SELF-LIMITATION AS AN EXPLANATION FOR SPECIES’ RELATIVE ABUNDANCES
AND THE LONG-TERM PERSISTENCE OF RARE SPECIES

by

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ABSTRACT

Self-limitation as an Explanation for Species’ Relative Abundances and the Long-term Persistence of Rare Species

by

Glenda M Yenni, Doctor of Philosophy

Utah State University, 2013

Much of ecological theory describes species interactions. These interactions often play an important theoretical role in facilitating coexistence. In particular, rarity in ecological communities, though often observed, provides a significant challenge to theoretical and empirical ecologists alike. I use a plant community model to simulate the effect of stronger 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 competitor, 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. To determine if ecological communities generally show the theoretical pattern, I estimate the strength of frequency-dependent population dynamics using species abundance data from 90 communities across a broad range of environments and taxonomic groups. In approximately half of the analyzed communities, rare species showed disproportionately strong negative frequency dependence. In particular, a pattern of increasing frequency dependence with decreasing relative abundance was seen in these communities, signaling the importance of this mechanism for rare species specifically. Insight into the special population dynamics of rare species will inform conservation efforts in response to climate change and other disturbance.
Further difficulties in the detection of theoretical patterns in ecological data may be a result of the ecological currency used. Though ecologists typically use abundance data to test theories, energy use is another ecological currency that may be more relevant in some cases. In particular when detecting patterns that are a result of species interactions, the currency used should be the one in which those interactions actually operate. I compare the results of using abundance and energy use to detect two processes with well-defined expectations. The first is a description of population dynamics, the above described relationship between relative abundance and self-limitation. The second, compensatory dynamics, is a description of community-level dynamics. I find that the currency used alters the results, and thus the species-level implications. It does not, however, alter the overall pattern that would have theoretical implications. Results in both currencies support the pattern of strong self-limitation for persistent rare species.

(130 pages)
PUBLIC ABSTRACT

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Ecological theories often hinge on species interactions, or how the species in an area “see” other species with whom they have to share food and space. Despite the contributions theoretical coexistence models have made to our understanding of species coexistence, it can still be difficult to match these theories with data from real communities. For example, we know of many species that are very rare where they occur. Theory predicts that these species should quickly go extinct, but they do not. I use simulations and real data to show that rare species are rare because they are more self-limiting. Self-limitation occurs when a species is more negatively affected by other members of the same species than it is by members of other species. The stronger this self-limitation is, the more a species is negatively affected when its numbers get too high. While this can prevent these species from becoming abundant, it also means that a species with strong self-limitation is more positively affected when its numbers are very low, i.e. it can rebound quickly when its population becomes small. I also show with simulations and data that rare species that are more self-limiting are less abundant, but they are also less likely to go extinct as a result, explaining why we see rare species so often in nature.

Another way to describe how species that co-occur at a site “see” each other, instead of using abundance, is to use energy use. Species that are very different sizes use very different
amounts of energy, because their metabolic rates are different. When co-occurring species are very different sizes, it is more likely that those species are more impacted by how much energy they each use, rather than just their abundances. I look at two different community patterns, the self-limitation described above and a measure of community variability called compensatory dynamics, to determine if energy use is a better currency to use when looking at community patterns. Energy use gives very different estimates for the dynamics I looked at, which could lead to different conclusions about what processes are important for a particular species. But energy is not as important when looking at large-scale patterns. The results across all species do not differ very much when using abundance compared to energy use. The conclusion using either abundance or energy use is that strongly self-limiting rare species are common.
Photos from the Portal project site in the Chihuahuan desert, a never-ending source of inspiration for pairing ecological theory with real data.
ACKNOWLEDGMENTS

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Two anonymous reviewers had insightful comments and suggestions that improved Chapter 1 for publication. I wish to thank all the researchers who have made their data publicly available and have permitted its use in this work. Please see the appendices for more detail about these data and the researchers responsible for their existence. In addition, thank you to Ryan O’Donnell, Sarah Supp and the Mammal Community Database, Elita Baldridge and the Life History Trait Database (for birds, mammals, and reptiles), and all the contributors to the Ecological Data Wiki for assistance in identifying available community datasets. This work was supported by USU’s Diversity Fellowship, an AAUW Selected Professions fellowship, a
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CHAPTER 1

INTRODUCTION

Community-level ecological theories focus on processes ranging from resource use and species interactions at the local scale to dispersal limitation and ecological equivalence at larger scales (Tilman 1982, Chesson 2000, Hubbell 2001, Levine and HilleRisLambers 2009). These processes often play an important theoretical role in facilitating coexistence or maintaining species diversity. Similarly, ecologists often have intimate knowledge of what species interactions, resource availability, dispersal, and species traits look like in their ecological system and assume that these are important for how the community operates as a whole (Brown et al. 2002, Gonzalez and Loreau 2009). Conclusions based on such results become more difficult, however, when one attempts to link expectations based on complex ecological models to data that one is able to collect in the field. The difficulty comes in determining what patterns to expect in ecological data, what patterns result from what processes, and what data are most appropriate to detect the patterns of interest.

In particular, rarity in ecological communities, though often observed, provides a significant challenge to theoretical and empirical ecologists alike. Rare species are observed often enough to inspire many explanations for why they occur (Main 1982). Yet rare species do not often achieve long-term persistence in theoretical models without employing very specific conditions. Negative interspecific effects make a species less abundant than it would be amongst less competitive species. At such low numbers, there also exists a relatively high probability of becoming so rare that the population cannot recover. The combination of the two makes persistent rarity, theoretically, unlikely. So it remains a puzzle how those species avoid the negative effects of stochastic extinction.
It has recently been suggested that disproportionately strong negative density-dependence may be a common cause of rarity (Mangan et al. 2010, Comita et al. 2010). Theory is also able to reproduce this pattern of rarity based on strong negative density-dependence (Chisholm and Muller-Landau 2011). Strong self-limitation thus provides a candidate for explaining species relative abundances with clear theoretical and empirical expectations. Processes linked to the prevalence of rare species are also likely candidates to be affecting their persistence. It is reasonable to expect that self-limitation should also promote the persistence of rare species by buffering them from extremely low population numbers.

To examine whether self-limitation can help rare-species persist, I 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. I then translate the results of this analysis into a well-defined pattern to expect out of ecological community data. To determine if ecological communities generally show the theoretical pattern, I use species abundance data from 90 communities across a broad range of environments and taxonomic groups.

While knowing what patterns to expect based on a particular process is important, it may also be the case that the type of data used in the analysis will affect your ability to detect that pattern. Standard methods of data collection are based primarily on convenience, not a consideration of what currency of species’ abundance is most appropriate for the processes of interest. For plants and invertebrates this is often biomass, while for vertebrates it is individual counts. But regardless of what the default currency is, when detecting patterns that are a result of species interactions, the currency used should be the one in which those interactions actually operate. I focus on the effect of currency choice in mammal communities. Large size differences in these communities likely create a need to account for species differences in resource use when describing species interactions. I compare the results of using abundance and energy use to detect
two processes with well-defined expectations. The first is a description of population dynamics, the above described relationship between relative abundance and self-limitation. The second, compensatory dynamics, is a description of community-level dynamics. If currency is an important choice when detecting these patterns, the two currencies should result in very different interpretations of when these processes are important and in which communities. Alternatively, currency choice may not impact the detection of ecological patterns. Still, the choice of currency should be motivated by theory, and not convenience.

References


CHAPTER 2

STRONG SELF-LIMITATION PROMOTES THE PERSISTENCE OF RARE SPECIES*

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 competitor, 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.

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 (Mangan et al. 2010, Comita 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 McPeek 2010).

Many tests of 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 (Figure 2 – 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 (Figure 2 – 1). This buffers a species against extremely low population numbers and stochastic extinction (e.g. Figure 2 – 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 use 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 introduce 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):

\[
N_{1,t+1} = \frac{r_1 N_{1,t}}{1 + a_{11} N_{1,t} + a_{12} N_{2,t}}
\]

\[
N_{2,t+1} = \frac{r_2 N_{2,t}}{1 + a_{22} N_{2,t} + a_{21} N_{1,t}}
\]

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 in this model are:

\[
S_1 = \frac{r_2}{1 + \left(\frac{a_{12}}{a_{22}}\right)(r_2 - 1)}
\]

\[
S_2 = \frac{r_1}{1 + \left(\frac{a_{21}}{a_{11}}\right)(r_1 - 1)}
\]

for species 1 and 2 respectively. Fitness equivalence, in this framework, is \(E_1 = \frac{r_1}{r_2}\) for species 1 and, assuming species 1 is the inferior competitor; \(E_1\) will always be between zero and one.

We calculated deterministic solutions for a range of possible parameter combinations \((r_1, r_2, a_{11}, a_{22})\) in which the deterministic abundance of species 1 was predicted to be 25% or less of the total community size. This produces scenarios for 14499 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 a species is suppressing conspecifics 7 times stronger than it suppresses heterospecifics. Very strong stabilization in this range has been observed in natural communities (Adler et al. 2010).

