosea* arrays; 0% reduction in seed set in *L. alba* in arrays with 8:8 plants *rosea:alba* relative to all *L. alba* arrays.
Grossenbacher and Stanton [2014]	*Mimulus guttatus, M. bicolor* yellow and white morphs	pollinator limitation/conspecific pollen loss	yes	seed set	60% reduction in seed set of *M. bicolor* yellow morph in the presence of yellow *M. guttatus*.
Animals					
Sato et al. [2014]	*Tetranychus urticae, T. evansi*	heterospecific mating	na	population growth	*T. evansi* not affected; *T. urticae* population growth reduced ca. 45% by *T. evansi*.
Vági and Hettyey [2016]	*Rana temporaria, R. dalmatina*	heterospecific mating	na	% fertilized eggs	Heterospecific matings reduce fertilization rates of *R. temporaria* eggs.
Rohde et al. [2015]	*Chorthippus montanus, C. parallelus*	heterospecific mating	yes	mating success	Females of *C. parallelus* were more often involved in interspecific matings (12×) than those of *C. montanus*.
Kyogoku and Nishida [2012]	*Callosobruchus chinensis, C. maculatus*	heterospecific mating	yes	# of hatched eggs per female	*C. maculatus* had ca. 40% reduction in fitness when rare; no effect of heterospecifics on *C. chinensis* at any density.
Noriyuki et al. [2012]	*Harmonia yedoensis, H. axyridis*	heterospecific mating	yes	mating opportunity, restricted niche	*H. yedoensis* female mating success decreased; *H. axyridis* females unaffected.
Friberg et al. [2013]	*Leptidea sinapis, L. juvernica*	heterospecific courtship	yes	conspecific mating	High frequency of heterospecifics reduces conspecific matings by 50–100%.
de Bruyn et al. [2008], Haddad et al. [2015]	*Arctocephalus gazella, Aptenodytes patagonicus*	hetero-class male harassment	no	survival	Seals attempt to mate with penguins, sometimes eat them.

