

CONCEPT
PAPER



Do persistent rare species experience stronger negative frequency dependence than common species?

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ABSTRACT

Understanding why so many species are rare yet persistent remains a significant challenge for both theoretical and empirical ecologists. Yenni *et al.* (2012, *Ecology*, 93, 456–461) proposed that strong negative frequency dependence causes species to be rare while simultaneously buffering them against extinction. This hypothesis predicts that, on average, rare species should experience stronger negative frequency dependence than common species. However, it is unknown if ecological communities generally show this theoretical pattern. We discuss the implications of this phenomenon for community dynamics, and develop a method to test for a non-random relationship between negative frequency dependence and relative abundance using species abundance data from 90 communities across a broad range of environments and taxonomic groups. To account for biases introduced by measurement error, we compared the observed correlation between species relative abundance and the strength of frequency dependence against expectations from a randomization procedure. In approximately half of the analysed communities, we found increasingly strong negative frequency dependence with decreasing relative abundance: rare species experienced stronger frequency dependence than common species. The randomization test never detected stronger negative frequency dependence in more common species. Our results suggest that strong negative frequency dependence is a signature of persistent, rare species in many communities.

Keywords

Coexistence, community, diversity, frequency dependence, persistence, rare species.

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INTRODUCTION

Most species are rare, but understanding the factors that cause them to be rare – and yet persist – is challenging. One complication is that there are so many different kinds of rarity (Preston, 1948; Main, 1982; Kunin & Gaston, 1997; Magurran & Henderson, 2003; Comita *et al.*, 2010). A geographically rare species or one that persists through dispersal and metapopulation dynamics is clearly different from a numerically rare species that can persist without spatial subsidies. We focus on the latter case: why are some species numerically rare in a community but still manage to persist over time?

One possibility is that persistent rare species occupy similar niches to superior competitors. In order for the rare

species to persist, niche overlap cannot be complete, but the greater the overlap, the fewer resources available to the inferior competitor and the smaller its population. Under this scenario, if the superior competitors were removed, the abundance of rare species would increase dramatically. A long history of removal experiments in plant communities suggests that this is sometimes the case, but in other cases rare species only increase modestly after removal of a dominant, do not respond or respond negatively (Sammul *et al.*, 2000; Fowler, 1981, 1995; Hils & Vankat, 1982; Silander & Antonovics, 1982; Miller, 1994; Page & Bork, 2005; Suding *et al.* 2006; Callaway & Howard, 2007; Rietsma *et al.*, 2010; Liancourt *et al.*, 2013). An alternative possibility is that persistent rare species specialize on unique, but narrow, niches.

These species would depend on a combination of resources, microsites or windows of opportunity which are ignored by dominant competitors but are in limited supply. The overlapping niche and unique niche scenarios represent two ends of a continuum.

The differences between these causes of persistent rarity have important implications. A species whose rarity is caused by niche overlap would respond readily to management interventions focused on the dominant species, but species that are rare because they specialize on narrow niches would not. Rare species affected by niche overlap will be sensitive to indirect effects of environmental change mediated by species interactions, whereas rare species with a unique niche will respond primarily to direct effects of environmental change (Adler *et al.*, 2012; Kleinhesselink & Adler, 2015). Perhaps most importantly, rare species occupying unique niches may be more effectively buffered against extinction than rare species affected by niche overlap (Yenni *et al.*, 2012). To understand this, we need to think about intra- and interspecific limitations.

A species whose rarity reflects niche overlap is sensitive to both intra- and interspecific competition. If a series of unfavourable years pushes it to the brink of extinction, it will still suffer from strong interspecific competition from more abundant competitors, limiting the rate at which it can rebound to its (stochastic) equilibrium abundance, and increasing the probability of its extinction. In contrast, a rare species that occupies a unique, narrow niche is far more sensitive to intra- than interspecific competition. When this kind of species falls to an unusually low abundance it will experience a relatively strong competitive release: intraspecific competition will decrease and interspecific competition was low to begin with. As a result, it has the potential to rebound quickly to its equilibrium abundance. A common species, in contrast, will almost never be in danger of stochastic extinction thanks to its large population size. This logic predicts that rare species occupying unique niches might be less sensitive to stochastic extinction (Yenni *et al.*, 2012) and more common in natural communities than rare species competing for contested niches.

Testing this hypothesis in natural communities would clearly be useful and interesting. But estimating the strength of intra- and interspecific interactions in species-rich communities, and for rare species in particular, is extremely difficult. Fortunately, a more tractable approach may be possible: the frequency dependence of a species' population growth rate provides an index of that species' sensitivity to intra- versus interspecific limitations. Frequency dependence arises indirectly from density dependence. Species often experience negative density dependence, but will not necessarily experience negative frequency dependence (NFD) as well, unless conspecific effects are more negative than heterospecific effects (see Appendix S2 in the Supporting Information for an in-depth discussion of density and frequency dependence). As a species increases from rare (low frequency) to common (high frequency) in a community, it interacts with

relatively more conspecifics and fewer heterospecifics. Frequency dependence describes how the per capita growth rate of a focal species changes across this gradient (Figure 1): if the focal species occupies a unique, narrow niche, its per capita growth rate will decline rapidly as its frequency in the community increases. On the other hand, if the focal species occupies a similar niche to other species, then conspecifics and heterospecifics will have similar impacts on individuals of the focal species, and the relationship between frequency and per capita growth rate will be weak. Thus, we expect species whose rarity is caused by specialization on rare resources or conditions to exhibit especially strong NFD relative to species that are rare due to niche overlap with dominants.