We calculated the covariance between deterministic abundance and strength of stabilization \((\nu)\) for each scenario. Note the results 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 Figure 2 – 1). We fit a logit regression model to determine the effects of fitness
equivalence, strength of stabilization, and $\nu$ on deterministic coexistence. This estimates the effect of $\nu$ 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 $\nu$ is negative (representing a strongly self-limiting rare species, see Figure 2 – 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. Simulations were initialized with 5 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 $\nu$ on the log 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 $\nu$ is negative (representing a strongly self-limiting rare species, see Figure 2 – 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 (Mangan et al. 2010, Comita et al. 2010, Bagchi 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 ($\nu$) between equilibrium abundance and strength of stabilization (i.e. the rare species experiencing disproportionately strong stabilization) promotes coexistence (Table 2–1).

Stochastic simulations

For rare species, the relationship between coexistence time and the strength of stabilization is log-linear (Figure 2–3): 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 (Figure 2–3). 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 2–1).

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. Though 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 Figure 2–1). 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 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. Figure 2–2). 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 explain the pervasiveness of rare species in real ecological communities by providing a mechanism which 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 multi-species models should generate the same pattern, where a negative relationship between abundance and stabilization of all the community members produces the most persistent community. While 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.

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 (Mangan et al. 2010, Comita 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 HilleRisLambers 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.

References


Table 2 – 1 A summary of the effect of the relationship between abundance and stabilization (ν) on deterministic coexistence and stochastic coexistence. 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 equivalence (of the rare species), negative covariances (ν) 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.

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Figure 2 - 1  Frequency dependence $\propto$ 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, grey 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 between mean population abundance and strength of stabilization ($\nu$) varies: (A) shows a positive relationship between mean population abundance and strength of stabilization ($\nu > 0$), (B) shows no relationship ($\nu \approx 0$), and (C) shows a negative relationship ($\nu < 0$). In the case in which $\nu < 0$, the rare species is experiencing much stronger positive growth rates, thus more opportunity for recovery from low density, than in either of the other two cases.
Asymmetric stabilization promotes stable coexistence: Example simulations showing the population dynamics when the rare species (solid line) is experiencing weak stabilization ($S_{\text{rare}} = 1$) vs strong stabilization ($S_{\text{rare}} = 5.17$). With weak stabilization (A), even though the deterministic equilibrium frequency of the rare species is relatively high (0.24), it is very vulnerable to stochastic extinction when abundance is low. With strong stabilization (B), 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 the first case, while it was 182 time steps in the second case.
The relationship between median coexistence time and the strength of stabilization experienced by the rare species (top row) and the dominant species (bottom row), shown as a histogram (grey bars), density plot (black curve) and median (black line). In each row, A: $1 < S < 2$; B: $2 < S < 3$; C: $3 < S < 4$, and D: $S > 4$, are the stabilization values experienced by either the rare species (top row) or the dominant species (bottom row). Though 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.
CHAPTER 3

EMPIRICAL EVIDENCE FOR THE DISPROPORTIONATELY STRONG SELF-LIMITATION OF PERSISTENT RARE SPECIES

Abstract

Rarity in ecological communities, though often observed, provides a significant challenge to theoretical and empirical ecologists alike. Yenni, Adler, and Ernest proposed a theoretical mechanism explaining persistent rare species in which the population dynamic that causes species to be rare (strong negative frequency dependence) is also what allows rare species to persist. However, it remains unclear if ecological communities generally show the theoretical pattern, or if rare species are perhaps controlled by other processes that shadow the effects of strong negative frequency dependence. The strength of frequency-dependent population dynamics was estimated using species abundance data from 90 communities across a broad range of environments and taxonomic groups. In approximately half of the analyzed communities, rare species showed disproportionately strong negative frequency dependence. In particular, a pattern of increasing frequency dependence with decreasing relative abundance was seen in these communities, signaling the importance of this mechanism for rare species specifically. Insight into the special population dynamics of rare species will inform conservation efforts in response to climate change and other disturbance.
Introduction

Rare species are ubiquitous in nature, but understanding why they occur and what mechanisms allow them to persist has proven challenging. While models describing interactions between well-studied common species perform well (Warner & Chesson 1985, Levine & Rees 2002, Thibault et al. 2010), reproducing realistic local-scale community structures with numerous rare species remains difficult using mechanistic models based on species interactions. Because rare species generally do not conform to our theoretical expectations and are empirically difficult to study (May 1999), progress in the study of rarity has been slow. However, most species within any community are rare and the low population sizes of rare species make them the most vulnerable to extinction. As such, rarity is a critical component for understanding mechanisms that maintain biodiversity and how to conserve it.

One of the conundrums of rarity is that while theoretically rare species are very vulnerable to stochastic extinction, they are also ubiquitous and unexpectedly persistent in nature. Since nature is rife with stochasticity, species with low population sizes need some mechanism that buffers their population dynamics from extinction in order to persist. One recently proposed mechanism for buffering small populations is the somewhat counter-intuitive, double-edged mechanism of self-limitation (see Chapter 2). Self-limitation occurs when a species’ population growth rate is more sensitive to the increasing presence of conspecifics than heterospecifics. Species with stronger self-limitation will also tend to be rare because of the strong decline in population growth rate with relatively small increases in the presence of conspecifics. However, when species with stronger self-limitation drop below their equilibrial state, they will also experience a stronger positive population growth rate which can rescue small populations from extinction (see Chapter 2). Because strong self-limitation can simultaneously create rare species
and allow their persistence, both aspects of this mechanism, referred to here as the self-limitation hypothesis for rarity, are required to promote coexistence and subsequently increase diversity.

While simulations suggest that strong self-limitation should be a common feature of persistent rare species, it is unclear whether this pattern occurs commonly in nature. One way to test the self-limitation hypothesis for rarity in ecological communities is to examine the strength of self-limitation exhibited by rarer species in comparison to more common species in the same community. There are four different scenarios (Fig 3 – 1) for how self-limitation could possibly be related to commonness or rarity (i.e. relative abundance) within a community: 1) persistent rare species exhibit weaker self-limitation than more common species, 2) all species may exhibit equal self-limitation, regardless of their relative frequency, 3) persistent rare species exhibit self-limitation that is greater than the most common species, but intermediate species exhibit no predictable relationship with their frequency, and 4) the strength of stabilization is directly related to the relative frequency of a species within the community, with rare species exhibiting the strongest self-limitation and self-limitation decreasing with increasing commonness. One of the challenges of testing the self-limitation prediction for rarity is that rare species only need strong enough self-limitation to buffer populations – not necessarily stronger or weaker than the more common species - and there is no a priori cut-off value for what constitutes ‘strong’ self-limitation. A rare species could have weaker self-limitation than a common species, but may still have strong enough self-limitation to buffer it against stochastic population dynamics (see Chapter 2). Because of this, the existence of scenarios 1-3 in empirical data cannot be used as support for or against the self-limitation prediction of rarity. In contrast, scenario 4, a predictable relationship between relative abundance and self-limitation, can be used to test the self-limitation hypothesis because the more common species provide a benchmark for measuring the self-limitation in the rarer species. Whether self-limitation is strong enough to provide a strong buffer
against stochastic dynamics is still not measurable from scenario 4, but it does show that rarer species will have more buffered population dynamics than more common species, which is consistent with the self-limitation hypothesis of rarity (see Chapter 2). While some examples of communities exhibiting scenario 4 have been reported (Harpole & Suding 2007, Adler et al. 2010, Comita et al. 2010, Mangan et al. 2010, Johnson et al. 2012), it remains unanswered if this community structure commonly occurs. Answering this issue is important because if strong self-limitation is a common mechanism for maintaining persistent rare species, it could provide an important theoretical explanation for why rarity exists and how rare species are maintained in nature.

Here we examine whether the predicted negative relationship between the strength of self-limitation and the rarity of a species is a pervasive structure in communities. We used estimates of negative frequency dependence and equilibrium frequency to explore the relationship between self-limitation and rarity in publicly available data from 90 communities across six major groups: fish, mammals, birds, plants, invertebrates, and herpetofauna. Negative frequency dependence directly describes the extent to which intraspecific interactions are stronger than interspecific interactions (Adler et al. 2007a), while equilibrium frequency is an estimate of a species’ intrinsic relative abundance in a community. Using these two measures, which are easily quantified from community time-series data, we can examine the persistently coexisting species within a community and estimate how sensitive individuals are to conspecifics and how this relates to their relative abundance.

Materials and Methods

Data

To estimate equilibrium frequency and the strength of negative frequency dependence of a species, it is necessary to have time series of abundance for a complete community at a well-

Communities were defined as within one habitat type and one trophic level. If datasets comprised data from multiple sites of the same habitat type, population dynamics were estimated for each local site separately, but the sites were pooled to describe one community dynamic. If datasets included multiple sites of different habitat types or multiple trophic levels, these data were treated as different communities and analyzed separately.