Table 1: Examples of reproductive interference since the review of Gröning and Hochkirch [2008] from diverse plants and animals. [†]Frequency-dependence or density-dependence.
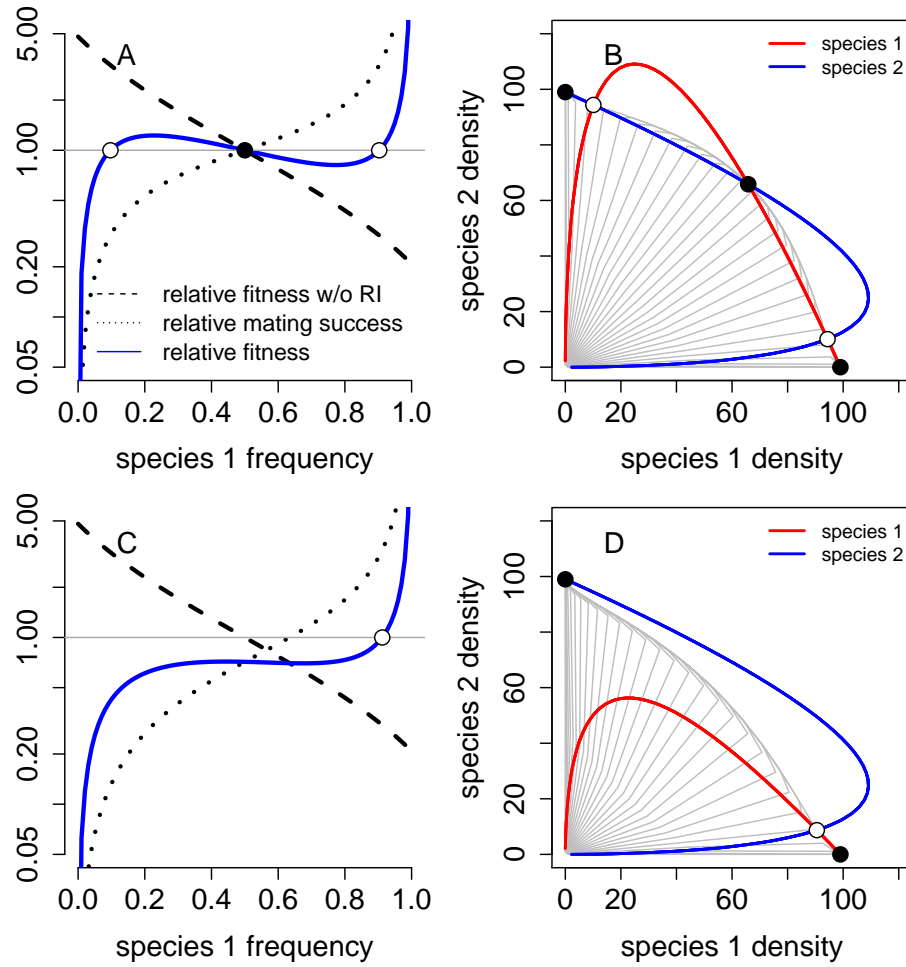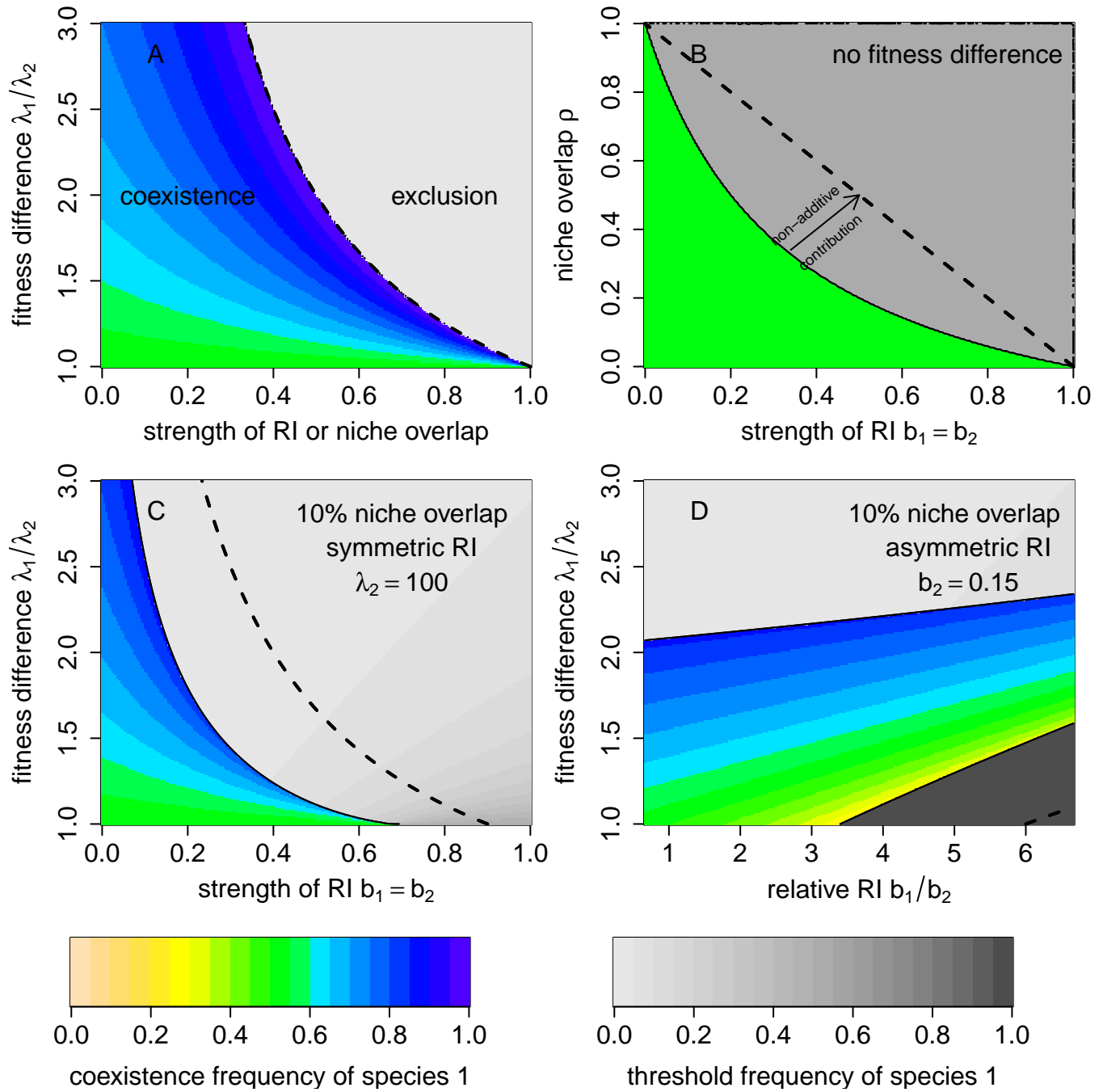
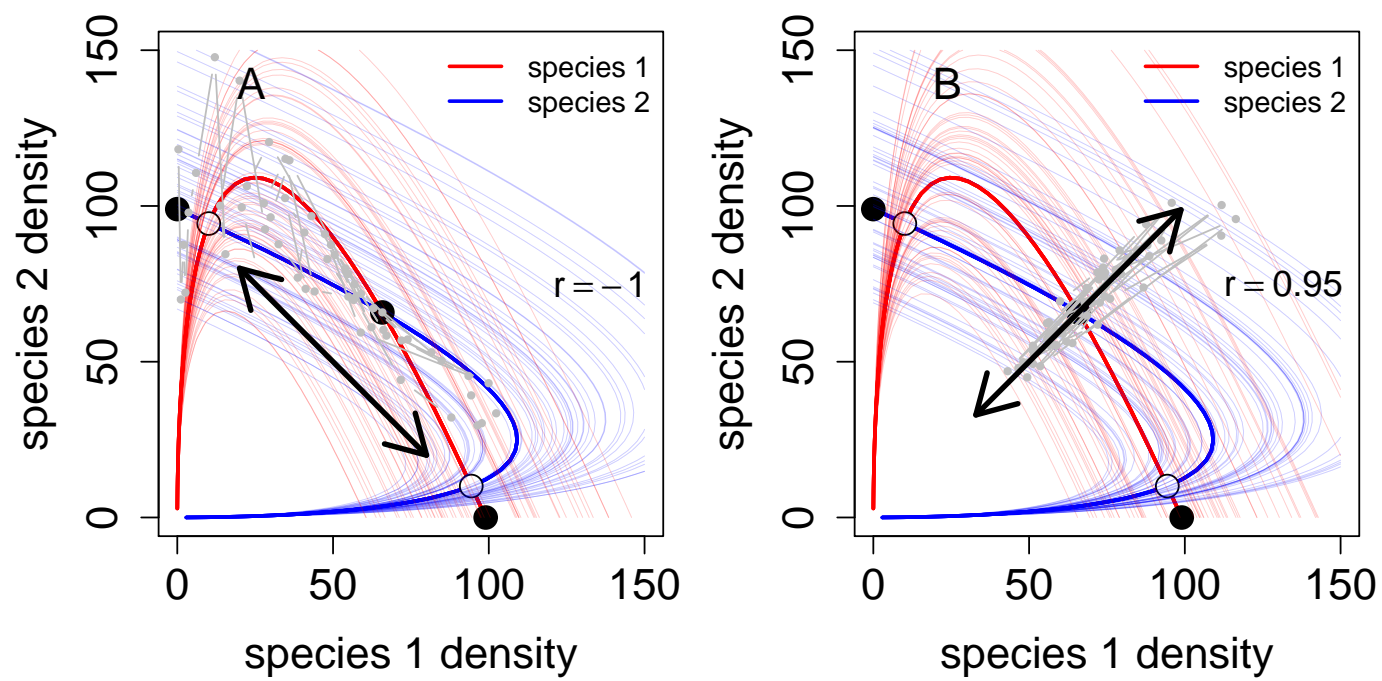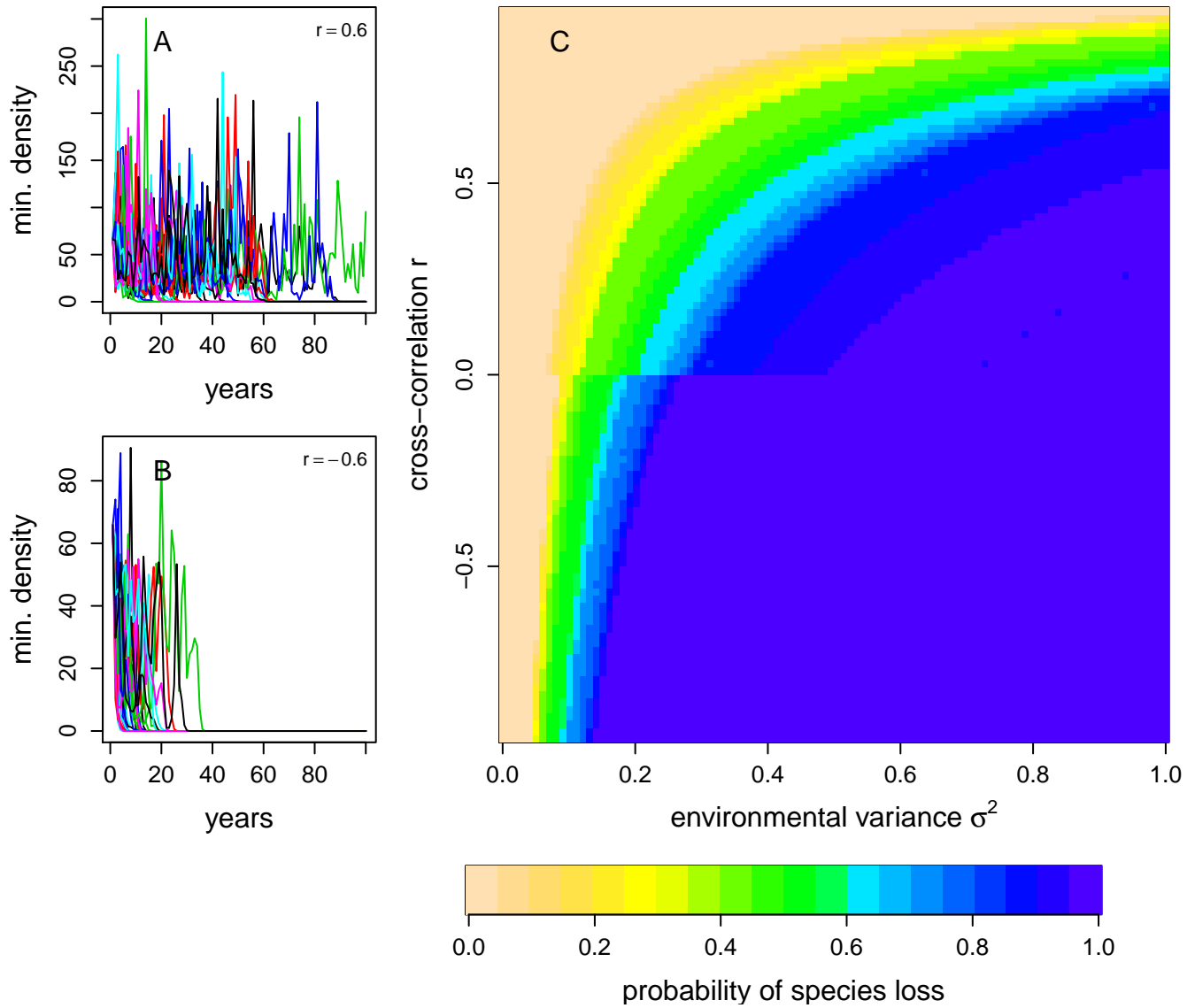# List of Figures

