

1 **Biodiversity-ecosystem function relationships change in sign and magnitude across the Hill**  
2 **diversity spectrum**

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12

13 **Summary**

14 Motivated by accelerating anthropogenic extinctions, decades of biodiversity-ecosystem function  
15 (BEF) experiments show that ecosystem function declines with species loss from local communities.

16 Yet, at the local scale, changes in species' total and relative abundances are more common than  
17 species loss. The consensus best biodiversity measures are Hill numbers, which use a scaling  
18 parameter,  $\ell$ , to emphasize rarer versus more common species. Shifting that emphasis captures  
19 distinct, function-relevant biodiversity gradients beyond species richness. Here, we surmised that Hill  
20 numbers that emphasize rare species more than richness may distinguish large, complex, and  
21 presumably higher-functioning assemblages from smaller and simpler ones. In this study, we tested  
22 which values of  $\ell$  produce the strongest BEF relationships in community datasets of ecosystem  
23 functions provided by wild, free-living organisms. We found that  $\ell$  values that emphasized rare species  
24 more than richness most often correlated most strongly with ecosystem functions. As emphasis  
25 shifted to more common species, BEF correlations were often weak and/or negative. We argue that  
26 unconventional Hill diversities that shift emphasis towards rarer species may be useful for describing  
27 biodiversity change, and that employing a wide spectrum of Hill numbers can clarify mechanisms  
28 underlying BEF relationships.

29

## 30 **Introduction**

31 A central question in community ecology is, “how will ongoing shifts in biodiversity affect ecosystem  
32 function?” In experiments that vary species richness while controlling other community properties,  
33 the answer has been clear for some time: ecosystem function has a positive, saturating relationship  
34 with species richness [1–3]. There is ongoing interest in “scaling up” research to resolve whether  
35 similar patterns hold in natural ecosystems [4,5]. However, richness is not a robust measure of  
36 biodiversity in observational data taken from natural ecosystems [6], in large part because most  
37 species are rare [7] and likely to be absent from samples. Further, richness often tracks real-world  
38 biodiversity gradients poorly, because species composition and abundance can change dramatically  
39 with little to no change in observed species richness [8–10]. Therefore, other metrics of biodiversity  
40 may provide improved clarity about the real-world linkages between biodiversity and ecosystem  
41 function (BEF).

42

43 There are both historical and conceptual reasons that BEF research has focused on richness as a  
44 measure of biodiversity. Since at least the 1960s, there has been extensive research on how  
45 productivity affects species richness [1]. Motivated by intensifying biodiversity loss in the 1980s,  
46 declines in richness were (at least implicitly) the global change pattern that seminal BEF studies, with  
47 their focus on species loss (e.g., [11]), aimed to understand. This prompted a wave of experiments on  
48 how species richness affects ecosystem function [2]. Thus, richness was a natural choice, both  
49 because of ecology’s long focus on how richness might *respond* to ecosystem functions like  
50 productivity, and because of a collective sense that species loss was the correct, or at least most  
51 convenient, way to frame anthropogenic changes in biodiversity. Furthermore, there may have been a  
52 sense that richness was an expedient measure of functional diversity and redundancy, which were  
53 considered the key mechanisms through which biodiversity maintains ecosystem function [12].  
54 However, the choice of richness may not have been based on theoretical expectation that richness,  
55 rather than other abundance-weighted diversity measures, best described functionally important  
56 biodiversity gradients.

57

58 Using species richness as the key biodiversity measure poses methodological problems for BEF  
59 research. Species richness is not only sensitive to the extent and depth of sampling, but also to the  
60 distribution of relative abundances in the sampled assemblage. To illustrate this, consider the

61 difficulty of accurately measuring species richness in a community with one hyper-dominant species  
62 and many very rare species, versus measuring richness in a community in which abundance is evenly  
63 distributed. Richness, like other diversity measures, summarizes the distribution of relative  
64 abundances in an assemblage, and when estimated from data, cannot be independent from that  
65 distribution, even if such a measure were desirable [6,13]. However, different diversity measures vary  
66 in the extent to which they emphasize rare vs. common species, with species richness heavily  
67 emphasizing rare species. A unified family of diversity measures, known as “Hill numbers” or “Hill  
68 diversities,” summarizes a distribution of relative abundances as the abundance-weighted,  
69 generalized mean rarity [14–16]. Hill numbers are governed by a scaling parameter,  $\ell$ , that scales  
70 species rarity when computing the mean, and higher values of  $\ell$  afford more leverage, or emphasis, to  
71 rare species, while lower values emphasize common species more [16].

