

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

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16 **Abstract**

17 Understanding why so many species are rare yet persistent remains a significant
18 challenge for both theoretical and empirical ecologists. Yenni, Adler, and Ernest (2012) proposed
19 that strong negative frequency dependence causes species to be rare while simultaneously
20 buffering them against extinction. This hypothesis predicts that, on average, rare species should
21 experience stronger negative frequency dependence than common species. However, it is
22 unknown if ecological communities generally show this theoretical pattern, or if rarity is
23 primarily determined by other processes that overwhelm the effects of strong negative frequency
24 dependence. We discuss the implications of this mechanism for natural communities, and
25 develop a method to test for a non-random relationship between negative frequency dependence
26 and relative abundance, using species abundance data from 90 communities across a broad range
27 of environments and taxonomic groups. To account for biases introduced by measurement error,
28 we compared the observed correlation between species relative abundance and the strength of
29 frequency dependence against expectations from a randomization procedure. In approximately
30 half of the analyzed communities, rare species showed disproportionately strong negative
31 frequency dependence compared to common species. Specifically, we found a pattern of
32 increasingly strong negative frequency dependence with decreasing relative abundance. Our
33 results suggest that strong negative frequency dependence is a signature of both rarity and
34 persistence for many species in many communities.

35 **Introduction**

36 Rare species are ubiquitous in nature, but understanding the factors limiting their
37 abundance and the mechanisms allowing them to persist has proven challenging. Reproducing

38 realistic local-scale community structures with numerous rare species remains difficult using
39 simple theoretical or statistical models of species interactions (Tilman, 2004; Angert *et al.*, 2009;
40 Clark *et al.*, 2010). One reason these models fail to predict realistic numbers of rare species is
41 that many rare species are simply ephemeral, and their occasional presence is likely explained by
42 metapopulation dynamics. Thus the number of these species in a local community can only be
43 explained when regional-scale processes are considered along with local-scale processes.
44 However, not all rare species are ephemeral. Some species manage to persist at low abundance
45 within a community for long periods of time without succumbing to stochastic extinction events.
46 Since stochasticity is pervasive in ecological systems, species with low population sizes need
47 mechanisms that buffer their population dynamics from extinction in order to persist (Tilman,
48 2004; Kobe & Vriesendorp, 2011). It is this subset of rare species, the persistent rare species,
49 which remain a paradox for coexistence. Despite the importance of understanding how these rare
50 species are able to persist, how to determine a rare species' role in a community as persistent or
51 ephemeral, how prevalent persistent rare species are, and what allows their persistence all remain
52 controversial (Preston, 1948; Main, 1982; Kunin & Gaston, 1997; Magurran & Henderson, 2003;
53 Comita *et al.*, 2010). Here we provide empirical evidence for a recently proposed mechanism
54 that, in theory, can buffer small populations against extinction: asymmetric negative frequency
55 dependence (Yenni *et al.*, 2012).

56 **The role of Negative Frequency Dependence in rarity and persistence**

57 Like density dependence, frequency dependence is a relationship between the population
58 growth rate and the frequency of a species in a community. However, because it is based on
59 relative frequency (i.e. abundance relative to other community members) rather than absolute
60 abundance, frequency dependence arises through both intra and inter-specific interactions (Adler

61 *et al.*, 2007). Negative frequency dependence occurs when a species' population growth rate is
62 more strongly limited by the density of conspecifics than by the density of heterospecifics (Fig
63 1A). When negative frequency dependence is strong, relatively small increases in a species'
64 density, and in turn its frequency in the community, will result in large declines in population
65 growth rate (Fig 1B). Holding the maximum population growth rate constant, species with
66 stronger negative frequency dependence must have lower relative abundance than species with
67 weak negative frequency dependence. In other words, for species experiencing strong negative
68 frequency dependence, intraspecific competition is the primary cause of rarity (Appendix S2 in
69 Supporting Information).