**Analysis**

A species’ negative frequency dependence can be estimated as the linear relationship between its relative frequency in a community in a year and the per capita population growth rate it experiences the following year. For each community time series obtained, relative abundance in each year $t$ for each species $s$ was calculated as $x_{t,s} = N_{t,s}/C_t$ (where $N$ is a species’ abundance and
C is the total community abundance. Log per capita population growth rates in each year $t$ for each species $s$ was calculated as $y_{t,s} = \log(N_{t+1,s}/N_{t,s})$. So the relationship between these population parameters was described as $Y_s = \beta_{0,s} + \beta_{1,s} X_s + \epsilon_s$ for each species. Equilibrium frequency, a species’ expected relative abundance in the community, is estimated as the x-intercept of this linear relationship, $-\beta_{0,s}/\beta_{1,s}$. The strength of a species’ negative frequency dependence is estimated as the negative slope of the linear relationship, $-\beta_{1,s}$. For consistency, the same model describing frequency dependence was used in all communities though more complex models would doubtless be appropriate in some communities.

Using the equilibrium frequency and frequency dependence, we identified which species observed at a site are likely persistent community members vs. ephemerally present. Because equilibrium frequency is estimated as the x-intercept of the fitted relationship between log per capita growth rate and relative abundance, it is possible for this value to be $< 0$ or $> 1$. If a species has an estimated equilibrium frequency below the expected range of 0 and 1, its expected relative abundance was 0 and thus unlikely to be a regular member of the community. Similarly, a species with estimated positive frequency dependence is expected to go locally extinct, as it is unlikely to have sufficiently large growth rates when rare. In these cases, the species is identified as ephemeral in the local community, as opposed to a persistent coexisting member of the community. All other species are retained as persistent community members. We examined how this method of identifying persistent species relates to actual persistence at a site by calculating the percent of years in which a species has non-zero abundance and comparing these values between ephemeral and persistent species.

To determine if persistent rare species are experiencing stronger negative frequency dependence than their dominant counterparts, we estimated the covariance between equilibrium frequency and the strength of negative frequency dependence in a community, $cov( \log(\beta_1/\beta_0), \cdots$.
log(−β_i)). Because most communities contain many species with very low equilibrium frequencies and a few dominants, and the negative frequency dependence of the few dominants was typically at least an order of magnitude lower than the remainder of the community, log-log relationships were most appropriate for calculating these covariances. Negative covariances indicate communities in which rare species are experiencing disproportionately strong negative frequency dependence relative to their dominant counterparts. Though there are several community scenarios in which rare species could be experiencing strong self-limitation (Figure 3–1), we only consider the cases in which there exists a significantly negative covariance between equilibrium frequency and negative frequency dependence (Figure 3–1A) as evidence in support of our hypothesis. This is a conservative approach, but it ensures an unbiased assessment of when a species is experiencing disproportionately strong self-limitation.

Randomized community estimates were used to determine which communities showed a significant negative covariance between equilibrium frequency and the strength of negative frequency dependence. Apparent negative frequency dependence can arise as a bias due to uncertainty in the abundance estimates (Knape & de Valpine 2012). There is the potential to overestimate the negative frequency dependence of rare species in particular, due to greater detection uncertainty, which would create a pattern similar to what is expected from rare species experiencing strong self-limitation. To maintain overall relative abundance and variability in the data, but remove negative density dependence, abundances from the original community time series were shuffled 5000 times, and all estimation methods were repeated with the shuffled data. This creates 5000 communities with the same community structure, but experiencing no real frequency dependence, thus any detection of frequency dependence in the randomized data is due to uncertainty alone. We compared the empirical pattern estimated from the original data to the distribution of these randomized values to estimate effect size and p-values. We report the
proportion difference in the observed pattern from the mean randomized pattern and calculate the p-value as the proportion of randomized pattern values that are less than or equal to the observed pattern. In addition to removing uncertainty bias, this has the added benefit of removing any effects of community structure (e.g. species richness) that may create a bias in the pattern of interest.

Results

In 44% (40 of 90) of the communities analyzed rarer species were experiencing significantly stronger negative frequency dependence increases (i.e. equilibrium frequency and the strength of negative frequency dependence were significantly negatively covariant). Removing species whose estimated equilibrium frequency was less than 0 and/or whose estimated frequency dependence was positive successfully identified a group of core species with higher percent presence as the persistent species (Figure 3–2). However, this may be a conservative approach for identifying ephemeral species as many species with low percent presence in the time series often remain. Among these remaining persistent species, the communities contain species experiencing a wide range of self-regulation, from very weak to surprisingly strong, and a wide range of equilibrium frequencies, from very dominant to extremely rare (Figure 3–3). Not only do persistent rare species in these communities experience extremely strong negative frequency dependence, but in many cases, it is the rare species specifically which are experiencing negative frequency dependence at the highest magnitude.

The prevalence of the relationship between equilibrium frequency and the strength of negative frequency dependence varied by group (Figure 3–4). While only 9% of herpetofauna communities had a significant self-limitation structure, in approximately half of bird, fish, invertebrate, mammal and plant communities (50%, 50%, 44%, 53% and 53%, respectively) were rare species more self-limiting than their dominant counterparts (Figure 3–4, also see Table C–
There is also a relationship between the pattern of negative density dependence in a community and species diversity. Communities in which the rare species were experiencing significantly stronger negative frequency dependence were more likely to be species-rich compared to the remaining communities (Figure 3–5).

Discussion

These results suggest that the relationship between self-limitation and rarity may be an important structuring factor in many ecological communities. Despite differences in diversity, complexity of species interactions and how species may achieve the necessary population dynamics, the phenomenon of rare species exhibiting stronger self-limitation than more common species is widespread. Though strong self-limitation is not universal among rare species, it does appear to be exclusive to rare species. There were only a few communities in which the dominant species had negative frequency dependence estimates higher than the rare species, and none in which they were significantly higher (see Table C–1). Because the strong self-limitation of persistent rare species is so common in these communities, it is no surprise that we also see the expected effects on diversity in general. Communities structured by self-limitation (i.e. those in which rare species were significantly more self-limiting than their dominant counterparts) were typically more diverse than those that were not structured by self-limitation (Figure 3–5). Presumably in those systems the buffering effects of strong self-limitation have resulted in increased diversity by allowing rare species to persist that would otherwise have succumbed to the combined effects of demographic stochasticity and competitive exclusion.

While many communities exhibited the predicted relationship between persistent rarity and the strength of self-limitation, it is important to note that many other communities did not. These non-significant communities likely fall into one of the other scenarios (Figure 3–1) for how self-limitation and commonness and rarity can potentially be related within a community.
Because of the complexities of assessing whether a particular value of self-limitation is strong enough to buffer populations, it is not possible to determine whether these non-significant communities support the self-limitation hypothesis of rarity or indicate the absence of the proposed mechanism. Therefore, it is not possible at this time to assess how widely the self-limitation hypothesis may apply to communities. However, even if all non-significant communities turn out to be inconsistent with the self-limitation hypothesis, our conservative approach allows us to state that at least 44% of tested communities exhibit a pattern consistent with the hypothesis. Interpreting what the non-significant communities mean for the self-limitation hypothesis of rarity will require more effort. It is already a worthwhile effort to directly estimate what magnitude of negative frequency dependence is sufficient to buffer a rare species from stochastic extinction. If it is possible to obtain, we could also use this information to determine whether rare species more frequently experience such strong frequency dependence that common species, without relying on the conservative approach we have used here.

The relevance of self-limitation for persistence occurs in a coexistence framework that employs a strict definition of what constitutes a local community. We are estimating the impact a species has on its own population dynamics relative to heterospecifics, which are restricted to other co-occurring species with a significant niche overlap (significantly shared resources). In our case, communities were assumed to be as defined by the dataset provider (with the exception of inter-trophic level datasets), rather than introduce any bias by removing species based on some arbitrary criteria. Species were only removed based on our estimates of their persistence as described in the methods. In most cases, of course, the community will be very well-defined by the dataset provider, with a classic coexistence concept in mind. Nonetheless, we have two possible scenarios of community misidentification. We may have been too exclusive in our community identification, or too inclusive. In either case, our estimate of the strength and
direction of the relationship between equilibrium frequency and strength of self-limitation is irrelevant if we have misidentified the community. But there is only one scenario in which we would expect to falsely conclude that a significant pattern exists; the one in which we falsely identify a rare species with weak self-limitation as nonpersistent and remove it from the community. This is the scenario we have tried to avoid with our very conservative identification of ephemeral rare species described in the methods. Interactions between distantly-related species have been detected in several systems (Valone et al. 1994; Keesing 1998; Muñoz et al. 2009), but these species are not typically included in the same community matrix because the interactions are unknown or the collection methods are different. In this analysis, only conventional community specifications were used, even if some knowledge that there may be significant interactions was available. Overall, we have taken a conservative approach to community identification and have still found our expected pattern widespread. With more precise community definition and estimation of population parameters by researchers in specific systems, strong self-limitation for rare species may prove to be even more prevalent than this study suggests.