In a community of stably coexisting species, all species should experience NFD; all species must limit conspecifics more than they limit heterospecifics (Chesson, 2000). But this requirement does not predict any relationship between equilibrium relative abundance and the strength of NFD. The two explanations for rarity offered above, however, do imply expectations about such a relationship. If rare species occupy similar niches to common species, their sensitivity to conspecific and heterospecific competition should also be similar, resulting in NFD of similar strength for rare and common species (Appendix S2). If rare species occupy unique, narrow niches, they will be very sensitive to conspecific competition but insensitive to heterospecific competition, implying a stronger NFD than we expect for common species (it is difficult for a species to become common if it experiences strong intraspecific competition).

The asymmetric NFD pattern

While simulations suggest that strong NFD should be a specific indicator of persistent rare species (Yenni *et al.*, 2012), few empirical studies have assessed this. Strong negative density or frequency dependence in some rare species has been documented (Harpole & Suding, 2007; Adler *et al.*, 2010; Comita *et al.*, 2010; Mangan *et al.*, 2010; Johnson *et al.*, 2012) but these few studies exclusively focused on selected plant communities. This limited number of studies does not tell us how general this pattern is across a variety of natural communities. Because there are many possible ways in which a rare species can be persistent, we would not necessarily expect one particular pattern to be present in all communities. Even if it were not common, asymmetric NFD would still be an indicator of rare species buffered from stochastic extinction where it did occur. If strong NFD is common among rare species, it would suggest (1) that those rare species are not rare because they are suppressed by superior competitors but rather because they are more strongly self-limiting, and (2) that rare species that do not experience a large release from competition at low density, as implied by strong NFD, often do not persist. If this is a general pattern across taxa and ecosystems, then this mechanism could be of

general importance to the coexistence and persistence of rare species.

Challenges to estimating asymmetric NFD

Using NFD as an indicator of the relative strength of intra- and interspecific effects is relatively easy because it relies only on abundance data. This approach comes with logistical costs of its own, however. Estimates of density dependence are often inflated as a result of measurement error (Freckleton *et al.*, 2006; Knape & de Valpine, 2012). Estimates of frequency dependence are subject to the same biases. The bias itself is not necessarily a problem, because asymmetric NFD describes the pattern of frequency dependence between all species in a community. If all species are subject to the same observation bias this alone would create no pattern in the NFD experienced by species based on their relative abundances. But we know that our ability to detect species does vary with abundance, implying higher measurement error for rare species and raising the potential for greater bias in the estimates of the NFD of rare species than of common species. Another known artefact comes when we estimate the relationship between NFD and frequency in the community, which requires us to calculate the covariance between two related estimates (the covariance of A/B with B expected to be negative). In order to use data from many different communities to assess whether there is empirical support that persistent rare species are more sensitive to intraspecific competition, we must account for these methodological issues related to the assessment of asymmetric NFD. In the course of describing our methods we also discuss the need for new approaches and data collection to rigorously pursue this important area in the research of diversity and the persistence of species.

METHODS

Overview of analysis

We assessed whether there is a general relationship between the rarity of a species and the strength of NFD by examining a large compilation of publicly available time series on the abundance of all species within one trophic guild. Our analysis involves the following steps: (1) identifying appropriate data, (2) estimating equilibrium frequency and NFD for each species in each community, (3) identifying the persistent community, (4) estimating a community-level pattern of NFD, and (5) accounting for known and unknown biases in the pattern of interest (see Fig. 2) before making a final conclusion about the NFD–rarity relationship in each community. Below, we describe each of these steps in detail. Our methods allow us to use commonly available data to conduct initial explorations into the relationship between NFD and rarity.

Identifying suitable data for community NFD patterns

Many of the coexistence mechanisms that generate NFD can operate at very small spatial scales (Chesson, 2000). This is also true in the framework defined in Yenni *et al.* (2012). Therefore, to assess whether persistent rare species have stronger NFD than common species, we required communities where the data were collected in a manner consistent with this local-scale concept. We restricted communities to all species within a study belonging to the same trophic level and occurring within a single habitat type as defined by the data collector. If the data collector indicated that the study included multiple sites of different habitat types or multiple trophic levels these data were treated as different communities and analysed separately. If a study collected data from multiple locations of the same habitat type, we examined those separately. However, to prevent a single study area from dominating the results because it had multiple sites, we treated multiple sites in a single study area as habitat replicates and only one datapoint was estimated from the entire resulting site data. Finally, to calculate frequency dependence, we used time-series data because there are few studies that have measured frequency dependence for all species in a community in an experimental manner. All of these data decisions were made to ensure we were only analysing populations that were likely to be directly interacting and to provide data for a large number and diversity of taxa and ecosystems. Using these criteria, we found suitable data for 90 different communities containing collectively 703 species (see Appendix S1). These communities represent six major taxonomic groups (birds, fish, herpetofauna, invertebrates, mammals, plants), five continents and three trophic levels, thus providing a general exploration of whether persistent rare species commonly exhibit stronger NFD, and thus stronger population buffering, than common species.

