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Strong self-limitation promotes the persistence of rare species

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Abstract. Theory has recognized a combination of niche and neutral processes each contributing, with varying importance, to species coexistence. However, long-term persistence of rare species has been difficult to produce in trait-based models of coexistence that incorporate stochastic dynamics, raising questions about how rare species persist despite such variability. Following recent evidence that rare species may experience significantly different population dynamics than dominant species, we use a plant community model to simulate the effect of disproportionately strong negative frequency dependence on the long-term persistence of the rare species in a simulated community. This strong self-limitation produces long persistence times for the rare competitors, which otherwise succumb quickly to stochastic extinction. The results suggest that the mechanism causing species to be rare in this case is the same mechanism allowing those species to persist.

Key words: coexistence; frequency dependence; niche theory; rare species; self-limitation; species diversity.

INTRODUCTION

Ecological communities are impressively diverse in species and in the roles that those species play. Empirical and theoretical studies have clearly shown that differences among species are important for preventing competitive exclusion (Tilman 1982, Chesson 2000, Clark and McLachlan 2003, Adler et al. 2010). Trait-based solutions to coexistence seem particularly important to produce persistent rare species, whereas common species can face little risk of extinction even under neutral dynamics. Rare species can result from specialization on a rare resource or from the negative effects of niche overlap with many other competitors (Main 1982). However, disproportionately strong negative density dependence may also cause rarity.

Two recent papers demonstrated empirically that negative density dependence (NDD) tended to be stronger for rare species than common species (Comita et al. 2010, Mangan et al. 2010). A theoretical model is also able to reproduce communities in which rare species experience strong self-limitation (Chisholm and Muller-Landau 2011). These studies suggest that rarity is caused by conspecific inhibition, and not by heterospecific suppression. However, this does not address the most important aspect of rarity in ecology: why is it that some rare species persist, while others do not? Species that

only occur incidentally or ephemerally are merely occupying the same area as the local species, but cannot be considered as interacting members of a community. Rare-but-persistent species, on the other hand, have solved the problem of how to remain interacting and permanent community members. In these cases, strong self-limitation may actually be a result of trait-based mechanisms that make a species rare but also promote long-term stable coexistence among species and thus higher diversity in communities.

In niche-based coexistence models, species differences promote coexistence because they create population dynamics in which species with unequal competitive ability can persist over extended periods of time (Adler et al. 2007). As formalized by Chesson (2000), it is the combination of fitness equivalence and stabilization that leads to species' persistence, where stabilizing mechanisms of coexistence operate by increasing the strength of intraspecific competition relative to interspecific competition (Chesson 2000). The strength of these stabilizing mechanisms can be estimated from the negative frequency dependence (NFD) that a species experiences in a community (Adler et al. 2007). Unlike negative density dependence (NDD), NFD will only arise if individuals are more sensitive to conspecifics than they are to other species (Adler et al. 2007). Stronger stabilization between species is reflected in more steeply negative frequency dependence shown by each species. For long-term persistence, the most crucial result of the negative relationship between per capita growth and the relative abundance of a species in the community is that it enables a species to increase when rare (Siepielski and McPeck 2010). Many tests of

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coexistence assume that competitive effects are pairwise and symmetric (Harpole and Suding 2007, Araya et al. 2011), which implies that the strength of negative frequency dependence is similar for all species. However, there is no a priori reason to expect this symmetry in natural communities.

Why should we expect self-limitation to be stronger for rare species than common species? One reason is deterministic: stronger negative frequency dependence simply increases a species' growth rate when rare, and even increases the likelihood that a rare species experiences a positive invasion growth rate at all (Fig. 1). In this case, stronger self-limitation allows the rare species to persist when symmetric frequency dependence would cause deterministic competitive exclusion. A second reason is that, once stochasticity is introduced, the role of self-limitation should become even more important for a rare species' persistence. Greater sensitivity to conspecifics leads to stronger negative feedback in population dynamics and a greater tendency for a species to remain close to its stochastic equilibrium abundance (Fig. 1). This buffers a species against extremely low population numbers and stochastic extinction (Fig. 2). In other words, the same self-limitation that causes a species to be rare also promotes its persistence. Furthermore, stochastic extinction should remove rare species that are not strongly self-limiting, while having little effect on common species at little risk of stochastic extinction.