Figure 1

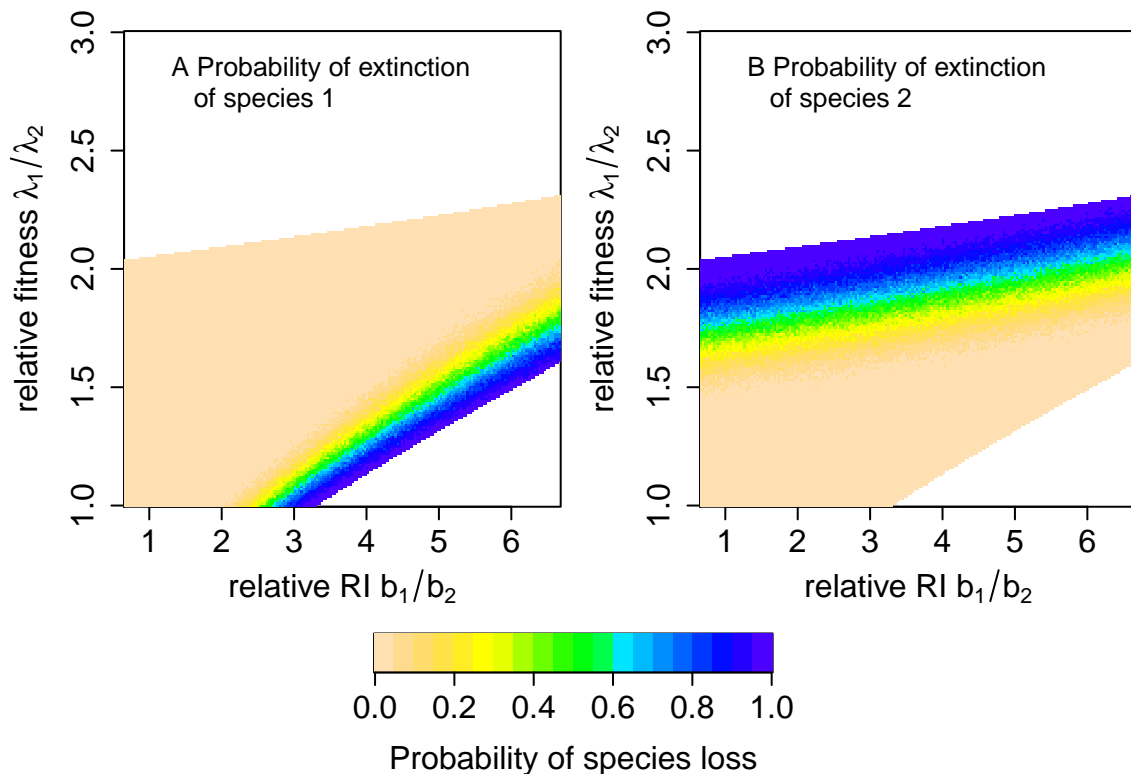Figure 2

Figure 3

Figure 4

Figure 5

Appendix S1 Deterministic Analysis

Analysis of the case of symmetric species

When the two species are identical ($b = b_1 = b_2$, $\lambda = \lambda_1 = \lambda_2$, $\alpha = \alpha_1 = \alpha_2$, and $\beta = \beta_1 = \beta_2$), the analysis can be simplified. This symmetric version of the model has a coexistence equilibrium, $N_1 = N_2 = \frac{\lambda - (1+b)}{(1+b)(\alpha+\beta)}$. For the equilibrium to be present and locally stable, the following conditions must hold:

$$\lambda - 1 - b > 0 \text{ and } \lambda(3\rho b + \rho + b - 1) + (1 - \rho)(1 + b)^2 < 0. \tag{6}$$

where $\rho = \beta/\alpha$ in this symmetric case. This is equivalent to the inequality (3) in Kishi and Nakazawa [2013]. Thus λ and ρ are equivalent to b/d and c, where b, d, and c are birth rate, death rate, and the relative strength of interspecific to intraspecific resource competition in the ODEs of Kishi and Nakazawa [2013]. This indicates that decreasing λ value results in reduced parameter regions for coexistence in the b-β plane (as Fig. 2B).

Analysis of the case of high fecundity: $\lambda_i \gg 1$

When $\lambda_i \gg 1$ for both species, we show that model (2) can be approximated by

$$
\begin{aligned}
N_{1,t+1} &= N_{1,t} \underbrace{\frac{N_{1,t}}{N_{1,t} + b_1 N_{2,t}} \frac{\lambda_1}{\alpha_1 N_{1,t} + \beta_1 N_{2,t}}}_{f_1(N_{1,t}, N_{2,t})} \\
N_{2,t+1} &= N_{2,t} \underbrace{\frac{N_{2,t}}{N_{2,t} + b_2 N_{1,t}} \frac{\lambda_2}{\alpha_2 N_{2,t} + \beta_2 N_{1,t}}}_{f_2(N_{1,t}, N_{2,t})}.
\end{aligned}
\tag{7}
$$