Issues of community misidentification notwithstanding, where self-limitation does not appear to be structuring local communities there are many other good candidates for factors controlling the structure of those systems. Dispersal-limitation, habitat connectivity, and species’ physiology could all be controlling and precluding any structuring based on self-limiting population dynamics (Tilman 1997; Ernest et al. 2003; Alexander et al. 2011). The herpetofauna provide a stark contrast to the frequency of the expected pattern in the other community types. The herp communities may be especially restricted by physiology or other constraints on population dynamics that reduce the relevance of structuring by self-limitation. Herpetofauna are also notoriously sensitive to anthropogenic disturbance (Collins & Storfer 2003), which can alter
population dynamics directly or disrupt the effects of self-limitation indirectly through changes in species interactions. Thus, factors overwhelming structuring by self-limitation can be intrinsic to the species or the system, or they can be imposed by some unnatural disturbance. Identifying the specific environmental factors that preclude structuring by self-limiting population dynamics should provide insight into the invasibility and stability of that system.

While the pattern of stronger self-limitation for persistent rare species is not universal, it is pervasive enough to warrant an additional question: How might rare species show stronger self-limitation? One possibility is that both the strong sensitivity to congeners and ability to increase rapidly when below the equilibrial frequency are traits of rare species, i.e. a product of the adaptation of the organism to the local environment. An alternative possibility is that some species may have plasticity in their biology that allows them to exhibit strong self-limitation when placed in a community structure where resource availability or biotic interactions will result in that species becoming rare. The limited availability of community time series data does not allow us to directly link strong self-limitation to species traits or to test whether some species may show weak self-limitation when they are dominant but strong self-limitation when they are rare. However, understanding whether some species can adjust their self-limitation based on community context or whether rarity is itself a life history ‘trait’, or both, is an important next step suggested by our results. The task should be fairly straightforward in specific systems. For systems in which the species traits and interactions are well-described, paired natural systems or designed experiments can be used to parse out what traits lead to strong self-limitation, and when the ability of self-limitation to structure a community is overwhelmed by environmental effects or altered by community composition. The advantage of self-limiting population dynamics is efficiency at increasing from low numbers. Traits that allow a species to achieve this efficiency are still environment-dependent. It is then possible for certain types of environmental changes
(e.g. those that enhance allee effects or demographic stochasticity) to impede the ability of self-limitation to buffer against extinction, and thus alter community structure.

Finally, the prevalence of this pattern does more than suggest that rare species are stabilized by strong self-limitation. We have identified 40 communities in which a species’ relative strength of self-limitation is predictable from its equilibrium relative abundance, not just for rare species, but for all community members. What does it imply if we assume a causal relationship between strength of self-limitation and equilibrium frequency for all community members? If rare species are created by strong self-limitation, then the inverse may be true as well. Common species may be created by weak self-limitation. This causal relationship predicts exactly the community structure we see in many of the communities included in this analysis, and prompts questions about what causes other communities to break the expected pattern. However, this is a difficult and dangerously circular question to answer, and requires that we first address the questions raised above. Once we have identified how rare species achieve strongly self-limiting population dynamics we will be able to explore the possibility that a species’ strength of self-limitation is not only important for allowing the persistence of rare species, but determines local community structure itself.

References


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Figure 3 – 1  Examples of 3-species communities in which the rare species is experiencing strong self-limitation (solid line). For each species, strength of self-limitation is determined by the slope of the line, and equilibrium frequency is determined by the x-intercept of the line. Panel 1 shows persistent rare species exhibiting weaker self-limitation than more common species (dashed and dotted lines). Panels 2 and 3 show scenarios in which there is no predictable relationship between equilibrium frequency and strength of self-limitation, though the strength of self-limitation experienced by the rarest species is equivalent to that in scenario 4. Panel 4 shows the expected pattern, in which the strength of self-limitation a species experiences is negatively related to its equilibrium frequency, creating a “fan” of self-limitation slopes.
Figure 3 – 2  Differences between the species determined by our methods to be persistent community members and species determined to be incidental or "Ephemeral." "% presence" is the proportion of years in the time series in which the species had non-zero abundance.
Figure 3 – 3  Relationship between a species' equilibrium frequency and the strength of its negative frequency dependence (NFD).
Figure 3–4  Relationship between a species' equilibrium frequency and the strength of its negative frequency dependence, results separated by group. The number in each box is the proportion of communities in that group in which the rare species are experiencing significantly stronger negative frequency dependence than the rest of the community.
Figure 3 – 5  Density plots of community species diversity (persistent species only) for communities in which the rare species are experiencing significantly stronger negative frequency dependence (p<0.1) and those in which they are not (p>0.1).
CHAPTER 4

THE IMPORTANCE OF CURRENCY IN DETECTING COMMUNITY DYNAMICS

Abstract

Community patterns are typically summarized and tested using abundance data, but abundance is not the only currency in which species interactions likely occur. For communities with large differences in species’ body sizes, energy use may provide a better currency with which to describe the effects species have on each other and the resulting community patterns. I look at two well-described community patterns, negative frequency dependence and compensatory dynamics, to demonstrate how the choice of currency can play a role in these cases. The results clearly show that, at the individual species level, the choice of currency can have a significant effect. As currency can alter species-specific estimates and community patterns, the choice of currency should be grounded in theory.
Introduction

Species interactions form the basis for most theoretical frameworks of community dynamics (Tilman 1982, 1994, Chesson 2000, Adler et al. 2007, Angert et al. 2009, Gonzalez and Loreau 2009, Adler 2010, Jochimsen et al. 2013). To test these theoretical frameworks against field data, much consideration is given to the patterns that may arise from the processes of interest, and how to detect those patterns in data. Species abundance is the currency typically used in vertebrate communities because a count of individuals is the standard unit of data to collect. In plant or invertebrate communities biomass is often the unit of data collection, either out of convenience or to explicitly examine competition (Trinder et al. 2013). Currencies other than abundance are also conceptually possible in vertebrate communities, they are simply non-standard.

If species interact directly through interference competition, then abundance is the appropriate currency to estimate the strength of these interactions (Case and Gilpin 1974). Even in communities with large size disparities in which the larger species competes more aggressively, the interaction is asymmetrical but no scaling is needed to deal with differences in size because interactions occur directly between two individuals. But the vast majority of the remaining species interactions are not individual-based, and likely in some way based on depletion of a shared resource (Tilman 1982, Chesson 2000). Conceptually, community dynamics are explicitly based on competitive interactions through resource use, and so using the most direct estimate of resource use (energy use) should provide clearer results than using a proxy for resource use (abundance). The depletion of this resource by each species in the community is a function of the energy requirements of that species, or its collective metabolic rate. For communities in which even moderate size disparities exist between species, species abundances will be an inaccurate estimate of each species’ actual energy use. To account for this type of
interaction, species energy use should be calculated directly. Where energy use is the best estimator of each species’ impact on its fellow community members it is also likely to be the best currency to use when estimating dynamics and patterns that arise from those interactions.

If the use of a specific currency is an important decision when detecting community dynamics, mammal communities are an ideal group to attempt to detect a difference. The life history data necessary to estimate energy use from abundance and mass data is readily available, as well as the relationship to make the conversion (Ernest and Brown 2001, Ernest 2003). It is not necessary to account for temperature when estimating the metabolic rate of homeotherms (Ernest et al. 2003). This removes the problem of obtaining reliable site-specific climate data for every trapping period in the time series. It is also common to take mass measurements on every individual when collecting small mammal data in particular, which improves accuracy in the estimate of energy use for these communities. To explore the potential importance in currency differences, I use mammal communities representing moderate (rodents), large (African ungulates), and extreme (Canadian carnivores) inequality in their body sizes.

To determine whether using different ecological currencies alter the interpretation of community dynamics, I use both abundance and an energy-use metric to examine two community patterns thought to potentially arise via population-level interactions between species: the relative-abundance/frequency-dependence relationship and compensatory dynamics. The relative-abundance/frequency-dependence pattern is the occurrence of an inverse relationship between a species’ equilibrium frequency and the strength of its’ negative frequency dependence (see Chapter 2; Fig 4 - 1, left). This pattern has been used to explain patterns of relative abundance and the persistence of rare species and is thought to be generated from the relative strength of intraspecific versus interspecific interactions. The second pattern, compensatory dynamics, predicts that competition for a common resource can generate dynamics whereby decreases in
population-level resource use by some species within a community will be compensated for by increases in resource use by other species, thus creating less variability at the community level (Figure 4 – 1, right). This pattern is based on resource-mediated interactions among species aggregated across the entire community. The choice of currency used to detect these dynamics should play an important role in how we are testing for and interpreting our tests of ecological theory.