Classical models of coexistence can accommodate asymmetric negative frequency dependence between species through unequal intra- and interspecific coefficients, and are thus suitable for a theoretical exploration of the potential importance of strong self-limitation for rare species. We used a well-known two-species coexistence model (Watkinson 1980, Rees and Westoby 1997, Levine and Rees 2002) to demonstrate two points about the role of asymmetric negative frequency dependence in promoting rare species persistence. First, we used a deterministic model to show that allowing the rare species to experience disproportionately strong stabilization relative to a more abundant competitor increases the parameter space that gives stable coexistence. Second, we introduced demographic stochasticity, which should cause the extinction of weakly stabilized rare species, but not strongly stabilized rare species or common species.

METHODS

To assess the role of asymmetric NFD in promoting coexistence, we used a two-species annual plant model (Watkinson 1980, Rees and Westoby 1997, Levine and Rees 2002):

$$\begin{aligned}
 N_{1,t+1} &= \frac{r_1 N_{1,t}}{1 + a_{11} N_{1,t} + a_{12} N_{2,t}} \\
 N_{2,t+1} &= \frac{r_2 N_{2,t}}{1 + a_{22} N_{2,t} + a_{12} N_{1,t}}
 \end{aligned}
 \tag{1}$$

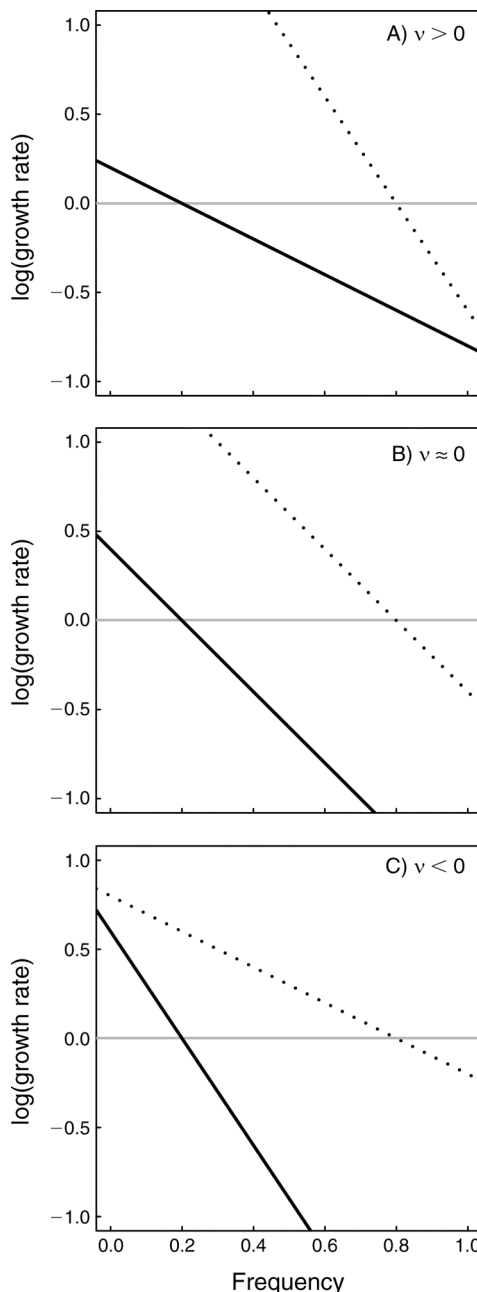


FIG. 1. Frequency dependence is proportional to strength of stabilization. For each species (1, solid line; 2, dotted line), the slope of the line (the negative frequency dependence, NFD) is an indication of the strength of stabilization (the steeper the line the greater the strength). The point at which a species crosses the zero line (its equilibrium frequency, gray line) is where it transitions from positive growth (above the line) to negative growth (below the line). In each panel, the equilibrium frequencies of each species are held constant ($F_1 = 0.2, F_2 = 0.8$). However, the relationship (v) between mean population abundance and strength of stabilization varies: (A) a positive relationship between mean population abundance and strength of stabilization ($v > 0$); (B) no relationship ($v \approx 0$); (C) a negative relationship ($v < 0$). In the case in which $v < 0$, the rare species is experiencing much stronger positive growth rates, and thus more opportunity for recovery from low density, than in either of the other two cases.