Calculating NFD and equilibrium frequency

Community time series can be used to estimate equilibrium frequency – the relative abundance when a species' population is in steady state – and the strength of NFD for all species that met our criteria for persistence within each community (Fig. 1). We estimated a species' NFD as the linear relationship between its relative abundance (frequency) in a community and its annual per capita population growth rate (Fig. 1b). For each community, relative abundance in each year t for each species s was calculated as $x_{t,s} = N_{t,s}/\sum_{i=1:S} N_{t,i}$ (where N is a species' absolute abundance) (Fig. 2, step 1). Log per capita population growth rates in each year t for each species s were calculated as $y_{t,s} = \log(N_{t+1,s}/N_{t,s})$ (Fig. 2, step 1). The relationship between these population parameters was described as $y_s = \beta_{0,s} + \beta_{1,s} x_s + \epsilon_s$ for each species s (Fig. 2, step 3). Equilibrium frequency (f), a species' expected relative abundance in the community, is estimated as the x -intercept of this linear relationship, $f = -\beta_{0,s}/\beta_{1,s}$

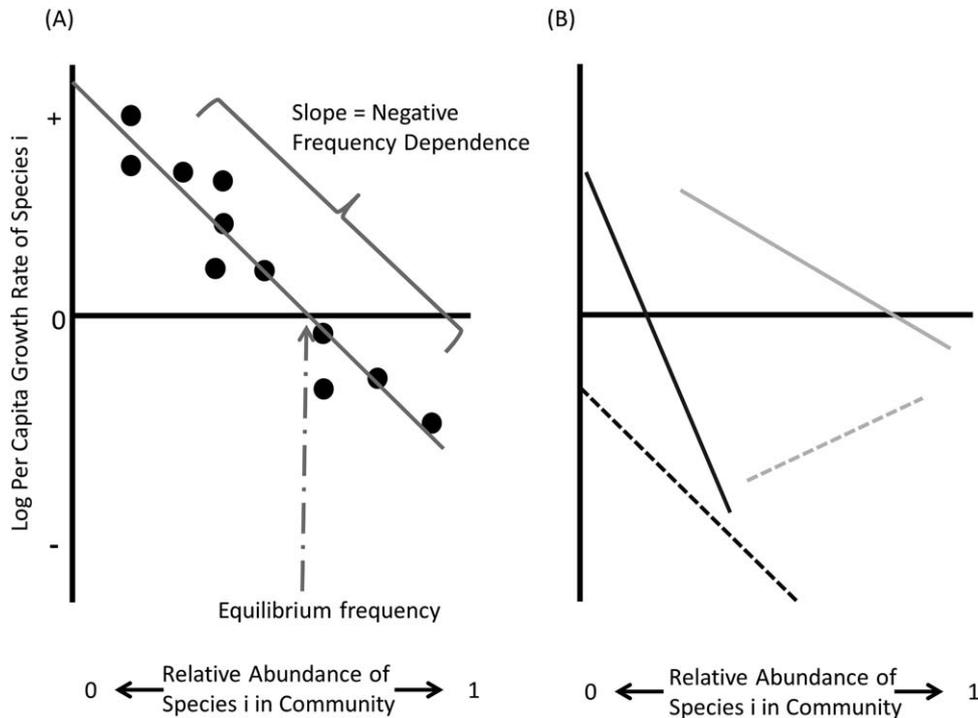


Figure 1 (a) Negative frequency dependence (NFD) and equilibrium frequency can be calculated from time-series community data. Each data point represents the relative abundance of species *i* at time *t* in its community (*x*-axis) and its log per capita population growth rate from time *t* to time *t* + 1 (*y*-axis). The slope of this line is the species' NFD (equal to $-\beta_1$ in the linear model). Equilibrium frequency – the expected relative abundance of species *i* in the community when its population growth is at equilibrium – is the fitted *x*-intercept of the relationship. The fitted *y*-intercept is the species' maximal growth rate. (b) The *x*-intercept and slope of the relationship indicate important biological information about each species. Steep slopes indicate stronger NFD, and thus higher sensitivity of population growth to changes in conspecifics than to changes in heterospecifics. In a linear relationship, high maximum growth rates, which buffer species from extinction, are achieved through high equilibrium frequencies (common species, solid grey line) or strong NFD (rare species, solid black line). *x*-intercepts < 0 indicate species that cannot maintain a stable presence within the community at their population equilibrium (dashed black line). Species exhibiting positive frequency dependence will often have difficulty invading when rare (dashed grey line). These latter two scenarios indicate species that are probably not stably coexisting within the current community.

(Fig. 2, step 3). Frequency dependence (FD) is estimated as the slope of the linear relationship, $FD = \beta_{1,s}$ (Fig. 2, step 3).