Methods

Data

To estimate equilibrium frequency and the strength of negative frequency dependence of a species, as well as compensatory dynamics in a community, it is necessary to have time series of abundance for a complete community at a well-defined local site. Data was obtained from 4 African ungulate communities (SANParks 1997, 2004, 2009), 12 Canadian carnivore communities (Novak et al. 1987), and 13 rodent communities (Grant 1976, Fryxell et al. 1998, Merritt 1999, Bartel et al. 2005, Stapp 2006, Bestelmeyer 2007, Friggins 2008, Ernest et al. 2009, Kaufman 2010) for which data was publicly available. Energy use was estimated using the known allometric relationship between body mass and metabolic rate, \( E=5.69*(mass)^{3/4} \) (Ernest 2005). In most cases the mass used to achieve this estimate was average mass from the literature (Ernest 2003), with the exception of 8 rodent communities for which individual mass data was available. This leads to a slightly improved estimate of energy use and these 8 communities (labeled Rodents 1 in the figures) were examined separately from the 5 rodent communities for which individual mass data was not collected (labeled Rodents 2 in the Figures).

Statistical Methods
Equilibrium abundance-frequency dependence relationship: For each community time series, relative abundance in each year \( t \) for each species \( s \) was calculated as \( x_{t,s} = N_{t,s}/C_t \) (where \( N \) is a species’ abundance or estimated energy use and \( C \) is the total community abundance or energy use). Log per capita population growth rates in each year \( t \) for each species \( s \) was calculated as \( y_{t,s} = \log(N_{t+1,s}/N_{t,s}) \). The relationship between these population parameters was estimated as in Chapter 3 to determine each species’ negative frequency dependence. Estimates were compared, within each mammal group, between abundance and energy use as the currency.

Compensatory dynamics: Following the methods from a recent paper on this topic (Jochimsen et al. 2013), detecting compensatory or synchronous community dynamics was done by calculating the covariance ratio for each community. The covariance ratio is the ratio of the summed community covariances over the summed individual species variances (Schluter 1984, Jochimsen et al. 2013). To account for the importance of time-scale in the operation of compensatory dynamics, covariance ratios were calculated in an expanding window, starting at 3 years and expanding yearly to include the entire time series. Covariance ratios were similarly calculated in a moving window fixed at 1/4, 1/3, and 1/2 the width of the total time series. Bootstrapped randomizations were done to assess significance using the boot package in R (Davidson and Hinkley 1997, Canty and Ripley 2012). Time series were phase-scrambled to account for the bias created by autocorrelation (Braun and Kulperger 1997, Solow and Duplisea 2007). To detect significant synchronous or compensatory dynamics, time series were phase-scrambled 5000 times and the randomized results were used to calculate a p-value.

While methods used in this paper follow recently published work on compensatory dynamics (Jochimsen et al 2013), it is important to note that these methods may be extremely conservative with regards to detecting significant compensatory dynamics. Mathematical restrictions on covariance ratios less than one and biases in detecting significance in the estimates
are known (Loreau and Mazancourt 2008), but attempts to introduce new methodology have been mostly ad hoc and have introduced their own methodology issues (Gonzalez and Loreau 2009). Clearly, the methodology for detecting compensatory dynamics needs to be updated, and systematic testing for bias done, before conclusions about the prevalence of compensatory dynamics generally can be assessed. However, for the purposes of this paper, where the question is focused on whether currency substantially changes detected dynamics, issues regarding how conservative tests may, or may not, be are largely irrelevant. By using the generally accepted current methodology, the inference is directly relatable to the current state of the literature on compensatory dynamics and whether those results may be sensitive to the currency used. All analyses were performed in R (R Development Core Team 2012).

Results

Negative frequency dependence

Converting to energy use compensated for large differences in metabolic rate by estimating smaller species to have greater frequency than would be calculated using abundance, and vice versa for very large species. This translates into differences in their estimated negative frequency dependence as well. The estimate of equilibrium frequency (relative abundance or relative energy use) was strongly affected by currency for the group with the largest inequality is species’ size, the Canadian carnivores, but less so for the other groups. This translated into weaker negative frequency dependence and stronger relationships between relative abundance and negative frequency dependence for the Canadian carnivores specifically (Figure 4 – 2). Across mammal groups, however, differences between the estimates were not large and occurred in no particular direction based on abundance or energy. Regardless of the currency used, rarer species tend to have strong negative frequency dependence, indicated by the prevalence of strong relationships between relative abundance and negative frequency dependence (Figure 4 – 2).
Compensatory dynamics

The differences in the results when using energy use versus abundance are more significant for compensatory dynamics. The frequency of synchronous or compensatory dynamics and their strength within a group of mammals varied widely with currency, though in no consistent direction (Figures 4–3, 4–4). Regardless of currency or timescale, significant synchronous dynamics were more frequent in the results than significant compensatory dynamics. Compensatory dynamics were slightly more prevalent when using energy as the currency (Figure 4–4), but the importance of community-specific results masks most of this tendency. However, in many individual communities the choice of currency made a significant difference in whether compensatory or synchronous dynamics were detected, and at what timescales (Figures 4–3, 4–4, also see Appendix for all individual community data).

Discussion

The choice of ecological currency clearly has the potential to significantly influence ecological inference for some questions. Accounting for the effects of resource availability on species interactions by converting to energy use (when appropriate) has important consequences for estimates of ecological parameters like negative frequency dependence and compensatory dynamics. The results include many communities in which an energy currency provided estimates of relative species energy uses and negative frequency dependences that were significantly different than the analogous estimates using an abundance currency. The detection of synchronous dynamics or compensatory dynamics (and at what timescales) was also significantly affected by currency. This translates to significantly different implications for the processes at work in those communities and their detection.
For an individual species or a local community, there are management and conservation implications based on the estimation of these parameters, making the choice of currency a crucial one. For example, the detection of negative frequency dependence can be used to determine whether a species is ephemeral or persistent. Some analyses using an energy currency detected an additional persistent rare species, or one that was at risk of local extinction. In some communities, compensatory dynamics were only detected using energy as the currency. The presence of compensatory dynamics at intermediate timescales indicates a much more stable community than one experiencing only synchronous dynamics. Compensatory dynamics suggest that competitive interactions between species should be particularly important for community stability. This should motivate different management actions than in a community where synchronous dynamics were dominant, indicating primarily environmental affects common to all species. The argument for an energy currency when estimating these parameters is based in theory, but the implications for conservation and management are no less relevant.

The choice of currency affects community-level patterns based on population dynamics, like the relationship between frequency and negative frequency dependence, because it clearly affects our estimates of relative abundance and NFD. Converting from abundance to energy use compensates for large inequalities in species’ metabolic rates and so ‘corrects’ relative abundances. This is apparent only in the mammal group with the largest inequality in body sizes, the Canadian carnivores, for which there is a much more equitable distribution of equilibrium frequencies using energy instead of abundance (Figure 4 – 2). But the correction is not significant enough to alter the shape of a pattern that is based as much or more on intraspecific interactions than it is on interspecific interactions (the inverse relationship between equilibrium frequency and negative frequency dependence). Very inequitable species size distributions are required to detect
a difference based on currency choice, but those examples provide evidence that while the shape of the pattern may not change in most cases, the strength of it will.

The choice of currency when examining community patterns based on whole-community dynamics had even greater impact than for the frequency dynamics. Conceptually, compensatory dynamics are explicitly based on competitive interactions and interactions with the environment affecting resource use (Ernest and Brown 2001). So it is not surprising that the choice of currency is an important one for detecting what dynamics are important for the community as a whole. There is much less agreement between the covariance ratio estimates using energy and abundance than for any of the negative frequency dependence parameters (compare Figures 4 – 2 and 4 – 3). In addition, my estimate of the overall prevalence of compensatory dynamics changes significantly when I use energy as the currency compared to abundance (Figure 4 – 4). Any post hoc explanation for why the estimate based on one currency is “correct” in contrast to the other would be completely subjective and invalid. Again, this suggests that the most appropriate currency to detect compensatory dynamics should be determined before performing the analysis, and based on the theoretical mechanisms creating the pattern.

Regardless of whether the use of a particular currency changes community patterns, there remain important conceptual reasons for actively choosing which currency to use in an analysis. To most closely pair theory with data, it is important to consider in which currency the processes of interest operate. For animals, it is relatively easy to use physiological data to convert population abundance to population energy use, especially if individual sizes have been measured in that community. When a community contains species of very unequal body masses, it is likely that abundance will not fully reflect dynamics based on indirect species interactions or whole-community fluctuations in energy use or output. On a larger scale, the choice of currency may not affect detection of processes operating within one trophic level, but energy is certainly more
appropriate to use when modeling the effect of those processes cascading to other trophic levels. The community-level patterns examined here appear robust in many ways to the choice of currency. That currency does not affect their detection, however, does not imply that the choice of currency is not important when estimating them. When looking at the site-level comparisons using abundance and energy, many differences align with expectations from ecological theory (e.g. that compensatory dynamics should appear at intermediate timescales, see Appendix), especially when familiar with the ecology of those systems specifically. But general ecological patterns less often come with such clear a priori expectations for what will be observed across multiple sites in multiple taxonomic groups. This only emphasizes the need for a clear theoretical grounding a priori for our choice of currency, rather than one based on convenience or convention.