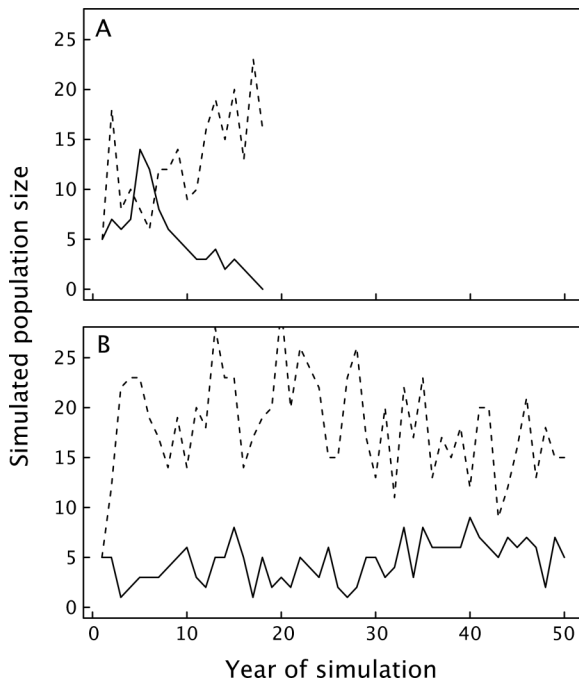


FIG. 2. Asymmetric stabilization promotes stable coexistence; example simulations show the population dynamics when the rare species (solid line) is experiencing (A) weak stabilization ($S_{\text{rare}} = 1$) vs. (B) strong stabilization ($S_{\text{rare}} = 5.17$); the dashed line represents the other (dominant) species in the simulation. With weak stabilization, even though the deterministic equilibrium frequency ($N_1/(N_1+N_2)$, where N is the deterministic abundance of species 1 and 2) of the rare species is relatively high (0.24), it is very vulnerable to stochastic extinction when abundance is low. With strong stabilization, the rare species' deterministic equilibrium frequency is lower (0.16), but strong stabilization allows it to repeatedly recover from low density. Median coexistence time over 2000 simulations was only 28 time steps in panel (A), whereas it was 182 time steps in panel (B).

where r_1 and r_2 represent the fecundity of species 1 and 2, a_{11} and a_{22} represent the per capita effects of species 1 and 2 on conspecifics, and a_{21} and a_{12} represent the per capita effects of species 1 and 2 on heterospecifics, respectively.

The parameter combinations that determine the strength of stabilization in this model are known (Adler et al. 2007), allowing the strength of stabilization to be directly manipulated to determine the effect on coexistence. The terms for the strength of stabilization (S) in this model are

$$S_1 = \frac{r_2}{1 + (a_{12}/a_{22})(r_2 - 1)}$$

$$S_2 = \frac{r_1}{1 + (a_{21}/a_{11})(r_1 - 1)} \quad (2)$$

for species 1 and 2, respectively. Fitness equivalence, in this framework, is $E_1 = r_1/r_2$ for species 1 and, assuming

species 1 is the inferior competitor, E_1 will always be between 0 and 1.

We calculated deterministic solutions for a range of possible parameter combinations (r_1 integers from 15 to 20, r_2 integers from 11 to 20, a_{11} from 0.7 to 3.0, a_{22} from 0.1 to 1.0, and the interspecific alphas between 0.1 and 1.0) in which the deterministic abundance of species 1 was predicted to be 25% or less of the total community size. This produces scenarios for 14 499 species combinations and S_1 stabilization values from 1 to 7. When stabilization is 1, the species suppresses conspecifics equally to heterospecifics. On the other end of the range, a stabilization of 7 indicates that a species is suppressing conspecifics seven times more strongly than it suppresses heterospecifics. Very strong stabilization in this range has been observed in natural communities (Adler et al. 2010).