70 In contrast, studies of competition often assume that rare species are primarily suppressed
71 by interspecific competition (Chesson, 2000; Tilman, 2004). But if interspecific competition is
72 the cause of rarity, how can we explain the long-term persistence of many rare species? Why
73 don't the superior competitors exclude rare species altogether? Our alternative explanation, that
74 rare species are strongly frequency-dependent, also explains persistence, because strong
75 population regulation buffers species against extinction. It is initially counter-intuitive that a
76 process causing rarity could also promote persistence. However, when a species with strong
77 negative frequency dependence drops below its equilibrium frequency, it will experience a large
78 increase in population growth rate (Fig. 1). Because species with strong negative frequency
79 dependence are more sensitive to increases in their own population numbers, they experience
80 relatively weak suppression by dominant community members; they are effectively released
81 from competitive effects as their densities approach zero. Thus, strong negative frequency
82 dependence can simultaneously limit species' average abundances while buffering them against
83 extinction if they fall to low density (Yenni *et al.*, 2012).

84 Strong negative frequency dependence should benefit rare species more than common
85 species (Yenni *et al.*, 2012). Common species are less vulnerable to stochastic extinction due to
86 their higher abundances. While common species might experience strong or weak negative
87 frequency dependence, rare species lacking strong negative frequency dependence would be
88 quickly lost from a local community due to stochastic extinction. In addition, if a rare and
89 common species experience the same degree of negative frequency dependence (equivalent
90 slopes in Fig 1), then the rare species must have a lower maximal growth rate. Holding the
91 equilibrium abundances constant, for the rare species to experience the same buffering against
92 stochastic extinction (i.e. similar maximal growth rates), it must have stronger negative
93 frequency dependence. Therefore, we expect a relationship between relative abundance
94 (frequency) and the strength of negative frequency dependence: species with lower relative
95 abundances should experience stronger negative frequency dependence.

96 **The Asymmetric Negative Frequency Dependence Pattern**

97 While simulations suggest that strong negative frequency dependence should be a common
98 feature of persistent rare species (Yenni *et al.*, 2012), few empirical studies have assessed this
99 mechanism. Strong negative density or frequency dependence in some rare species has been
100 documented (Harpole & Suding, 2007; Adler *et al.*, 2010; Comita *et al.*, 2010; Mangan *et al.*,
101 2010; Johnson *et al.*, 2012; Xu *et al.*, 2015) but these few studies exclusively focused on select
102 plant communities. If this is a general pattern across taxa and ecosystems, then this mechanism
103 could be of general importance to the coexistence and persistence of rare species. However, this
104 limited number of studies does not tell us how general this pattern is across a variety of natural
105 communities. Testing the asymmetric negative frequency dependence hypothesis is challenging
106 because there is no a priori cut-off value for what constitutes strong enough negative frequency

107 dependence to buffer species against stochastic extinction. However, we can examine whether
108 rarer species have stronger negative frequency dependence than more common species, which is
109 equivalent to testing whether rare species are more sensitive to intra- than interspecific
110 competition when compared to common species. If strong negative frequency dependence is
111 more common among rare species, it would suggest 1) that rare species are not rare because they
112 are suppressed by superior competitors, but rather because they are more strongly self-limiting,
113 and 2) that rare species that do not experience a large release from competition at low density, as
114 implied by strong negative frequency dependence, often do not persist.

115 **Testing for Asymmetric Negative Frequency Dependence**

116 To explore the relationship between rarity and negative frequency dependence in
117 ecological communities, we decided to assess whether there is a general relationship between the
118 rarity of a species and the strength of negative frequency dependence by examining a large
119 compilation of publicly available time-series on the abundance of all species within one trophic
120 guild. Using this approach to evaluate the relationship between abundance and rarity requires 1)
121 identification of appropriate data, 2) estimating equilibrium frequency and negative frequency
122 dependence for each species in each community, 3) identifying the persistent community, 4)
123 estimating a community-level pattern of negative frequency dependence, and 5) accounting for
124 known and unknown biases in the pattern of interest before making a final conclusion about the
125 negative frequency dependence-rarity relationship in each community. The methods we
126 developed to deal with these issues have allowed us to use commonly available data to begin to
127 explore the relationship between negative frequency dependence and rarity. We hope our results
128 will spur future research and collection of even more useful data.