To show that the simplified model (7) provides a good description of the dynamics of the global attractor of (2), we begin by showing that non-zero solutions of (7) ultimate yield population sizes of order λ_i. To this end, let $A = \max\{\alpha_1, \alpha_2, \beta_1, \beta_2\}$, $B = \max\{b_1, b_2, 1\}$, and $R = \min\{\lambda_1, \lambda_2\}$. If $n_t = N_{1,t} + N_{2,t}$, then

$$
\begin{aligned}
n_{t+1} &= \sum_i N_{i,t} \frac{N_{i,t}}{N_{i,t} + b_i N_{j,t}} \frac{\lambda_i}{1 + \alpha_i N_{i,t} + \beta_i N_{j,t}} \\
&\geq \sum_i N_{i,t} \frac{1}{B} \frac{N_{i,t}}{n_t} \frac{R}{1 + A n_t} \\
&\geq \frac{R}{2B} \frac{n_t}{1 + A n_t}
\end{aligned}
$$

where the final inequality follows from $a^2 + b^2 \geq (a + b)^2/2$ for any $a \geq 0$ and $b \geq 0$. Hence, by monotonicity, if $n_0 > 0$, then

$$\liminf_{t\to\infty} n_t \geq \frac{R/(2B) - 1}{A} \geq R/(2BA)$$

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In particular, if we define $a = \min\{\alpha_1, \alpha_2, \beta_1, \beta_2\}$, then $\alpha_i N_{i,t} + \beta_i N_{j,t} \geq aR/(2BA)$ for sufficiently large t. Hence, provided that $N_{1,0} + N_{2,0} > 0$, $(N_{1,t}, N_{2,t})$ enters the set

$$\Gamma = \{(N_1, N_2) : \alpha_i N_i + \beta_i N_j \geq aR/(2BA) \text{ for } i = 1, 2, j \neq i\}$$

for t sufficiently large.

Now assume that $\lambda_2 = C\lambda_1$ for some $C > 0$ and $\lambda_1 \gg 1$. As (2) is equivalent to

$$N_{1,t+1} = N_{1,t} \frac{N_{1,t}}{N_{1,t} + b_1 N_{2,t}} \frac{1}{1/\lambda_1 + \alpha_1 N_{1,t}/\lambda_1 + \beta_1 N_{2,t}/\lambda_1}$$

$$N_{2,t+1} = N_{2,t} \frac{N_{2,t}}{N_{2,t} + b_2 N_{1,t}} \frac{1}{1/\lambda_2 + \alpha_2 N_{2,t}/\lambda_2 + \beta_2 N_{1,t}/\lambda_2}$$

Let $c = \min\{1, C\}$. For $(N_1, N_2) \in \Gamma$, we have that $\alpha_i N_i/\lambda_i + \beta_i N_j/\lambda_i \geq c/(2BA) > 0$. Hence provided that $(N_1, N_2) \in \Gamma$ and $\lambda_1 \gg 1$ is sufficiently large

$$\frac{1}{1/\lambda_i + \alpha_i N_i/\lambda_i + \beta_i N_j/\lambda_i} \approx \frac{1}{\alpha_i N_i/\lambda_i + \beta_i N_j/\lambda_i} = \frac{\lambda_i}{\alpha_i N_i + \beta_i N_j}$$

and we have justified the approximation (7) of the long-term dynamics of (2).

Analysis of the simplified model (7)

Equation 7 can be reduced to a one-dimensional model via the change of coordinates $y = \frac{N_1}{N_2}$. In this coordinate system

$$y_{t+1} = y_t^2 \frac{1 + b_2 y_t}{y_t + b_1} \frac{\lambda_1}{\lambda_2} \frac{\alpha_2 + \beta_2 y_t}{\alpha_1 y_t + \beta_1} \tag{8}$$

For our analysis of (8), we first verify the two assertions in the main text about the relative fitness function and then analyze the dynamics of (8).

In the y coordinate system, the relative fitness function f_1/f_2 is given by

$$R_1 = \underbrace{\frac{y(1 + b_2 y)}{y + b_1}}_{=:\phi} \underbrace{\frac{\lambda_1}{\lambda_2} \frac{\alpha_2 + \beta_2 y}{\alpha_1 y + \beta_1}}_{=:\psi}$$

where ϕ corresponds to the "relative mating success" of species 1 and ψ corresponds to the "relative reproductive potential" of species 1. A direct computation of the derivatives yields:

$$\frac{d\phi}{dy} = \frac{b_2 y^2 + 2b_1 b_2 y + b_1}{y^2 + 2b_1 y + b_1^2} \text{ and } \frac{d\psi}{dy} = \frac{\lambda_1}{\lambda_2} \frac{\beta_1 \beta_2 - \alpha_1 \alpha_2}{\alpha_1^2 y^2 + 2\alpha_1 \beta_1 y + \beta_1^2}.$$

$\frac{d\phi}{dy}$ is always positive, and $\frac{d\psi}{dy}$ is negative if and only if $\alpha_1 \alpha_2 > \beta_1 \beta_2$ i.e. $\rho < 1$. To get the derivatives with respect to the frequency ($x = N_1/(N_1 + N_2)$) of species 1, notice that $y = x/(1-x)$ and $dy/dx = \frac{1}{(x-1)^2} > 0$ for $x \neq 1$. Therefore, by the chain rule

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$$\frac{d\phi}{dx} = \frac{d\phi}{dy}\frac{dy}{dx} \text{ and } \frac{d\psi}{dx} = \frac{d\psi}{dy}\frac{dy}{dx}, \text{ and}$$

the derivatives $d\phi/dx$ and $d\psi/dx$ have the same signs as the derivatives $d\phi/dy$ and $d\psi/dy$, respectively. Therefore, as claimed in the main text, ϕ is an increasing function of x and ψ is a decreasing function of x if and only if $\alpha_1\alpha_2 > \beta_1\beta_2$ i.e. $\rho > 1$.