Ephemeral versus persistent species

As discussed in the Introduction, asymmetric NFD is a mechanism for maintaining small populations near their steady state despite stochasticity, and thus only applies to stably coexisting common and rare species. Because other mechanisms are expected to dominate the population dynamics of invading, declining or transient species, we used three criteria to identify and exclude species with population characteristics that would make them likely to be ephemeral and not stably coexistent (Figure S15 in Appendix S5): (1) too few occurrences to estimate parameters (typically only or nearly all zero abundances, the inclusion of this type of species in a dataset is typically an arbitrary decision by the data collectors, and was highly variable between datasets – 52% of species included in the raw data files), which indicates that a species is exceptionally transient; (2) negative equilibrium frequency (Fig. 1b),

which indicates the species cannot persist in the community (7.7% of species; Chesson, 2000; Adler *et al.*, 2007); and (3) positive frequency dependence (Fig. 1b), which is related to a negative invasion growth rate and likely results in either the extinction of that species or an ever increasing invader (11% of species; Chesson, 2000; Adler *et al.*, 2007). 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 less than 0 or greater than 1 (Fig. 1a). Besides the fact that these species are obviously ephemeral and thus irrelevant to our analysis, it would make the relationship between equilibrium frequency and frequency dependence nonsensical to include negative equilibrium frequencies or positive frequency dependences.

All other species are retained as persistent community members. Our criteria are only a weak filter for removing ephemeral species. Some of the species retained in the analysis are also likely to be ephemeral, but we abstained from further filtering to avoid possibly biasing the results. After all, it is not the goal of this analysis to determine which