129 **Identifying Suitable Data for Community Negative Frequency Dependence Patterns**

130 Many of the coexistence mechanisms that generate negative frequency dependence can
131 operate at very small spatial scales (Chesson, 2000). This is also true in the framework defined in
132 Yenni et al. (2012). Therefore, to assess whether persistent rare species have stronger negative
133 frequency dependence than common species, we required communities where the data was
134 collected in a manner consistent with this local-scale concept. We restricted communities to all
135 species within a study belonging to the same trophic level and occurring within a single habitat
136 type as defined by the data collector. If the data collector indicated that the study included
137 multiple sites of different habitat types or multiple trophic levels these data were treated as
138 different communities and analyzed separately. If a study collected data from multiple locations
139 of the same habitat type, we examined those separately. However, to keep a single study area
140 from dominating the results because it had multiple sites, we treated multiple sites in a single
141 study area as habitat replicates and only one covariance was estimated from the entire resulting
142 site data. Finally, to calculate frequency dependence, we used time series data because studies
143 measuring frequency dependence for all species in a community in an experimental manner are
144 rare. All of these data decisions were made to ensure we were only analyzing populations that
145 were likely to be directly interacting and to provide data for a large number and diversity of taxa
146 and ecosystems. Using these criteria, we found suitable data for 90 different communities
147 containing collectively 703 species (Appendix S1 in Supplementary Information). These
148 communities represent six major taxonomic groups (birds, fish, herpetofauna, invertebrates,
149 mammals, and plants), 5 continents, and 3 trophic levels, thus providing a general exploration of
150 whether persistent rare species commonly exhibit stronger negative frequency dependence, and
151 thus, stronger population buffering, than common species.

152 **Calculating Negative Frequency Dependence and Equilibrium Frequency**

153 Community time series can be used to estimate equilibrium frequency – the relative
154 abundance when a species' population is in steady state – and the strength of negative frequency
155 dependence for all species that met our criteria for persistence within each community (Fig 1A).
156 We estimated a species' negative frequency dependence as the linear relationship between its
157 relative abundance (frequency) in a community and its annual per capita population growth rate.
158 For each community, relative abundance in each year t for each species s was calculated as $x_{t,s} =$
159 $N_{t,s} / \sum_{s=1:S} N_{t,s}$ (where N is a species' absolute abundance). Log per capita population growth
160 rates in each year t for each species s were calculated as $y_{t,s} = \log(N_{t+1,s}/N_{t,s})$. The relationship
161 between these population parameters was described as $\mathbf{Y}_s = \beta_{0,s} + \beta_{1,s} \mathbf{X}_s + \boldsymbol{\varepsilon}_s$ for each species s .
162 Equilibrium frequency (f), a species' expected relative abundance in the community, is estimated
163 as the x-intercept of this linear relationship, $f = -\beta_{0,s}/\beta_{1,s}$. Frequency dependence (FD) is
164 estimated as the slope of the linear relationship, $FD = \beta_{1,s}$.

165 **Ephemeral vs. Persistent Species**

166 As discussed in the introduction, asymmetric negative frequency dependence is a
167 mechanism for maintaining small populations near their steady state despite stochasticity, and
168 thus only applies to stably coexisting common and rare species. Because other mechanisms are
169 expected to dominate the population dynamics of invading, declining, or transient species, we
170 used three criteria to identify and exclude species with population characteristics that would
171 make them likely to be ephemeral and not stably coexisting (Supplementary Figure S15): 1) too
172 few occurrences to estimate parameters (i.e. few or no adjacent non-zero abundances, the
173 inclusion of this type of species in a dataset is typically an arbitrary decision by the data

174 collectors, and was highly variable between datasets), which indicates a species is likely
175 transient, 2) negative equilibrium frequency (Fig 1B), which indicates the species cannot persist
176 in the community (7.7% of species, (Chesson, 2000; Adler *et al.*, 2007)), and 3) positive
177 frequency dependence (Fig 1B), which is related to a negative invasion growth rate and likely
178 results in either the extinction of that species or an ever increasing invader (11% of species,
179 (Chesson, 2000; Adler *et al.*, 2007)). Because equilibrium frequency is estimated as the x-
180 intercept of the fitted relationship between log per capita growth rate and relative abundance, it is
181 possible for this value to be < 0 or > 1 (Fig 1B). Besides the fact that these species are obviously
182 ephemeral and thus irrelevant to our analysis, it would make the relationship between
183 equilibrium frequency and frequency dependence nonsensical to include negative equilibrium
184 frequencies or positive frequency dependences.