We calculated the covariance (v) between deterministic abundance and strength of stabilization for each scenario. Note that the result of each parameter combination consists of two points from which a covariance can be calculated: the absolute abundance and strength of stabilization of species 1, and the absolute abundance and strength of stabilization of species 2 (also see Fig. 1). We fit a logit regression model to determine the effects of fitness equivalence, strength of stabilization, and v on deterministic coexistence. This estimates the effect of v on deterministic coexistence, after accounting for the known (positive) effects of fitness equivalence and strength of stabilization. If the rarer species benefits deterministically from stronger stabilization, then coexistence is predicted more often when v is negative (representing a strongly self-limiting rare species; see Fig. 1).

We then incorporated demographic stochasticity by drawing the absolute abundance of each species at each time step from a Poisson distribution in which the mean was the predicted abundance from the model (Supplement). Simulations were initialized with five individuals in each case for each species ($N_0 = 5$). We ran these simulations until one species went extinct and repeated this process 2000 times for each parameter combination. Population summary statistics were saved, as well as the mean and median coexistence times, from the multiple iterations done for each parameter combination. In this case, a simple linear regression model was fit to estimate the effect of v on the log-transformed median coexistence time, after accounting for the known (positive) effects of fitness equivalence and strength of stabilization. In a stochastic setting, if the rarer species benefits from stronger stabilization, then median coexistence time will increase when v is negative (representing a strongly self-limiting rare species; see Fig. 1). One strength of the approach used in this study is that it deals directly with differences in NFD, which is the signature of stabilizing mechanisms of coexistence, rather than NDD, which may or may not lead to NFD and play a role in coexistence (Adler et al. 2007).

Thus, we are able to directly implicate asymmetrical NFD as a facilitator of coexistence in this simple model. However, this does not restrict the potential mechanisms that species may employ to produce the asymmetric stabilization structure. Mechanisms may be direct forms of intraspecific competition, or they may be indirect density-dependent processes (Bagchi et al. 2010, Comita et al. 2010, Mangan et al. 2010).

RESULTS

Deterministic solutions

A logit regression of the effects of the covariance between abundance and stabilization on the deterministic coexistence of the two species indicates that, after accounting for the known effects of fitness equivalence and strength of stabilization, a negative relationship (v) between equilibrium abundance and strength of stabilization (i.e., the rare species experiencing disproportionately strong stabilization) promotes coexistence (Table 1).

Stochastic simulations

For rare species, the relationship between coexistence time and the strength of stabilization is log-linear (Fig. 3): coexistence times increase dramatically with greater strength of stabilization. The dominant species does not show the same results. The strength of stabilization it is experiencing is not an important factor in determining coexistence times (Fig. 3). The simple linear model in this case shows that, after accounting for the known effects of stabilization and equivalence, a stronger negative relationship leads to longer median coexistence times (Table 1).

DISCUSSION

Our results demonstrate that a stochastic model relying on a simple form of niche differences can readily produce long-term coexistence when an asymmetric stabilization structure disproportionately impacts rare species. Although the model consistently supports strong self-limitation of rare species as a factor promoting coexistence, the deterministic and stochastic results suggest qualitatively different mechanisms creating this effect. In the deterministic case, a coexistence solution is more likely to be observed when rare species are strongly self-limiting. This is a mathematically intuitive result, given that a rare species is more likely to experience strong positive growth rates (or even positive growth rates at all) if it has stronger negative frequency dependence, whereas a dominant species has a large range of relative abundance values over which it experiences positive growth rates (see Fig. 1). The result does appear to contradict the common assumption that any factor that makes a species rare increases its risk of stochastic extinction (Kobe and Vriesendorp 2011). However, this assumption ignores the fact that strong NFD has a positive effect when a species is at very low abundance (e.g., below its stochastic equilibrium). The

TABLE 1. Summary of the effect of the relationship between abundance and stabilization (covariance, v) on deterministic coexistence and stochastic coexistence.