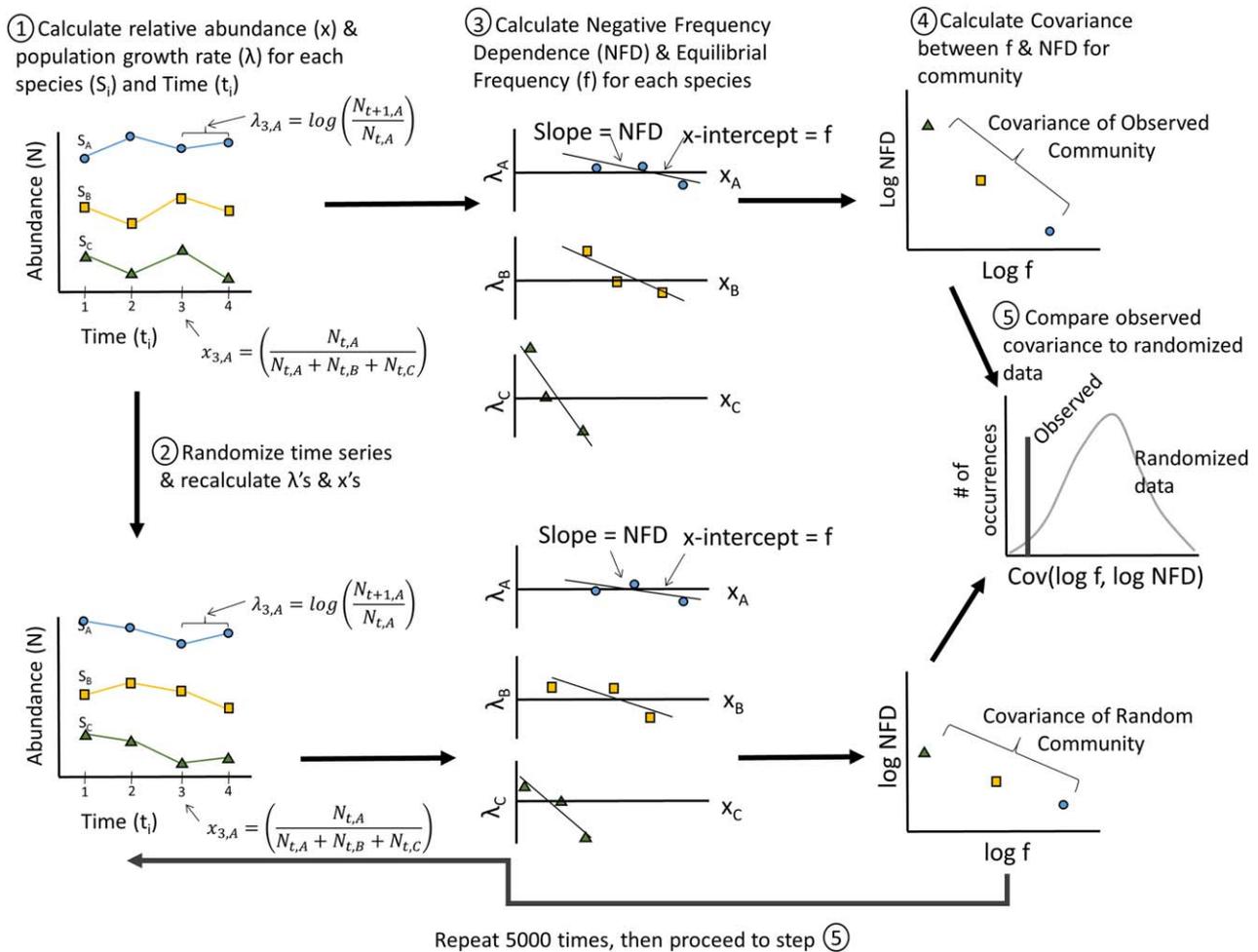


Figure 2 A diagram of our analysis. (1) We calculated relative abundance and per capita growth rate for each species at each time step. (2) The data are randomized (within each species, independently from other species) and relative abundance and growth rate are recalculated for the 'Null' expectation. From this point, each of 5000 iterations of the randomized data receives the same treatment as the observed data in the analysis. (3) The relationship between relative abundance and growth rate is fitted for each species. The slope of this relationship is the strength of negative frequency dependence (NFD) for each species, and the x-intercept is the equilibrium frequency (f). (4) Using each species as a data point, the covariance between these two parameters is the value of interest, but it contains known biases. (5) Now, the randomizations of the time series are used to create a baseline expectation for each unique community based on these biases, and the observed relationship is considered relative to this baseline (the randomized covariance). Thus, we use the proportional difference in the empirical covariance from random (observed covariance/mean randomized covariance). P -values are calculated as the proportion of randomized values larger than the observed asymmetry value.

individual species are ephemeral or persistent. We only seek to determine, among species that appear to be experiencing NFD, whether there is a relationship with rarity. We examined how this method of identifying persistent species relates to actual persistence at a site by calculating the percentage of years in which a species has non-zero abundances and comparing these values between ephemeral and persistent species. Our approach identified a group of more persistent species that were on average present over a greater fraction of the time series (Figure S14 in Appendix S5).

Quantifying asymmetric NFD at the community level

Our goal is not to characterize the absolute strength of NFD experienced by individual species, which might reflect

estimation biases, but rather to estimate the pattern in relative abundance and NFD across all persistent species in the community. To quantify the relationship between rarity and NFD within a community, we calculated the covariance between equilibrium frequency and the strength of NFD (Fig. 2, step 4). The covariance calculation uses each species in a community as a single data point in the calculation (Fig. 2, step 4): $cov[\log(f), \log(-FD)]$. Negative covariances indicate communities in which rare species are experiencing stronger NFD than their dominant counterparts (note that the expectation for $cov[\log(f), \log(-FD)]$ is already negative due to issues with calculating NFD as discussed in the Introduction; we discuss how we addressed this in the following section). Log-log relationships were most appropriate for calculating

these covariances because most communities contain many species with very low equilibrium frequencies and only a few dominants, and because the observed NFD of the few dominants was typically at least an order of magnitude lower than for the remainder of the community. To explore how our assumptions about the shape of the relationship affected our results, we also explored a nonlinear model of frequency dependence. These results are in Appendix S6.

Dealing with known and unknown biases

Time-series data with significant observation uncertainty can show the signature of negative density or frequency dependence even when none exists (Freckleton *et al.*, 2006; Knappe & de Valpine, 2012) because the calculation can create a negative bias in the resulting estimates of population growth. Our interest is not in the individual estimates, however, but the overall community pattern. We designed a randomization procedure to determine which communities showed a significant negative covariance between equilibrium frequency and the strength of NFD. We reshuffled abundances from the original community time series 5000 times for each species independently (Fig. 2, step 2), and then repeated all estimation methods with the time-randomized data (Fig 2, steps 3 and 4). This procedure maintains relative abundances and observed variability, but the frequency dependence detected in the randomized data is due to statistical artefacts alone. We compared the covariance estimated from the original data with the distribution of covariance estimated from the randomized data sets to estimate effect size and *P*-values (Fig. 2, step 5). We report the 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. Simulations using known relationships confirm that this approach accounts for known biases resulting from uncertainty in the observations. It also accounts for the fact that the expectation for the covariance is already negative (see Appendix S3 for details of our simulations). In addition to removing these known biases, the randomization method has the added benefit of removing any unknown statistical artefacts or effects of community structure (e.g. richness) that may create a bias in the pattern of interest, because it creates a randomized expectation specifically for each community. This is a conservative approach, but it enables us to identify communities in which the observed relationship between rarity and NDF is extremely unlikely to arise due to chance or statistical artefacts. The significance of the asymmetric NFD pattern was assessed using Strimmer's approach (Strimmer, 2008) to estimate the number of true null hypotheses, controlling the false discovery rate at 0.1 (Benjamini & Hochberg, 1995, 2000; Verhoeven *et al.*, 2005). All analyses were performed using R software (R Development Core Team, 2012), and code is provided in Methods S1.

Immigration might create an additional bias in our estimates of NFD which our randomization procedure does not

account for. Intuition suggests that if immigration maintains populations of a rare species in a sink habitat, our approach would detect very strong density and frequency dependence. For example, adding one immigrant to a small population represents a very large population growth rate but would have little effect on the population growth rate of a large population. We used both our NFD simulation and a more traditional Lotka–Volterra model (Chesson, 2000) to evaluate this intuition and explore how immigration might influence NFD in common and rare species (Appendix S4). Results from both models were similar: immigration did not create patterns of asymmetric frequency dependence and, if anything, significant amounts of immigration decrease the ability of our method to detect true *in situ* asymmetric NFD (models and results in Appendix S4).