References


Merritt, J. 1999. Long Term Mammal Data from Powdermill Biological Station. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication knb-lter-vcr.67.11.


Figure 4 – 1 Demonstration of the two community patterns of interest. Frequency dependence creates a pattern in which rarer species (solid line) experience stronger (more negative, steeper line) frequency dependence than more common species (dashed or dotted lines). Compensatory dynamics creates a pattern in which species fluctuations are offset (solid and dashed lines), resulting in less variability at the community level (dash-dot line).
Comparisons of estimates of the frequency dependence parameters using abundance (x-axis) or energy (y-axis) as the currency on a one-to-one line (grey). Rodents 1 includes rodent communities for which individual mass data was available. Rodents 2 includes other rodent communities for which mass data was not collected and energy use was estimated based on average species mass (as for the African Ungulate and Canadian Carnivore data). The first panel shows the estimates of equilibrium relative abundance or relative energy use. The second panel shows estimates of the strength of negative frequency dependence (NFD) using
abundance or energy. The third panel shows $S$, the estimated effect size of the relationship between NFD and relative abundance or relative energy use. A larger value of $S$ represents a relationship between relative abundance and NFD that is much stronger than expected from the randomized data. Estimates were clearly affected by the choice of currency, but not in a consistent direction or across mammal groups. The clearest differences occur in the group with the most inequitable distribution of species’ masses, the Canadian carnivores. These communities tend to have more equitable distributions of equilibrium relative energy use, weaker negative frequency dependence, and a stronger relationship between the two estimates using energy as the currency.
Figure 4 – 3  Comparisons of the covariance ratio estimates using abundance (x-axis) or energy (y-axis) as the currency on a one-to-one line (grey), for each of the ‘expanding window’ or ‘moving window’ analyses. Covariance ratios, R, were found to be significant (p-value < 0.05) using both energy and abundance (blue), using abundance but not energy (red), using energy but not abundance (green), or for neither currency (purple). The dark shaded region indicates the area in which the estimate of covariance ratio using abundance (RA) and the estimate using energy (RE) agree on the presence of compensatory dynamics (RA < 1 and RE < 1). The unshaded
region indicates the area in which the estimates using abundance and energy agree on the presence of synchronous dynamics (RA > 1 and RE > 1). And the lightly shaded regions indicate the areas in which the estimates using abundance and energy disagree on whether compensatory or synchronous dynamics are present (RA > 1 and RE < 1, or RA < 1 and RE > 1).
Figure 4 – 4  Comparison of the prevalence of compensatory dynamics found in a community in each of the moving window analyses, using abundance (x-axis) or energy (y-axis) as the currency. Black-outlined points represent the proportion of significant compensatory dynamics found, all other points are the proportion indicating a compensatory trend (R<1), significant or not.
CHAPTER 5
CONCLUSION

Though strong self-limitation seems at first a counter-intuitive candidate to explain the persistence of rare species, it arises as a relatively prevalent pattern across many types of ecological communities. This remains, however, the beginning of the story for how self-limitation produces and affects rare species, and species in general. Many questions remain about how biotic and abiotic conditions could affect the relationship between relative abundance and self-limitation. Does anthropogenic disturbance break the relationship, or make it stronger? Can the pattern be used as an indicator of a stable community, or its absence as a signal of community-wide change? Can we link the strength of a species’ self-limitation to that species’ traits? Is rarity caused by self-limitation even a species trait, or is it simply dependent on the local conditions? Though some of these questions will prove very complicated to answer, most of them already have relatively clear paths to follow to attempt an answer.

The effect of currency on our detection of ecological patterns also raises more questions. Though it may not change our inference about patterns at large scales and across communities, the choice of currency clearly has the ability to alter our inference of the presence of local-scale processes in a specific community. A method for determining which currency drives the other, and thus which is at the root of ecological processes, could better address which currency is the “correct” one to use in a particular community. Structural equation modeling and hierarchical modeling both have potential to shed light on this question, or at least utilize both currencies to improve detection of significant ecological patterns.
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To Permissions Editor:

I am preparing my dissertation in the Biology department at Utah State University. I hope to complete my degree in the Spring of 2013. An article, STRONG SELF-LIMITATION PROMOTES THE PERSISTENCE OF RARE SPECIES, of which I am first author, and which appeared in your journal Ecology reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation. (Reprinting the chapter may necessitate some revision.) Please note that USU sends Dissertations to Bell & Howell Dissertation Services to be made available for reproduction. I will include an acknowledgment to the article on the first page of the chapter, as shown below. Copyright and permission information will be included in a special appendix. If you would like a different acknowledgment, please so indicate.

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APPENDIX B:

DATASET SOURCES
Appendix B: Dataset sources

   Some data used in this publication were obtained by scientists of the Hubbard Brook Ecosystem Study; this publication has not been reviewed by those scientists. The Hubbard Brook Experimental Forest is operated and maintained by the Northeastern Research Station, U.S. Department of Agriculture, Newtown Square, Pennsylvania.
   2 datasets: Hubbard and White Mountain
   http://www.hubbardbrook.org/data/dataset.php?id=81

2. Detection of Density-Dependent Effects in Annual Duck Censuses
   1 dataset: Redvers
   http://dx.doi.org/10.2307/1939462

3. The Land-Bird Community of Skokholm: Ordination and Turnover
   1 dataset: Skokholm
   http://www.jstor.org/stable/3544096

   Data for CBP01 was supported by the NSF Long Term Ecological Research Program at Konza Prairie Biological Station
   2 datasets: Konza Waterfowl, Konza Songbirds

5. Neotropical Migratory Bird Communities in a Developing Pine Plantation
   1 dataset: Texas birds

1 dataset: Eastern Wood birds

7. The North American Breeding Bird Survey Results and Analysis. Version 96.4. Patuxent Wildlife Research Center

Data sets were provided by the Shortgrass Steppe Long Term Ecological Research group, a partnership between Colorado State University, United States Department of Agriculture, Agricultural Research Service, and the U.S. Forest Service Pawnee National Grassland. Significant funding for these data was provided by the National Science Foundation Long Term Ecological Research program (NSF Grant Number DEB-0823405).

2 datasets: Pawnee songbirds, Pawnee Raptors
http://www.sgslter.colostate.edu/dataset_view.aspx?id=avrc_usgs

8. Mountain Bird Watch

Thanks to the Vermont Center for Ecostudies for supplying data and to the hundreds of Mountain Birdwatch volunteers who gathered data for the project.

3 datasets: Maine, New York, Green Mountains
http://www.vtecostudies.org/MBW/

9. Avian populations Long-Term Monitoring. Luquillo LTER

This data was supported by grants BSR-8811902, DEB 9411973, DEB 0080538, DEB 0218039, and DEB 0620910 from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and to the International Institute of Tropical Forestry USDA Forest Service, as part of the Luquillo Long-Term Ecological Research Program. The U.S. Forest Service (Dept. of Agriculture) and the University of Puerto Rico gave additional support.

1 dataset: Luquillo Birds
http://luq.lternet.edu/data/luqmetadata23
10. The marine community at Hinkley Point
2 datasets: Hinkley Flatfish, Hinkley Gadoidfish
http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html

11. Time-series data for a selection of forty fish species caught during the International Bottom Trawl Survey
4 datasets: Northsea Demersal, Northsea Flatfish, Northsea Gadoid, Northsea Pelagic
http://icesjms.oxfordjournals.org/content/53/6/1079

12. Anole Population Dynamics. Luquillo LTER
This data was supported by grants BSR-8811902, DEB 9411973, DEB 0080538, DEB 0218039, and DEB 0620910 from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and to the International Institute of Tropical Forestry USDA Forest Service, as part of the Luquillo Long-Term Ecological Research Program. The U.S. Forest Service (Dept. of Agriculture) and the University of Puerto Rico gave additional support.
1 dataset: Luquillo anoles
http://luq.lternet.edu/data/luqmetadata4

13. Long-term sampling of a herpetofaunal assemblage on an isolated urban bushland remnant, Bold Park, Perth
3 datasets: Bold Park Snakes, Bold Park Lizards

14. Effects of rangeland management on community dynamics of the herpetofauna of the tallgrass prairie
2 datasets: Cowley County Snakes, Cowley County Lizards
http://www.bioone.org/doi/abs/10.1655/0018-0831%282006%2962%5B378%3AEORMOC%5D2.0.CO%3B2

15. Temporal variations in reptile assemblages in the goldfields of Western Australia
2 datasets: Ora Banda Snakes, Ora Banda Lizards

16. Historic and Legacy Data on Snakes. Kansas Biological Survey

Thank you to Dr. Henry S. Fitch for his efforts and to Alice Fitch Aechelle, George Pisani, and the Kansas Biological Survey for making this data publicly available and allowing its inclusion in this publication.