Parameter	Deterministic estimate	Stochastic estimate
Intercept	-42.64	0.6391
Stabilization	17.77	0.5766
Equivalence	23.83	1.173
v	-0.006528	-0.001256

Notes: A logit regression was used to model deterministic coexistence of the two species. A simple linear model was used to model the log of the median coexistence time of the two species in the stochastic simulations. After accounting for the known effects of stabilization and fitness equivalence (of the rare species), negative covariances (v) are more likely to result in coexistence in the deterministic case, and a stronger negative covariance leads to longer median coexistence times in the stochastic case.

positive effect is crucial for helping rare species resist the negative effects of demographic stochasticity.

When uncertainty is added in the form of demographic stochasticity, the asymmetric stabilization structure becomes a buffering mechanism for rare species. Strong stabilization becomes much more critical for long-term coexistence, and rare species that are only weakly stabilized quickly go extinct. Models that attempt to capture realistic levels of uncertainty in the factors affecting coexistence have generated similar results, showing that demographic stochasticity dramatically increases the probability of extinction for rare species, even when deterministic criteria for coexistence are satisfied (Tilman 2004). Thus, dynamics that guard against stochastic extinction are especially valuable for the persistence of rare species. Disproportionately strong stabilization helps rare species to persist by limiting the amount of time they spend at very low densities (e.g., Fig. 2). Stronger NFD for rare species has already been observed in experimental (Harpole and Suding 2007) and natural communities (Adler et al. 2010). Additional empirical support will be necessary to determine whether asymmetric stabilization is a general feature of natural communities.

Our simulations help to explain the pervasiveness of rare species in real ecological communities by providing a mechanism that causes species to be rare but also buffers them against stochastic extinction when population numbers become critically low. A two-species model was used here for simplicity, but multispecies models should generate the same pattern, where a negative relationship between abundance and stabilization of all the community members produces the most persistent community. Although our model generates strong NFD through phenomenological differences in intra- and interspecific competition coefficients, in real systems such differences could reflect a wide variety of coexistence mechanisms of low or high dimensionality (Clark 2010). Future modeling efforts could also determine how our findings are affected when coexistence mechanisms are incorporated more explicitly.