RESULTS

Asymmetric patterns of NFD appear to be common

When compared with the randomized time series, 46% (41 of 90) of communities demonstrated a significant relationship between relative abundance and NFD, indicating that rare species experience stronger NFD than common species (Fig. 3a, Table 1). While negative relationships between rarity and the strength of NFD often arose in randomized data as well, in the communities where the observed pattern was statistically significant, the stronger NFD of rare species could not be explained solely as a result of bias related to uncertainty in the abundance estimates. These results indicate real differences between rare and common species in the sensitivity of population growth rates to the abundance of heterospecifics and conspecifics.

The prevalence of asymmetric NFD within communities varied by taxonomic group (Fig. 3b–g). In approximately half of bird, fish, invertebrate, mammal and plant communities (50%, 50%, 48%, 53% and 53%, respectively) rare species experienced stronger NFD than their dominant counterparts (Table 1, Fig. 3). However, only 9% of herpetofauna communities had a significant asymmetric NFD structure. Why asymmetric NFD is less prevalent in herpetofauna communities is unclear, though a likely explanation is the difficulty in achieving reliable abundance data for such communities. Noise in the observed abundances could make it difficult to detect NFD in many of these communities. Additional figures are provided in Appendix S5.

Across all taxa, only a few communities had dominant species with stronger NFD estimates than the rare species, but this pattern was never significant (see Table S1). Thus, while rare species often, but not always, showed significantly stronger NFD than common species, common species never showed stronger NFD than rare species. Despite differences in diversity, complexity of species interactions and how species may achieve the necessary population dynamics, the phenomenon of rare species exhibiting stronger NFD than more common species appears to be widespread across community types.