Now we perform the dynamical analysis of (8). As the right-hand side of (8) is an increasing function of y for $x \geq 0$, all solutions either approach an equilibrium or approach $+\infty$ which corresponds to species 2 going extinct in (7). The non-zero (and non-infinite) equilibria are given by the solutions of $R_1 = 1$. Equivalently, the roots of the cubic:

$$b_2\beta_2\lambda_1 y^3 + ((\beta_2 + \alpha_2 b_2)\lambda_1 - \alpha_1\lambda_2)y^2 + ((-\beta_1 - \alpha_1 b_1)\lambda_2 + \alpha_2\lambda_1)y - b_1\beta_1\lambda_2 \tag{9}$$

Contingent coexistence occurs when there are three positive solutions to this cubic equation i.e. two unstable equilibria and one stable equilibrium. Contingent exclusion occurs when there is only one positive real root to the equation. As this equation is negative at $y = 0$ and approaches $+\infty$ as $y \to +\infty$ (i.e. the cubic coefficient is positive), there never can be exactly two positive solutions.

As the cubic (9) is negative at $y = 0$ and approaches $+\infty$ as $y \to +\infty$, three positive solutions are possible only if the first derivative of this cubic is positive at $y = 0$ and the second derivative at $y = 0$ is negative. Namely,

$$\frac{\lambda_1}{\alpha_1}\frac{\alpha_2}{\lambda_2} > \frac{\beta_1}{\alpha_1} + b_1 \text{ and } \frac{\lambda_2}{\alpha_2}\frac{\alpha_1}{\lambda_1} > \frac{\beta_2}{\alpha_2} + b_2.$$

In the special case where $\alpha_1 = \alpha_2$ and $\beta_1 = \beta_2$, the ratios β_i/α_i equal ρ, and the coexistence condition becomes

$$\frac{\lambda_1}{\lambda_2} > \rho + b_1 \text{ and } \frac{\lambda_2}{\lambda_1} > \rho + b_2$$

as presented in the main text.

While these coexistence conditions are only necessary, a necessary and sufficient condition is given by considering the discriminant of the (9). Specifically, define

$$\Delta = 18c_0 c_1 c_2 c_3 - 4c_2^3 c_0 + c_2^2 c_1^2 - 4c_3 c_1^3 - 27c_3^2 c_0^2$$

where $c_0 = -b_1\beta_1\lambda_2$, $c_1 = ((-\beta_1 - \alpha_1 b_1)\lambda_2 + \alpha_2\lambda_1)$, $c_2 = ((\beta_2 + \alpha_2 b_2)\lambda_1 - \alpha_1\lambda_2)$, and $c_3 = b_2\beta_2\lambda_1$. If $\Delta > 0$, then (9) has three real roots which are all positive if the necessary condition for coexistence is satisfied. Unfortunately, while this expression provides a quick computational method for identifying whether coexistence occurs or not, it is not readily interpretable.

Finally, in the special case of species symmetry (i.e. $\lambda_1 = \lambda_2 =: \lambda$, $\alpha_1 = \alpha_2 =: \alpha$, $\beta_1 = \beta_2 =: \beta$ and $b_1 = b_2 =: b$), $y = 1$ is solution of (9) i.e. equal frequencies of both species. In this case, there are two other equilibria if and only if the derivative of (9) is negative at $y = 1$. This derivative is given by

$$((3b + 1)\beta + \alpha b - \alpha)\lambda$$

and is negative if and only if

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$$\frac{\beta}{\alpha} < \frac{1-b}{3b+1}$$

Equivalently, as $\rho = \beta/\alpha$ in this symmetric case, coexistence occurs if and only if

$$b + \rho + 3b\rho < 1.$$

This is a special case of the conditions (6) when $\lambda \gg 1$

General model: Carrying Simplices and Coexistence Criteria

To analyze the full model, we use the theory of monotone maps [Smith, 1998, Hirsch and Smith, 2005]. Define

$$
\begin{aligned}
F(N_1, N_2) &= N_1 \overbrace{\frac{N_1}{N_1 + b_1 N_2} \frac{\lambda_1}{1 + \alpha_1 N_1 + \beta_1 N_2}}^{=:N_1 f(N_1,N_2)} \\
G(N_1, N_2) &= N_2 \underbrace{\frac{N_2}{N_2 + b_2 N_1} \frac{\lambda_2}{1 + \alpha_2 N_2 + \beta_2 N_1}}_{=:N_2 g(N_1,N_2)}
\end{aligned}
$$

Then the dynamics of (2) is given by

$$(N_{1,t+1}, N_{2,t+1}) = (F(N_{1,t}, N_{2,t}), G(N_{1,t}, N_{2,t})) = H(N_{1,t}, N_{2,t}).$$

We recall a few definitions. The competitive ordering of the non-negative cone $C = [0, \infty)^2$ is given by $(N_1, N_2) \geq_K (M_1, M_2)$ if $N_1 \geq N_2$ and $M_1 \leq M_2$, $(N_1, N_2) >_K (M_1, M_2)$ if $(N_1, N_2) \geq_K (M_1, M_2)$ and either $N_1 > N_2$ or $M_1 < M_2$, and $(N_1, N_2) \gg_K (M_1, M_2)$ if $N_1 > N_2$ and $M_1 < M_2$. We will show that (2) is *strongly competitive*: $H(N_1, N_2) \gg_K H(M_1, M_2)$ whenever $(N_1, N_2) >_K (M_1, M_2)$. By Smith [1998, Proposition 2.1], H being strongly competitive follows from the derivative map $DH =$