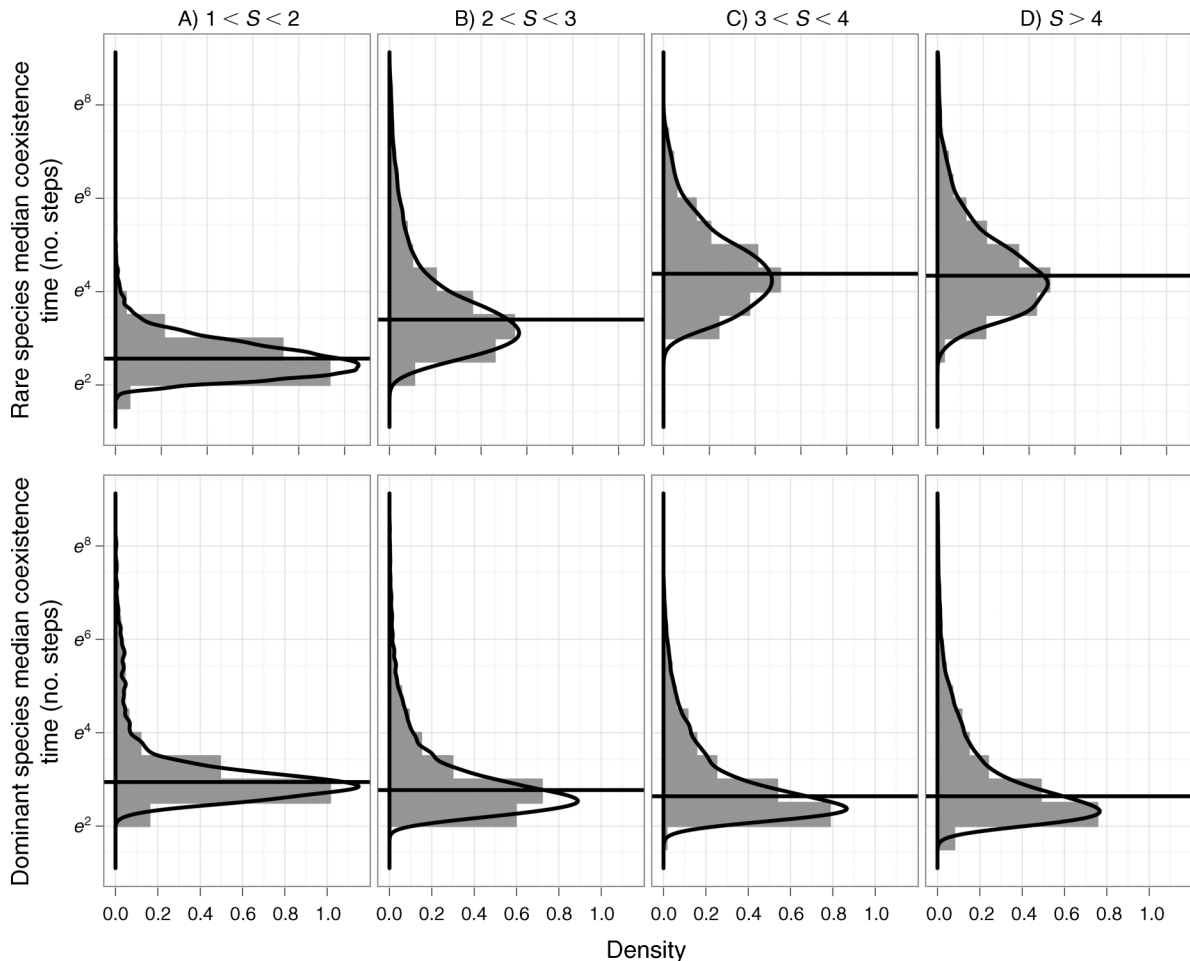


FIG. 3. Relationship between median coexistence time (the number of time steps, shown on a natural log scale, e) and the strength of stabilization experienced by the rare species (top row) and the dominant species (bottom row), shown as a histogram (gray bars), density plot (black curve), and median (black line). “Density” in this figure is simultaneously the value of the density plot and the frequency of the histogram bins. In each row, four levels of stabilization values (S) are given (A–D). Although demographic stochasticity often causes rapid extinction, dragging down median coexistence time in all cases, the prevalence of exceptionally long median coexistence times rapidly increases as stabilization increases for the rare species. In contrast, strength of stabilization for the dominant species does not directionally influence coexistence times.

Recent empirical papers have suggested that rarity may be the result of species-specific traits that make a species particularly sensitive to conspecifics in its local community, resulting in lower abundances in nature (Comita et al. 2010, Mangan et al. 2010). Our study emphasizes that strong NFD is not only why rare species are rare, but also why they are persistent, despite being rare. Rare species that do not have strong NFD may also be observed in a local community, but they should be incidental, rather than a persistent and interacting community member. Attempts to link species traits directly to the strength of self-limitation should help us to predict rarity, reconstruct more realistic community structures in restoration, and improve conservation and management of species requiring specific population dynamics for persistence. For example, it is possible to obtain fitness equivalence and stabilization estimates

from multispecies communities (e.g., Levine and Hille-RisLambers 2009, Adler et al. 2010) and use them as parameter values to simulate community dynamics through time. Such simulations could distinguish persistently rare species from at-risk species, as well as the strength of stabilization required to keep a species of interest in the community. Our prediction is that rare but persistent species will have some combination of intrinsic species traits that produce stronger NFD than dominant or incidental species experience.

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SUPPLEMENTAL MATERIAL

Supplement

R code to simulate frequency-dependent population growth for specific parameter combinations (*Ecological Archives* E093-042-S1).