1 dataset: Fitch Snakes
http://kifs.ku.edu/media/kufs/libres/snakedata.htm

17. Population estimates of Appalachian salamanders. Coweeta LTER

1 dataset: Coweeta Salamanders
http://tropical.lternet.edu/knb/metacat/knb-lter-cwt.1044.4/lter


1 dataset: ES George Turtles
http://www3.imperial.ac.uk/cpb/databases/gpdd

19. Long-Term Studies of Vertebrate Communities

1 dataset: Rainbow Bay Frogs

20. Marine Mammals and Fisheries

1 dataset: CA Coastline Molluscs


Hubbard Brook Experimental Forest

Some data used in this publication were obtained by scientists of the Hubbard Brook Ecosystem Study; this publication has not been reviewed by those scientists. The Hubbard Brook Experimental Forest is operated and maintained by the Northeastern Research Station, U.S. Department of Agriculture, Newtown Square, Pennsylvania.

1 dataset: Hubbard Brook Leps
http://www.hubbardbrook.org/data/dataset.php?id=82

22. **Arthropod Pitfall Traps at LTER II NPP sites. Jornada LTER**

Data sets were provided by the Jornada Basin Long-Term Ecological Research (LTER) project. Funding for these data was provided by the U.S. National Science Foundation (Grant DEB-0618210).

4 datasets: Jornada Pitfalls Creosote, Jornada Pitfalls Grassland, Jornada Pitfalls Mesquite, Jornada Pitfalls Tarbush


23. **Community Ecology of Land Snails Survey (Long-term population dynamics of snails in the tabonuco forest). Luquillo LTER**

1 dataset: Luquillo Snails

http://tropical.lternet.edu/knb/metacat/knb-lter-luq.107.3/lter


Some data used in this publication was obtained by scientists, staff, and students at the Cornell Biological Field Station; this publication has not been reviewed by them. The Cornell Biological Field Station is operated and maintained by Cornell University, Ithaca, NY.

1 dataset: Oneida Lake Zooplankton

http://knb.ecoinformatics.org/knb/metacat/kgordon.17.27/knb

25. **MARINe Core Surveys: Species Counts**

11 datasets: Pacific Coast Arthropods CAY, Pacific Coast Echinoderms, Pacific Coast Molluscs BOA, Pacific Coast Molluscs CAY, Pacific Coast Molluscs GPT, Pacific Coast Molluscs HAZ, Pacific Coast Molluscs MCR, Pacific Coast Molluscs OCC, Pacific Coast Molluscs PSN, Pacific Coast Molluscs SAD, Pacific Coast Molluscs SHB

http://osu.piscoweb.org/cgi-bin/showDataset.cgi?docid=MLPA_intertidal.81.2

6 datasets: UK Butterflies Agricultural, UK Butterflies Coastal, UK Butterflies Grassland, UK Butterflies Forest, UK Butterflies Mixed, UK Butterflies Wetland


27. Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA

1 dataset: Portal

http://www.esajournals.org/doi/abs/10.1890/08-1222.1

28. Small Mammal Mark-Recapture Population Dynamics at Core Research Sites at the Sevilleta National Wildlife Refuge, New Mexico.

Data sets were provided by the Sevilleta Long Term Ecological Research (LTER) Program. Significant funding for collection of these data was provided by the National Science Foundation Long Term Ecological Research program.

3 datasets: Sev 5p grass, Sev 5p larrea, Sev rs larrea

http://sev.lternet.edu/data/sev-008

29. Seasonal summary of numbers of small mammals on the LTER traplines in prairie.

Konza Prairie LTER

Data for CSM04 was supported by the NSF Long Term Ecological Research Program at Konza Prairie Biological Station.

1 dataset: Konza


2 datasets: Curlew, INEEL

http://www.esajournals.org/doi/abs/10.1890/04-1607
31. Small Mammal Exclosure Study. Jornada LTER

Data sets were provided by the Jornada Basin Long-Term Ecological Research (LTER) project. Funding for these data was provided by the U.S. National Science Foundation (Grant DEB-0618210).

2 datasets: Jornada Grassland rodents, Jornada Shrubland rodents

http://jornada-www.nmsu.edu/studies/lter/datasets/animals/smlmamex/smesrdnt/smesrdnt.csv

32. Long Term Mammal Data from Powdermill Biological Station

Data sets were provided by the Virginia Coast Reserve LTER project of the University of Virginia. Funding for these data was provided by the U.S. National Science Foundation (NSF Grants BSR-8702333-06, DEB-9211772, DEB-9411974, DEB-0080381 and DEB-0621014).

2 datasets: Powdermill squirrels, Powdermill rodents

http://metacat.lternet.edu/knb/metacat/knb-lter-vcr.67.11/lter

33. SGS-LTER Long-Term Monitoring Project: Small Mammals on Trapping Webs

Data sets were provided by the Shortgrass Steppe Long Term Ecological Research group, a partnership between Colorado State University, United States Department of Agriculture, Agricultural Research Service, and the U.S. Forest Service Pawnee National Grassland. Significant funding for these data was provided by the National Science Foundation Long Term Ecological Research program (NSF Grant Number DEB-0823405).

http://sgs.cnr.colostate.edu/dataset_view.aspx?id=LTMrntrSmlMamWebs

1 dataset: Shortgrass rodents

34. Long-Term Dynamics of Small-Mammal Populations in Ontario

1 datasets: Ontario rodents

http://www.esajournals.org/doi/abs/10.1890/0012-9658%281998%29079%5B0213%3ALTDOSM%5D2.0.CO%3B2
35. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec
   1 dataset: Hilaire rodents
   http://www.nrceresearchpress.com/doi/abs/10.1139/z76-249#.UHXy31HZ2eg

   1 dataset: Karoo NP
   http://dataknp.sanparks.org/sanparks/metacat/peggym.117.10/sanparks

37. Census totals for large herbivores in the Kruger National Park summarized by year and region 1965-1997
   1 dataset: Kruger NP
   http://dataknp.sanparks.org/sanparks/metacat/judithk.814.4/sanparks

38. Golden Gate Highland National Parks Census Data
   1 dataset: Goldengate NP
   http://dataknp.sanparks.org/sanparks/metacat/peggym.113.6/sanparks

39. Long-term population dynamics of individually mapped Sonoran Desert winter annuals from the Desert Laboratory, Tucson AZ
   2 datasets: Desert Lab Open habitats, Desert Lab Shrub habitats
   http://www.eebweb.arizona.edu/faculty/venable/LTREB.htm

40. Spatial and Temporal Patterns of Net Primary Production in Chihuahuan Desert Ecosystems (NPP Study). Jornada LTER
    Data sets were provided by the Jornada Basin Long-Term Ecological Research (LTER) project. Funding for these data was provided by the U.S. National Science Foundation (Grant DEB-0618210).
    10 datasets: Jornada CS, Jornada CW, Jornada GS, Jornada GW, Jornada MS, Jornada MW, Jornada PS, Jornada PW, Jornada TS, Jornada TW
http://jornada-www.nmsu.edu/studies/lter/datasets/plants/nppqdbio/nppqdbio.dsd

41. Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants

2 datasets: Kansas Annuals, Kansas Perennials

http://www.esajournals.org/doi/abs/10.1890/0012-9658%282007%2988%5B2673%3ALMQFKP%5D2.0.CO%3B2

42. Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA

2 datasets: Portal Summer annuals, Portal Winter annuals

http://www.esajournals.org/doi/abs/10.1890/08-1222.1

43. Mapped quadrats in sagebrush steppe: long-term data for analyzing demographic rates and plant–plant interactions

1 dataset: Steppe plants

http://www.esajournals.org/doi/abs/10.1890/10-0404.1


12 datasets: Alberta, BC, Manitoba, New Brunswick, Newfoundland, Nova Scotia, NW Territories, Ontario, Prince Edwards Is, Quebec, Saskatchewan, Yukon
APPENDIX C:

CHAPTER 3: COMMUNITY-LEVEL RESULTS
Table C – 1  Community level results for Chapter 3

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“Observed S” is the number of species provided in the raw data. Species included in a community matrix with no or few non-zero abundances, for which estimation of population parameters was obviously not possible, were removed from the dataset before analysis and are not included in the “Observed S”. “Persistent S” is the number of species determined persistent by the methods described in the text. “Effect Size” is the proportional difference in the empirical pattern from random, or “Pattern”/”Random Pattern”. “Pattern” is the estimated covariance between equilibrium frequency and strength of negative frequency dependence for the community. “Random Pattern” is the mean covariance between equilibrium frequency and strength of negative frequency dependence found in the randomized data. “P-val” is the proportion of randomized pattern values that are less than or equal to the observed pattern.