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$\begin{pmatrix} \frac{\partial F}{\partial N_1} & \frac{\partial F}{\partial N_2} \\ \frac{\partial G}{\partial N_2} & \frac{\partial G}{\partial N_2} \end{pmatrix}$ having the sign pattern $\begin{pmatrix} + & - \\ - & + \end{pmatrix}$. Taking the partial derivatives yields:

$$\frac{\partial F}{\partial N_1} = (2b_1\beta_1\lambda_1 N_1 N_2^2 + ((\beta_1 + \alpha_1 b_1)\lambda_1 N_1^2 + 2b_1\lambda_1 N_1)N_2 + \lambda_1 N_1^2)/$$
$$(b_1^2\beta_1^2 N_2^4 + ((2b_1\beta_1^2 + 2\alpha_1 b_1^2\beta_1)N_1 + 2b_1^2\beta_1)N_2^3 +$$
$$((\beta_1^2 + 4\alpha_1 b_1\beta_1 + \alpha_1^2 b_1^2)N_1^2 + (4b_1\beta_1 + 2\alpha_1 b_1^2)N_1 + b_1^2)N_2^2$$
$$+((2\alpha_1\beta_1 + 2\alpha_1^2 b_1)N_1^3 + (2\beta_1 + 4\alpha_1 b_1)N_1^2 + 2b_1 N_1)N_2$$
$$+\alpha_1^2 N_1^4 + 2\alpha_1 N_1^3 + N_1^2) > 0$$

$$\frac{\partial F}{\partial N_2} = -\frac{b_1\lambda_1 N_1^2}{(b_1 N_2 + N_1)^2(\beta_1 N_2 + \alpha_1 N_1 + 1)} - \frac{\beta_1\lambda_1 N_1^2}{(b_1 N_2 + N_1)(\beta_1 N_2 + \alpha_1 N_1 + 1)^2}$$
$$< 0$$

$$\frac{\partial G}{\partial N_1} = -\frac{b_2\lambda_2 N_2^2}{(N_2 + b_2 N_1)^2(\alpha_2 N_2 + \beta_2 N_1 + 1)} - \frac{\beta_2\lambda_2 N_2^2}{(N_2 + b_2 N_1)(\alpha_2 N_2 + \beta_2 N_1 + 1)^2}$$
$$< 0$$

$$\frac{\partial G}{\partial N_2} = (((\beta_2 + \alpha_2 b_2)\lambda_2 N_1 + \lambda_2)N_2^2 + (2b_2\beta_2\lambda_2 N_1^2 + 2b_2\lambda_2 N_1)N_2)/$$
$$(\alpha_2^2 N_2^4 + ((2\alpha_2\beta_2 + 2\alpha_2^2 b_2)N_1 + 2\alpha_2)N_2^3 +$$
$$((\beta_2^2 + 4\alpha_2 b_2\beta_2 + \alpha_2^2 b_2^2)N_1^2 + (2\beta_2 + 4\alpha_2 b_2)N_1 + 1)N_2^2 +$$
$$((2b_2\beta_2^2 + 2\alpha_2 b_2^2\beta_2)N_1^3 + (4b_2\beta_2 + 2\alpha_2 b_2^2)N_1^2 +$$
$$2b_2 N_1)N_2 + b_2^2\beta_2^2 N_1^4 + 2b_2^2\beta_2 N_1^3 + b_2^2 N_1^2) > 0$$

Hence, H is strongly competitive.

The sign of the determinant of DH is positive due to the following truly horrific calculation:

$$f(N_1, N_2)g(N_1, N_2)(2b_1\beta_1 N_2^3 + ((b_1\beta_2 + (2b_1 b_2 + 1)\beta_1 + \alpha_2 b_1 b_2 + \alpha_1 b_1)N_1$$
$$+2b_1)N_2^2 + (((2b_1 b_2 + 1)\beta_2 + b_2\beta_1 + (\alpha_1 b_1 + \alpha_2)b_2)N_1^2 + (3b_1 b_2 + 1)N_1)N_2$$
$$+2b_2\beta_2 N_1^3 + 2b_2 N_1^2)/(\alpha_2 b_1\beta_1 N_2^4 + ((b_1\beta_1\beta_2 + (\alpha_2 b_1 b_2 + \alpha_2)\beta_1$$
$$+\alpha_1\alpha_2 b_1)N_1 + b_1\beta_1 + \alpha_2 b_1)N_2^3 + ((((b_1 b_2 + 1)\beta_1 + \alpha_1 b_1)\beta_2$$
$$+\alpha_2 b_2\beta_1 + \alpha_1\alpha_2 b_1 b_2 + \alpha_1\alpha_2)N_1^2 + (b_1\beta_2 + (b_1 b_2 + 1)\beta_1 + \alpha_2 b_1 b_2 + \alpha_1 b_1$$
$$+\alpha_2)N_1 + b_1)N_2^2 + (((b_2\beta_1 + \alpha_1 b_1 b_2 + \alpha_1)\beta_2 + \alpha_1\alpha_2 b_2)N_1^3 + ((b_1 b_2 + 1)\beta_2$$
$$+b_2\beta_1 + (\alpha_1 b_1 + \alpha_2)b_2 + \alpha_1)N_1^2 + (b_1 b_2 + 1)N_1)N_2 + \alpha_1 b_2\beta_2 N_1^4$$
$$+(b_2\beta_2 + \alpha_1 b_2)N_1^3 + b_2 N_1^2) > 0$$

From these two calculations, we get that DH is invertible and all of its entries are strictly positive.