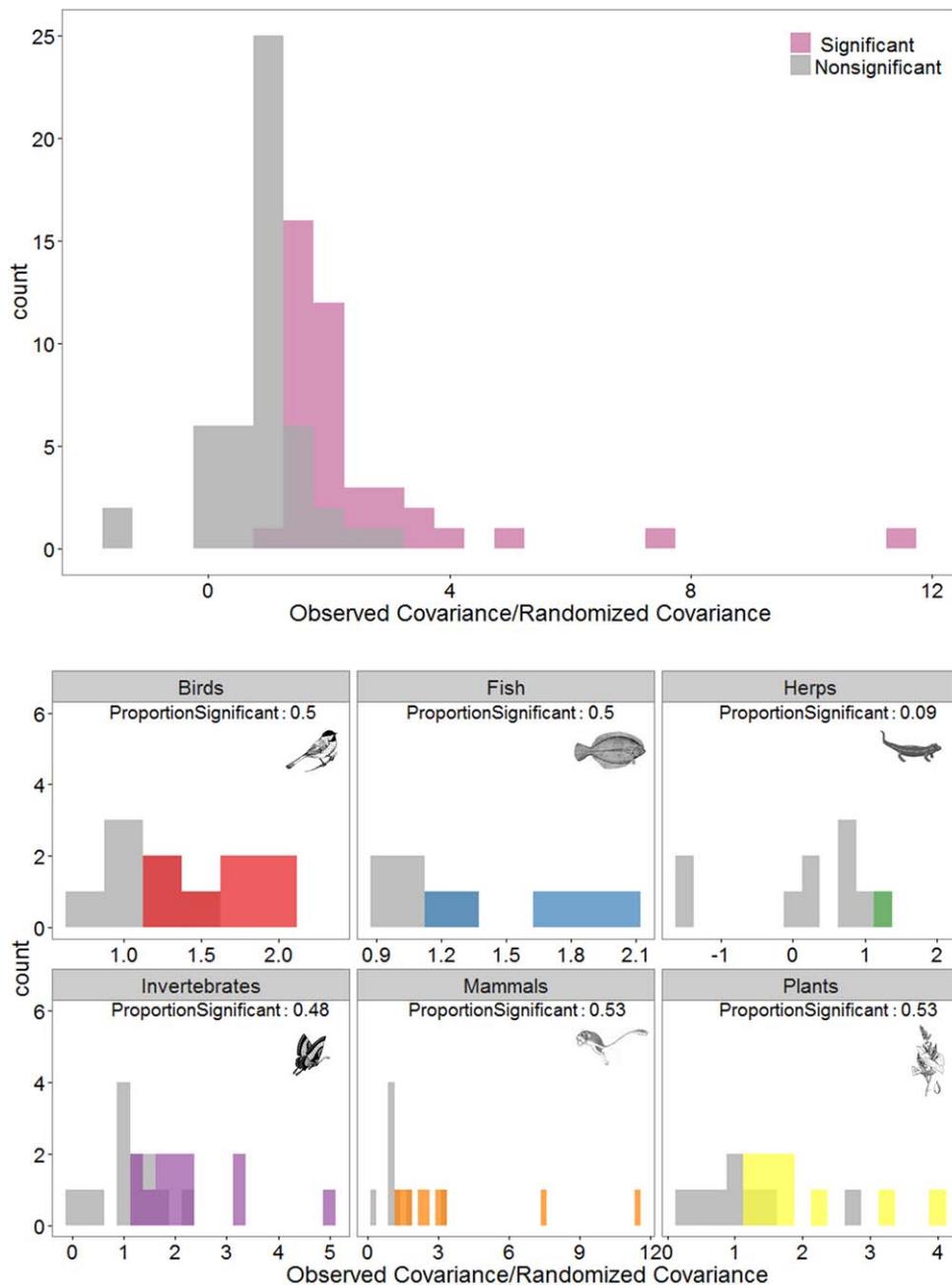


Figure 3 Results were compared with randomized data to account for bias introduced by measurement error and determine which relationships were significant (coloured bars) or not (grey bars). *P*-values were calculated as the proportion of randomized values larger than the observed asymmetry value. (a) All results for the 90 communities included in the analysis. We detected a significantly asymmetric negative frequency dependence (NFD) pattern in 46% of these communities. (b) Results separated by taxonomic group, showing the relative size of the asymmetry in NFD between species in each community (observed covariance/randomized covariance). The proportion value in each panel is the proportion of communities in that group with a significant asymmetric NFD pattern.

Simulations testing our randomization procedure for addressing bias caused by measurement error (Appendix S3) demonstrated that our method consistently assigns significance when the relationship between equilibrium frequency and NFD is strong, but it typically fails to detect weak relationships. Therefore, our non-significant results probably include some communities where a relationship

between relative abundance and NFD exists but is too weak for our method to detect. If so, then the prevalence of strong NFD in rare species is probably more common than our results indicate. Overall, our results suggest that in many communities, persistent rare species may commonly exhibit stronger NFD than the more common species in the community.

Table 1 Summary results of community-level analyses by taxonomic group.

Taxonomic group	No. of communities	Mean values across communities				Covariance strength (ρ/ρ_0)	No. of significant communities	Proportion significant
		Species/community	Persistent species/community	Observed covariance (ρ)	Randomized covariance (ρ_0)			
Birds	14	25.9	21.1	-1.68	-1.29	1.38	7	0.50
Fish	6	8.8	7.0	-9.02	-7.41	1.40	3	0.50
Herpetofauna	11	11.4	7.0	-0.41	-0.67	0.27	1	0.09
Invertebrates	25	42.0	12.2	-3.86	-2.84	1.69	12	0.48
Mammals	17	7.8	4.6	-1.70	-1.08	2.65	9	0.53
Plants	17	82.0	22.6	-3.74	-2.61	1.64	9	0.53
Total	90						41	0.46

Covariances (ρ and ρ_0) were calculated as $\text{cov}[\log(f), \log(-\text{FD})]$. The number of significant communities is those in which the covariance was determined significant after control for false discovery rate ($\alpha = 0.1$).

DISCUSSION

Implications

Our results, which are consistent with the theory developed by Yenni *et al.* (2012), suggest that in many communities persistent rare species do not share similar niches with competitors having higher fitness but rather occupy unique, narrow niches. The resulting differences between rare and common species in their sensitivity to intra- and interspecific interactions may explain the existence of persistent rare species in many communities. However, the pattern we have detected raises questions about mechanisms. Compared with common species, why do rare species appear to be so much more sensitive to intra- than interspecific interactions? One possibility is that both strong sensitivity to congeners and an ability to increase rapidly when the population falls below its equilibrium frequency are traits of rare species, for example a result of specialization on a rare resource or susceptibility to virulent species-specific natural enemies. An alternative explanation is that strong NFD is not a fixed trait but is context-dependent. Some species might show strong NFD when conditions cause them to be rare members of the community but weaker NFD in communities when they are more dominant. The limited availability of community time-series data does not allow us to directly link strong NFD to species traits or to test whether some species may show weak NFD when they are dominant but strong NFD when they are rare.

Our simulations further support the idea that the prevalence of asymmetric NFD is not merely an artefact of uncertainty due to sampling biases or immigration. This is not to say that immigration or processes such as facilitation and interaction networks, cycles, chaotic dynamics and nonlinear NFDs could not also create or modify patterns of NFD. For example, while we explored a particular implementation of immigration, it is still possible that immigration might be able to generate asymmetric NFD under specific circumstances. Clearly it is important for coexistence theory to assess whether these other processes can also generate or enhance

community-level patterns of asymmetric frequency dependence, especially as it relates to the concept of persistent rare species.

Regardless of the underlying mechanisms, or whether strong NFD is a fixed or plastic trait of rare species, our results suggest that exploring the causes and consequences of asymmetric NFD may be important not only for coexistence theory, but also for designing management strategies for rare species. If intraspecific competition is the primary cause of rarity, then indirect effects of environmental change mediated by competitive interactions (Adler *et al.*, 2012; Chu *et al.*, 2016) might be relatively weak for rare species compared with common species. Similarly, we might expect management actions intended to increase the abundance of a rare species by reducing the density of interspecific competitors to be unsuccessful. However, if asymmetric NFD is being generated by other mechanisms such as immigration, then the implications for designing management strategies will be very different. Investigating the mechanisms that lead to asymmetric NFD is an important step for understanding, and potentially managing, the many rare species in natural communities.