185 All other species are retained as persistent community members. Our criteria are only a
186 weak filter for removing ephemeral species. Some of the species retained in the analysis are
187 likely also ephemeral, but we abstained from further filtering to avoid possibly biasing the
188 results. We examined how this method of identifying persistent species relates to actual
189 persistence at a site by calculating the percent of years in which a species has non-zero
190 abundance and comparing these values between ephemeral and persistent species. Our approach
191 identified a group of more persistent species that were on average present over a higher fraction
192 of the time series (Supplementary Information Figure S14).

193 **Quantifying Asymmetric Negative Frequency Dependence at the Community Level**

194 We currently have no way to objectively characterize a species as experiencing weak or
195 strong negative frequency dependence. We can, however, estimate the relationship between
196 relative abundance and negative frequency dependence across all persistent species in the

197 community. To quantify the relationship between rarity and negative frequency dependence
198 within a community, we calculated the covariance between equilibrium frequency and strength
199 of negative frequency dependence (Fig 2B). The covariance calculation uses every species in a
200 community as a single data point in the calculation (Fig 2B): $cov(\log(f), \log(-FD))$. Negative
201 covariances indicate communities in which rare species are experiencing stronger negative
202 frequency dependence than their dominant counterparts (note that the expectation for $cov(\log(f),$
203 $\log(-FD))$ is already negative, we discuss how we addressed this in the following section). Log-
204 log relationships were most appropriate for calculating these covariances because most
205 communities contain many species with very low equilibrium frequencies and only a few
206 dominants, and because the observed negative frequency dependence of the few dominants was
207 typically at least an order of magnitude lower than the remainder of the community.

208 **Dealing with Uncertainty in Abundance Estimates**

209 Time series data with significant observation uncertainty can show the signature of
210 negative density or frequency dependence even when none exists (Freckleton *et al.*, 2006; Knappe
211 & de Valpine, 2012) because the calculation can create a negative bias in the resulting population
212 growth estimates. We designed a randomization procedure to determine which communities
213 showed a significant negative covariance between equilibrium frequency and the strength of
214 negative frequency dependence. We reshuffled abundances from the original community time
215 series 5000 times for each species independently, and then repeated all estimation methods with
216 the time-randomized data. This procedure maintains relative abundances and observed
217 variability, but the frequency dependence detected in the randomized data is due to uncertainty
218 alone. We compared the covariance estimated from the original data to the distribution of
219 covariance estimated from the randomized data sets to estimate effect size and p-values. We

220 report the difference in the observed pattern from the mean randomized pattern and calculate the
221 p-value as the proportion of randomized pattern values that are less than or equal to the observed
222 pattern. Simulations confirm that this approach accounts for known biases resulting from
223 uncertainty in the observations, as well as sampling biases for rare species (see Supplementary
224 Information for details). In addition to removing uncertainty bias, this has the added benefit of
225 removing any effects of community structure (e.g. richness) that may create a bias in the pattern
226 of interest, because it creates a randomized expectation for each community. This is a
227 conservative approach, but it enables us to identify communities in which the observed
228 relationship between rarity and NDF is extremely unlikely to arise due to chance or statistical
229 artifacts. The significance of the asymmetric negative frequency dependence pattern was
230 assessed using Strimmer's approach (Strimmer, 2008) to estimate the number of true null
231 hypotheses, controlling the false discovery rate at 0.1 (Benjamini & Hochberg, 1995, 2000;
232 Verhoeven *et al.*, 2005). All analyses were performed in the R platform ((R Development Core
233 Team, 2012) see Supplementary Information).

234 **Immigration or Competition?**

235 While Yenni et al (2012) predicted asymmetric frequency dependence emerging from
236 competition, it is possible that other mechanisms could generate the same pattern. While, only
237 competition has been explored theoretically, it is possible to imagine scenarios where other
238 processes could generate or modify negative frequency dependence patterns. We explored one of
239 the more likely processes to generate asymmetric frequency dependence: immigration.
240 Immigration is an important process influencing the persistence of species (Brown & Kodric-
241 Brown, 1977) and is expected to have particular influence on populations of rare species, thus
242 creating the potential for immigration to influence or even create patterns of asymmetric

243 frequency dependence. We used both our NFD simulation and a more traditional Lotka-Volterra
244 based model (Chesson, 2000) to explore how immigration influenced negative frequency
245 dependence in common and rare species (Appendix S4). Results from both models were similar:
246 immigration did not create patterns of asymmetric frequency dependence and, if anything,
247 significant amounts of immigration decreases the ability of our method to detect true *in situ*
248 asymmetric negative frequency dependence (models and results in Appendix S4).