<table>
<thead>
<tr>
<th>Plants</th>
<th>Jornada LTE R – Tarbush</th>
<th>Summer Annuals</th>
<th>Observed S</th>
<th>Persistent S</th>
<th>Effect Size Pattern</th>
<th>Effect Size Random Pattern</th>
<th>P-val</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plants</strong></td>
<td>Jornada LTE R – Tarbush</td>
<td>Winter Annuals</td>
<td>81</td>
<td>21</td>
<td>19</td>
<td>1.31928</td>
<td>-5.73949</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td>Kansas mixed-grass prairie</td>
<td>Annuals</td>
<td>34</td>
<td>4</td>
<td>39</td>
<td>2.674102</td>
<td>0.101421</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td>Kansas mixed-grass prairie</td>
<td>Perennials</td>
<td>102</td>
<td>39</td>
<td>41</td>
<td>0.426919</td>
<td>-1.12883</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td>Portal</td>
<td>Summer Annuals</td>
<td>68</td>
<td>33</td>
<td>32</td>
<td>1.101736</td>
<td>-3.36264</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td>Portal</td>
<td>Winter Annuals</td>
<td>71</td>
<td>34</td>
<td>32</td>
<td>1.349654</td>
<td>-3.89468</td>
</tr>
<tr>
<td><strong>Plants</strong></td>
<td>Sagebrush Steppe</td>
<td>Annuals</td>
<td>73</td>
<td>6</td>
<td>27</td>
<td>3.993184</td>
<td>-1.78516</td>
</tr>
</tbody>
</table>
APPENDIX D:

CHAPTER 4: COMMUNITY-LEVEL RESULTS
Figure D – 1  Overall relationship between equilibrium frequency and negative frequency dependence (NFD) using abundance and energy (red and blue, respectively). Though individual species estimates vary, both currencies give the approximately equivalent relationship overall. Rodents 1 includes rodent communities for which individual mass data was available. Rodents 2 includes other rodent communities for which mass data was not collected and energy use was estimated based on average species mass (as for the African Ungulate and Canadian Carnivore data). Lines are the modeled log-linear relationship between equilibrium frequency and NFD, with 95% confidence intervals (grey).
Figures D – 2 – D – 30 Covariance ratios at multiple timescales for all communities included in the analysis. Top panels: Covariance ratios estimated in an expanding window and 3 widths of moving window using abundance. Bottom panels: Covariance ratios estimated in an expanding window and 3 widths of moving window using energy use. Solid points indicate significant compensatory (below the grey line, R<1, p-value<0.05) or synchronous (above the grey line, R>1, p-value<0.05) dynamics. Open points indicate non-significant trends. Community data information is provided in Appendix 2.
Expanding window

CanadaCarnivores/quebecA

15-year moving window

21-year moving window

31-year moving window

Expanding window

CanadaCarnivores/quebecE

15-year moving window

21-year moving window

31-year moving window
APPENDIX E:

METADATA FOR ONLINE SUPPLEMENTARY INFORMATION
Chapter 2 code: R code to simulate frequency-dependent population growth for specific parameter combinations

File list

annualplant_2spp_stoch_par.r
updateN_function.r
simul_rare.txt
simul_rare_README.txt

Description

The ‘annualplant_2spp_stoch_par.r’ file is the R code written to simulate frequency-dependent population growth. The file ‘updateN_function.r’ is the population growth function used by ‘annualplant_2spp_stoch_par.r’, incorporating demographic stochasticity. The file ‘simul_rare.txt’ describes all parameter combinations used in the simulations, as well as their deterministic solutions. The file simul_rare_README.txt contains column definitions for the simul_rare.txt file.

Chapter 3 code: R code to calculate equilibrium frequency and negative frequency dependence, and determine the covariance between them.

File list

stabil_function.R
null_function.R

Description

The stabil_function code calculates equilibrium frequency and the strength of negative frequency dependence for each species in a community matrix, as well as the covariance between the two for the whole community. It also calls the null_function.R code, which randomizes the data to get a null expectation for the covariance to compare to the observed value.

Chapter 4 code: R code to calculate covariance ratios and get bootstrapped randomizations in a moving window for community time series data

File list

varianceratios.R
vartest_function.R

Description

The varianceratios.R code defines window sizes and functions to move an expanding window and a series of moving windows through a community time series. It runs the function vartest_function.R, which calculates the covariance ratio for a given community matrix, and performs phase-scrambled bootstrapping to assess significance. The code described in the Chapter 3 section is also used in this chapter.
CURRICULUM VITAE

Glenda Marie Yenni
(March 2013)

Research Summary
I am interested in general questions of community dynamics, coexistence and species diversity. I use a synthesis of theory and empirical observations to find processes that are widespread among ecological communities.

EDUCATION
Utah State University, May 2013 (expected)
**PhD in Biology, Ecology** GPA: 3.8
Advisor: S. K. Morgan Ernest

Utah State University, May 2011
**MS in Statistics** GPA: 3.74
Thesis: “Climate change and community dynamics: A hierarchical Bayesian model of resource-driven changes in a desert rodent community”
Advisor: Mevin Hooten

University of California, Davis, June 2004
**BS in Animal Science**, specialization Conservation Biology, with Honors GPA: 3.58

PROFESSIONAL EXPERIENCE

**Graduate Research Assistant.** Department of Biology, Utah State University, Logan UT. Desert small mammal community ecology, management of the Portal LTREB, small mammal live trapping, database management. 2006-2008, 2012-present

**Research Assistant.** School of Natural Resources, University of Arizona. Mt. Graham, AZ. Tamiasciurus hudsonicus grahamensis radio telemetry, habitat classification, database maintenance, threatened/endangered species protocol. 2006

**Field Technician.** University of Alaska, SE and USDA Forest Service, Pacific Northwest Research Station. Prince of Wales Island, AK. Winston P. Smith, Ph.D. (Research Wildlife Biologist). Glaucomys sabrinus live trapping, PIT tagging, tissue/blood/hair sampling, spool releases, nighttime radio telemetry triangulation, homing and den site surveys, vegetation surveys in old growth, clear cuts, and second growth, management and instruction of EarthWatch volunteers, set up and operation of Silent Image cameras for vigilance behavior study, data management. 2005

**Field Assistant.** Department of Evolution and Ecology, UC Davis. Karen Mabry (Population Biology Graduate Group). Peromyscus boylii live trapping, tagging, tissue sampling, data recording, nighttime radio telemetry and triangulation and homing, fluorescent powder tracking, GPS, vegetation surveys of nest sites. 2004-2005

**Internship.** Department of Evolution and Ecology, UC Davis. Judy Stamps and Kyria Mills. Drosophila observations, experiment design, yeast cultures, purification of genomic DNA, PCR, DNA sequencing. 2004
Lab Assistant. Herman J. Phaff Yeast Culture Collection, UC Davis. Kyria Mills. Purification and transfer of yeast strains, lab management. 2004


Lab Assistant, Pet and Health Care Center, Department of Molecular and Cellular Biology, UC Davis. 2000-2001

TEACHING EXPERIENCE
Teaching Assistant. Biology II, BIOL 1620, Utah State University. 2012
Teaching Assistant. Human Physiology, BIOL 2420, Utah State University. 2009
Teaching Assistant. Biology I, BIOL 1610, Utah State University. 2009
Outdoor Adventures Wilderness Guide. UC Davis. 2003-2004
Biology/Statistics Tutor, Learning Skills Center, UC Davis. 2002-2003

IN PREP
Yenni, Glenda Marie. Empirical Evidence for the Disproportionately Strong Self-Limitation of Persistent Rare Species.

PUBLICATIONS

PRESENTATIONS

AWARDS
USU Research and Graduate Studies Graduate Student Travel Award – August 2012
USU Center for Women and Gender Travel Grant – July 2012
USU Ecology Center Travel Award – June 2007, June 2009, July 2012
USU School of Graduate Studies Dissertation Fellowship – 2012
USU Ecology Center Assistantship - 2010-2011
AAUW Selected Professions Fellowship – 2008-2009
USU Diversity Fellowship in Science and Engineering – 2006-2008
American Society of Animal Science Scholastic Achievement Award 05/28/2004
Animal Science Academic Scholarship – UC Davis 1999-2001

MEMBERSHIPS
Ecological Society of America
American Society of Mammalogists
American Statistical Association
USU Biology Graduate Student Association

SKILLS
Quantitative: Bayesian, likelihood-based, and frequentist statistics, multivariate statistics, mathematical models of ecological concepts, simulation, database design and management, experimental design and implementation
Field: Leading/managing field crews, live small mammal trapping and handling, vegetation surveys, plant identification, PIT tagging, radio collaring, radio telemetry (including triangulation), blood sampling, Silent Image cameras, wildlife observation, GPS, bat mist-netting
Computer: Microsoft, Macintosh, Linux, virtual machines, using the shell, version control, web design
Language: Spanish, R, Python, SQL, MATLAB, SAS