Future analyses

Our analysis also highlights analytical and theoretical limitations to our understanding of NFD that need to be addressed for research into NFD to progress further. For example, that herpetofaunal communities would display different dynamics from the other taxa may not be surprising. The documented sensitivity of herpetofauna to disturbance is one possibility for their differing dynamics (Collins & Storfer, 2003). If these communities are not governed by competition dynamics because they are responding primarily to disturbance, then we would not expect them to show a pattern that reflects avoidance of competition. However, we are unable to make this inference because we cannot assume that the apparent lack of NFD is accurate. These may simply be communities in which, due to inaccurate estimates of abundance, we

cannot detect the NFD that species are experiencing. Our analysis allows us to create a conservative estimate for the prevalence of NFD for rare species in natural communities. But accurate estimates that will allow us to make inferences like the ones above remain a challenge.

Definitive statements about the absolute strength of NFD in common and rare species would require unbiased estimates of maximum population growth rates and density dependence. In contrast, our randomization test focuses on the relative strength of NFD in common versus rare species. Direct, unbiased estimates of NFD would remove the need for our conservative randomization test, and might reveal the role of asymmetric NFD in additional communities. An additional challenge for future research is disentangling the effects of intra- and interspecific competition from other potential mechanisms of NFD, such as immigration or nonlinear dynamics. Addressing this challenge will also require more sophisticated methods for correcting NFD for bias or, alternatively, individual-level data on vital rates and dispersal.

Summary

Our work suggests that strong NFD in persistent rare species could be a mechanism that helps offset stochastic extinction risk. If true, this concept has wide-ranging implications for our understanding of coexistence and community dynamics. However, in exploring this idea, we found severe limitations in the current state of data, statistics and theory that prevented us from conducting robust empirical analyses or interpreting rigorously the mechanism behind the patterns we uncovered. Given the importance, and possible generality, of asymmetric frequency dependence, we hope that our work here will inspire others to help solve these challenges so we may all better understand the mechanisms that allow rare species to persist in nature.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Dataset sources.

Appendix S2 Discussion of negative frequency dependence.

Appendix S3 Simulations to test methodology.

Appendix S4 Immigration simulations.

Appendix S5 Supplementary figures (Figs S14–S19).

Appendix S6 Testing an alternative (nonlinear) model of negative frequency dependence.

Table S1 Community-level results.

Table S2 Summary of the parameter values used in our simulations.

Table S3 Summary of the parameter values used in simulating immigration.

Figure S1 The frequency-dependence relationships simulated in each community scenario.

Figure S2 The resulting actual species abundances in simulated community scenarios 1–4.

Figure S3 The resulting observed species abundances in the nine simulated communities, after incorporating sampling noise.

Figure S4 Results of simulation of scenario 1, using the same methodology applied to the real community data.

Figure S5 Results of simulation of scenario 2, using the same methodology applied to the real community data.

Figure S6 Results of simulation of scenario 3, using the same methodology applied to the real community data.

Figure S7 Results of simulation of scenario 4.

Figure S8 The frequency-dependence relationship simulated in the focal community and the resulting actual species abundances in the simulated community for the stabilized scenario.

Figure S9 The resulting observed species abundances in the simulated community for the stabilized scenario, after incorporating sampling noise.

Figure S10 Results from simulated and sampled communities in the stabilized scenario, using the same methodology applied to the real community data.

Figure S11 The frequency-dependence relationship simulated in the focal community and the resulting actual species abundances in the simulated community for the randomized scenario.

Figure S12 The resulting observed species abundances in the simulated community for the randomized scenario, after incorporating sampling noise.

Figure S13 Results from simulated and sampled communities in the randomized scenario, using the same methodology applied to the real community data.

Figure S14 Differences between the species determined by our methods to be persistent community members and species determined to be incidental or 'ephemeral'.

Figure S15 Number of species (and their relative abundances) determined to be persistent or ephemeral based on estimated equilibrium frequency and whether or not they are experiencing positive or negative frequency dependence.

Figure S16 Results separated by group. The value in each panel is the proportion of communities in that group that show the asymmetric negative frequency dependence pattern significantly.

Figure S17 Relationship between a species' equilibrium frequency and the strength of its negative frequency dependence.

Figure S18 Results separated by taxonomic group, showing the relationship between equilibrium frequency and strength of negative frequency dependence experienced in each individual community.

Figure S19 In contrast to the strength of negative frequency dependence, there is no clear relationship between equilibrium frequency and the maximal growth rate estimate for each species (estimated as the y-intercept of the frequency dependence relationship).

Figure S20 Results were compared to randomized data to account for bias introduced by measurement error and determine which relationships were significant or not.

Figure S21 Results separated by taxonomic group, showing the relative size of the asymmetry in negative frequency dependence between species in each community.

BIOSKETCHES

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