249 **Asymmetric Patterns of Negative Frequency Dependence Appear to be Common**

250 When compared to the randomized time series, 46% (41 of 90) of communities
251 demonstrated a significant relationship between relative abundance and negative frequency
252 dependence, indicating that rare species experience stronger negative frequency dependence than
253 common species (Fig 3A, Table 1). While negative relationships between rarity and the strength
254 of negative frequency dependence often arose in randomized data as well (Fig 2B, 2C), in the
255 communities where the observed pattern was statistically significant, the stronger negative
256 frequency dependence of rare species could not be explained solely as a result of bias related to
257 uncertainty in the abundance estimates. These results indicate real differences between rare and
258 common species in the sensitivity of population growth rates to the abundance of heterospecifics
259 and conspecifics.

260 The prevalence of asymmetric negative frequency dependence within communities varied
261 by taxonomic group (Fig 3B-G). In approximately half of bird, fish, invertebrate, mammal and
262 plant communities (50%, 50%, 48%, 53% and 53%, respectively) rare species experienced
263 stronger negative frequency dependence than their dominant counterparts (Table 1, Fig 3).
264 However, only 9% of herpetofauna communities had a significant asymmetric negative

265 frequency dependence structure. Why asymmetric negative frequency dependence is less
266 prevalent in herpetofauna communities is unclear, though the documented sensitivity of
267 herpetofauna to disturbance is one possibility for their differing dynamics (Collins & Storer,
268 2003). Across all taxa, only a few communities had dominant species with stronger negative
269 frequency dependence estimates than the rare species, but this pattern was never significant (see
270 Table S1 in Supplementary Information). Thus, while rare species often, but not always, showed
271 significantly stronger negative frequency dependence than common species, common species
272 never showed stronger negative frequency dependence than rare species. Despite differences in
273 diversity, complexity of species interactions and how species may achieve the necessary
274 population dynamics, the phenomenon of rare species exhibiting stronger negative frequency
275 dependence than more common species appears to be widespread across community types.

276 Simulations testing our randomization procedure for addressing bias caused by measurement
277 error (Supplementary Information) demonstrated that our method consistently assigns
278 significance when the relationship between equilibrium frequency and negative frequency
279 dependence is strong, but it typically fails to detect weak relationships. Therefore, our non-
280 significant results likely include some communities where a relationship between relative
281 abundance and negative frequency dependence exists, but is too weak for our method to detect.
282 If so, then the prevalence of strong negative frequency dependence in rare species is likely more
283 common than our results indicate. Overall, our results suggest that in many communities,
284 persistent rare species may commonly exhibit stronger negative frequency dependence than the
285 more common species in the community.

286 **Implications**

287 The theory developed in Yenni et al. (2012) and the results presented here imply that
288 differences between rare and common species in their sensitivity to intraspecific and interspecific
289 competition may explain the existence of persistent rare species in many communities. This
290 finding leads to a variety of interesting research questions. Why are rare species more sensitive
291 to intraspecific than interspecific competition? One possibility is that both strong sensitivity to
292 congeners and an ability to increase rapidly when the population falls below its equilibrium
293 frequency are traits of rare species, e.g. a result of specialization on a rare resource or
294 susceptibility to virulent species-specific natural enemies. An alternative explanation is that
295 strong negative frequency dependence is not a fixed trait but is context-dependent. Some species
296 might show strong negative frequency dependence when conditions cause them to be rare
297 members of the community but weaker negative frequency dependence in communities when
298 they are more dominant. The limited availability of community time series data does not allow us
299 to directly link strong negative frequency dependence to species traits or to test whether some
300 species may show weak negative frequency dependence when they are dominant but strong
301 negative frequency dependence when they are rare.

302 Yenni et al (2012) described a theoretical framework in which the stronger negative
303 frequency dependence of rare species emerges from intraspecific competition. Our empirical
304 results are consistent with the theory and suggest that asymmetric density dependence may
305 structure many communities. Our simulations, provided in the Supplementary Information,
306 further support the idea that the prevalence of asymmetric negative frequency dependence is not
307 merely an artifact of uncertainty due to sampling biases or immigration. That is not to say that
308 immigration as an ecological process, along with other processes such as facilitation and
309 interaction networks, cycles, chaotic dynamics, and nonlinear negative frequency dependences

310 could not also create or modify patterns of negative frequency dependence. For example, while
311 we explored a particular implementation of immigration, it is still possible that immigration
312 might be able to generate asymmetric negative frequency dependence under specific
313 circumstances. Clearly it is important for coexistence theory to assess whether these other
314 processes can also generate or enhance community-level patterns of asymmetric frequency
315 dependence, especially as it relates to the concept of persistent rare species.