Using these facts, the work of [Smith, 1986, 1998] implies two key results. First, all solutions with $N_{1,0} N_{2,0} > 0$ converge to a continuous (in fact Lipschitz), invariant curve Γ. This curve is known as the carrying simplex of the system. It has the important property that all radial lines in C intersect Γ in exactly one point. Thus, all possible frequencies of the species have a unique representation on this curve. One can view the dynamics of H restricted to Γ as describing the asymptotic frequency dynamics of the competing species. Second, all solutions of (2) converge to an equilibrium. We note: in the limiting case of $\lambda_i \to \infty$ for $i = 1, 2$, the simplified model (8) can be viewed as a radial projection of the dynamics on the carrying simplex onto the standard simplex $\{(N_1, N_2) : N_1 \geq 0, N_2 \geq 0, N_1 + N_2 = 1\}$.

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As the boundary equilibria on Γ are stable, coexistence is possible if and only if there exist equilibria (N_1^+, N_2^+) and (N_1^-, N_2^-) on Γ such that (i) $N_1^+/(N_1^+ + N_2^+) > N_1^-/(N_1^- + N_2^-)$ and (ii) there are no other equilibria $(N_1^*, N_2^*) \in \Gamma$ satisfying $0 < N_1^*/(N_1^* + N_2^*) < N_1^-/(N_1^- + N_2^-)$ or $N_1^+/(N_1^+ + N_2^+) < N_1^*/(N_1^* + N_2^*) < 1$. These equilibria correspond to the critical frequencies on Γ such that when the species lie on Γ between these critical frequencies, the species converge to an equilibrium supporting both species. Conversely, when the species initially lie on Γ outside these critical frequencies, the species dynamics converge to one of the boundary equilibria.

Appendix S2   Stochastic Analysis

Analysis of the simplified model (7)

In the relative density coordinate system $y = \frac{N_1}{N_2}$, the stochastic simplified model takes the form

$$y_{t+1} = y_t^2 \frac{1 + b_2 y_t}{y_t + b_1} \frac{\lambda_{1,t}}{\lambda_{2,t}} \frac{\alpha_2 + \beta_2 y_t}{\alpha_1 y_t + \beta_1}. \tag{10}$$

Assume that $b_i > 0$, $\alpha_i > 0$, $\beta_i > 0$, and $(\log \lambda_{1,t}, \log \lambda_{2,t})$ are a sequence of independent, identically distributed random vectors with a multivariate normal distribution with mean vector (μ_1, μ_2) and covariance matrix $\Sigma^2 = \begin{pmatrix} \sigma_1^2 & r\sigma_1\sigma_2 \\ r\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}$ where $\sigma_1 > 0$ and $\sigma_2 > 0$.

If $\sigma_1^2 = \sigma_2^2$ and $r = 1$, then $\lambda_{1,t}/\lambda_{2,t} = \exp(\mu_1 - \mu_2)$ is constant for all time t. Hence, the dynamics are deterministic and the analysis from Appendix S1 applies.

If $\sigma_1^2 \neq \sigma^2$ or $r < 1$, then $\log \lambda_{1,t}/\lambda_{2,t}$ is normally distributed with mean $\mu_1 - \mu_2$ and variance $\sigma_1^2 - 2r\sigma_1\sigma_2 + \sigma_2^2 > 0$. As $y = 0$ is a stable equilibrium, the proof of Roth and Schreiber [2014, Theorem 4.1] implies that for all $\varepsilon > 0$ there exists $\delta > 0$ such that

$$\mathbb{P}\left[\lim_{t\to\infty} y_t = 0 \mid y_0 \in [0, \varepsilon)\right] \geq 1 - \delta.$$

Namely, for initial values y_0 sufficiently close to zero, the probability of losing species 1 is arbitrarily close to 1. Making the change of variables $z_t = 1/y_t$, the dynamics of (10) become

$$z_{t+1} = z_t^2 \frac{1 + b_1 z_t}{z_t + b_2} \frac{\lambda_{2,t}}{\lambda_{1,t}} \frac{\alpha_1 + \beta_1 z_t}{\alpha_2 z_t + \beta_2}. \tag{11}$$

Reapplying the proof of Roth and Schreiber [2014, Theorem 4.1] implies that for all $\varepsilon > 0$ there exists $\delta > 0$ such that

$$\mathbb{P}\left[\lim_{t\to\infty} z_t = 0 \mid z_0 \in [0, \varepsilon)\right] \geq 1 - \delta.$$

Namely, for initial values z_0 sufficiently close to zero, the probability of losing species 2 is arbitrarily close to 1.

Since $\log \lambda_{1,t}/\lambda_{2,t}$ is normally distributed with positive variance, for any $M > 0$ there exists $\gamma > 0$ such that

$$\mathbb{P}\left[\text{there exists } t \geq 1 \text{ such that } y_t \in [0, 1/M] \cup [M, \infty) \mid y_0 > 0\right] \geq \gamma.$$

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Consequently, the proof of Roth and Schreiber [2014, Theorem 3.2] implies that

$$\mathbb{P}\left[\lim_{t\to\infty} y_t = 0 \text{ or } \lim_{t\to\infty} y_t = \infty \mid y_0 > 0\right] = 1.$$

Hence, for any initial condition y_0, with probability one, species 1 or species 2 goes extinct asymptotically. Moreover, whenever $y_0 > 0$, there is a positive probability that either species goes extinct asymptotically.