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

329 **Future Analyses**

330 Our analysis also highlights analytical and theoretical limitations to our understanding of
331 negative frequency dependence that need to be addressed for research into negative frequency

332 dependence to progress further. Definitive statements about the absolute strength of negative
333 frequency dependence in common and rare species would require unbiased estimates of
334 maximum population growth rates and density dependence. In contrast, our randomization test
335 focuses on the relative strength of negative frequency dependence in common vs. rare species.
336 Direct, unbiased estimates of negative frequency dependence would remove the need for our
337 conservative approach, and could reveal the role of asymmetric negative frequency dependence
338 in additional communities. An additional challenge for future research is disentangling the effects
339 of intra- and interspecific competition from other potential mechanisms of negative frequency
340 dependence such as immigration or nonlinear dynamics. Addressing this challenge will also
341 require more sophisticated methods for correcting negative frequency dependence for bias or,
342 alternatively, individual-level data on vital rates and dispersal.

343 **Summary**

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

352

353

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364

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429

430 Biosketches

431 Glenda Yenni is a multidisciplinary ecologist interested in drawing connections between
432 theory and observation in community ecology. Peter Adler is a plant ecologist interested in
433 explaining population and community dynamics in space and time. S.K. Morgan Ernest is a
434 macroecologist and community ecologist studying the temporal dynamics of community
435 assembly.
436

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

Taxonomic Group	Num. communities	<u>Mean Values Across Communities</u>					Num. significant communities	Proportion significant.
		Spp/community	Persistent spp/community	Observed covariance (ρ)	Randomized covariance (ρ_0)	Covariance strength (ρ/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

438 Covariances (ρ and ρ_0) were calculated as $cov(\log(f), \log(-FD))$. The number of significant
 439 communities are those in which the covariance was determined significant after false discovery
 440 rate control ($\alpha=0.1$).
 441

442 Figure Legends

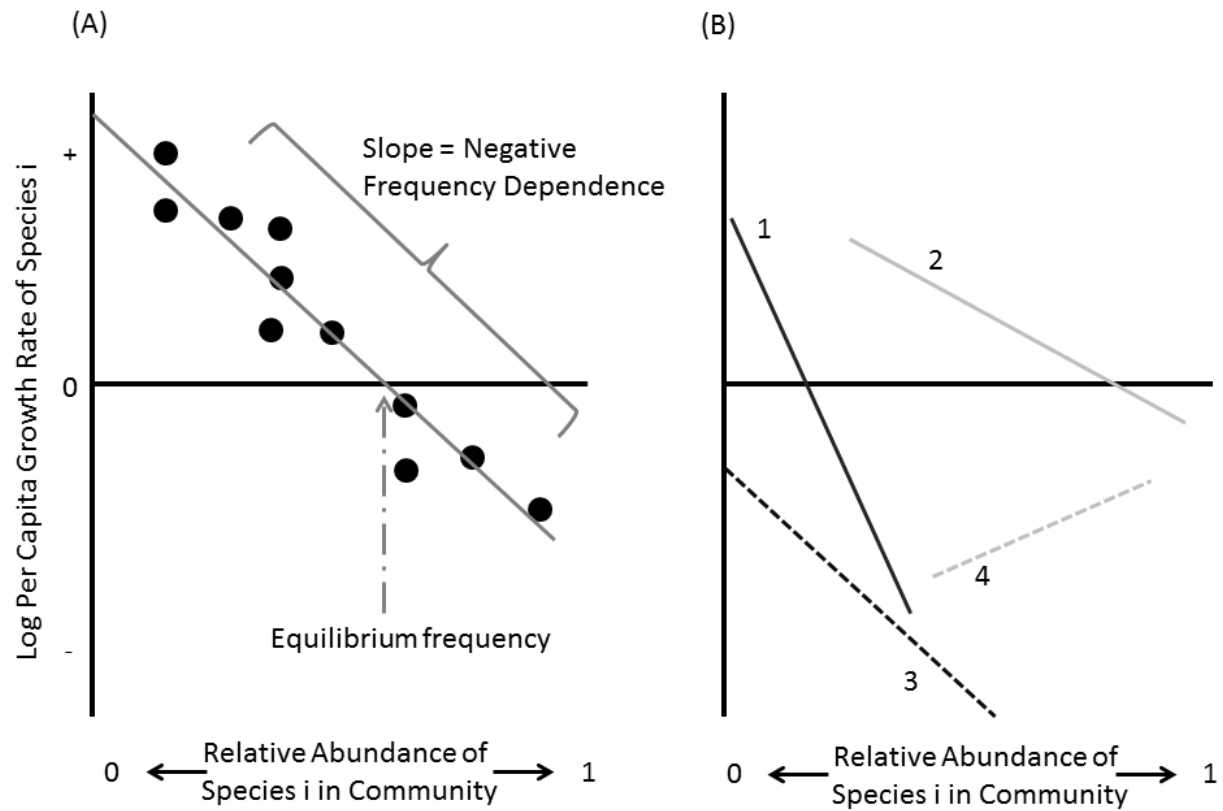
443 Figure 1: A) Negative frequency dependence and equilibrium frequency can be calculated from
444 time-series community data. Each data point represents the relative abundance of species i at
445 time t in its community (x-axis) and its log per capita population growth rate from time t to time
446 $t+1$ (y-axis). The slope of this line is the species' negative frequency dependence ($NFD = -\beta_1$ in
447 the linear model). Equilibrium frequency – the expected relative abundance of species i in the
448 community when its population growth is at equilibrium - is the fitted x-intercept of the
449 relationship. The fitted y-intercept is the species' maximal growth rate. B) The x-intercept and
450 slope of the relationship indicate important biological information about each species. Steep
451 slopes indicate stronger negative frequency dependence, and thus higher sensitivity of population
452 growth to changes in conspecifics than to changes in heterospecifics. In a linear relationship,
453 high maximal growth rates, which buffer species from extinction, are achieved through high
454 equilibrium frequencies (common species, solid grey line), or strong negative frequency
455 dependence (rare species, solid black line). X-intercepts < 0 indicate species that cannot maintain
456 a stable presence within the community at their population equilibrium. Species exhibiting
457 positive frequency dependence will often have difficulty invading when rare. These latter two
458 scenarios indicate species that are likely not stably coexisting within the current community.

459 Figure 2: An example of our analyses using the Portal rodent community. (A) The relationship
460 between relative abundance and growth rate is fit for each species. The slope of this relationship
461 is the "Strength of NFD" for each species, and the x-intercept is the "Equilibrium Frequency."
462 (B) Using each species as a datapoint, the covariance between these two parameters (-1.17 in this
463 example) is the value of interest, but it contains known biases. Randomizations of the time series
464 were used to create a baseline expectation for each unique community, and the observed

465 relationship was considered relative to this baseline (the Randomized Covariance, -0.46 in this
466 example). Thus, we use the proportional difference in the empirical covariance from random
467 (observed covariance/mean randomized covariance, $-1.17/-0.46 = 2.54$). The empirical pattern in
468 this community (solid black line, with shaded 95% confidence intervals) compared to one
469 realization from the randomized results (out of 5000 randomizations), accounts for the bias in the
470 negative frequency dependence estimates introduced by measurement error and the artificial
471 relationship this creates (dashed line, with shaded 95% confidence intervals). (C) P-values were
472 calculated as the proportion of randomized values larger than the observed asymmetry value (-
473 1.17, p-value = 0.0032 in this example).

474 Figure 3: Results were compared to randomized data to account for bias introduced by
475 measurement error and determine which relationships were significant (colored bars) or not (grey
476 bars). P-values were calculated as the proportion of randomized values larger than the observed
477 asymmetry value. (A) All results for the 90 communities included in the analysis. We detected a
478 significantly asymmetric negative frequency dependence pattern in 46% of these communities.
479 (B) Results separated by taxonomic group, showing the relative size of the asymmetry in
480 negative frequency dependence between species in each community (Observed
481 Covariance/Randomized Covariance). The proportion value in each panel is the proportion of
482 communities in that group with a significant asymmetric negative frequency dependence pattern.

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