72  
73 The Hill diversity of an assemblage is not a single value, but rather a spectrum that varies  
74 continuously across  $\ell$  [6,14] (figure 1), raising the question of how ecosystem function relates to  
75 biodiversity measures with different emphasis on common vs. rare species. While several recent  
76 studies have compared whether richness ( $\ell = 1$ ), exponentiated Shannon ( $\ell = 0$ ), and inverse Simpson  
77 ( $\ell = -1$ ) best predicts ecosystem function [17–20], there has been no examination of how Hill numbers  
78 predict ecosystem function across a wide range of  $\ell$  values. This is a striking knowledge gap because,  
79 although nearly all studies of the relationship between biodiversity and ecosystem function have used  
80 species richness as a measure of diversity [3], other diversity measures could both better describe real  
81 world variation in biodiversity, and also have stronger links to ecosystem functioning. Thus,  
82 biodiversity-function studies may be *underestimating* the importance of biodiversity for function by  
83 not considering Hill diversities with different emphases on rare and common species via different  
84 values of the scaling parameter  $\ell$ .

85  
86 Despite clear declines in richness at the global scale, local changes in biodiversity are likely better  
87 captured by measuring total abundance and species’ relative abundances, for at least three reasons.  
88 First, as already discussed, observed richness is a poor predictor of true richness [21], and good  
89 estimators of true richness based only on species frequencies in samples may never exist [22]. Thus,  
90 even if underlying variation in species richness correlates strongly with, or even drives, ecosystem  
91 function, estimating richness from samples could severely obscure the underlying pattern. Second,

92 although observed richness does increase with observed abundance, to the extent that abundance  
93 *per se* drives function, Hill diversities that better reflect abundance (i.e., when  $\ell \gg 1$ ) should be  
94 stronger correlates of function than richness ( $\ell = 1$ ) is. Third, if diversity effects on function are  
95 mediated by positive species interactions [3,23–25], more probable and stronger between equally  
96 abundant species [26,27], Hill diversities that better reflect the probability of interspecific encounter  
97 (e.g. Hill-Simpson diversity, at  $\ell = -1$  [28]) may outperform richness as a predictor of function.

98  
99 Here, we conduct an in-depth examination of Hill numbers across a wide range of values of the scaling  
100 parameter  $\ell$ , and outline the ecological insight that can be gained by knowing which value of  $\ell$  best  
101 predicts ecosystem function. We focus on ecosystem functions that can be expressed as the product  
102 of mean per-capita function and total abundance, which works well for many functions [29,30]. This  
103 provides the opportunity to consider how biodiversity relates to both mean per-capita and total  
104 community function, which are both key targets of BEF research [31–33]. In this endeavor, we use only  
105 simple correlational analyses, omitting other important variables underlying function [34–36].

106  
107 In this study, we use observational community datasets on three ecosystem functions to ask:

- 108 1) Which values of the Hill diversity scaling factor  $\ell$  produce the strongest biodiversity-  
109 ecosystem function correlations?
- 110 2) How do biodiversity-ecosystem function correlations change in sign and strength over a wide  
111 range of Hill diversities?
- 112 3) What is the role of absolute abundance in shaping BEF correlations over the Hill diversity  
113 spectrum?

114  
115 It is not our aim to exhaustively review data in search of a single, best  $\ell$  value for BEF research,  
116 because developing insight does not require that the same  $\ell$  is predictive for all functions. Instead, we  
117 aim to provide a framework that allows researchers interested in biodiversity-function questions to  
118 think about diversity as a spectrum, almost certainly leading to the conclusion that Hill diversities  
119 besides richness can better predict ecosystem function.

120

## 121 **Materials and Methods**

122 To find how biodiversity-ecosystem function correlations change with different diversity scaling, we  
123 used previously published community datasets that recorded both the abundance and function of  
124 species at multiple sites. We chose datasets of disparate ecosystem functions and spatial scales:  
125 pollination by wild bee visitors to a landscape-scale array of three plant species (update ref when DOI  
126 is available: Genung et al. 2022, *in press*) [37], reef fish biomass from dive surveys replicated within 32  
127 globally distributed geographic regions [38,39], and above-ground tree biomass in census plots  
128 replicated within four tropical forests [40,41] (Table 1). In each system, total function of a community  
129 can be estimated as the summed contribution across species (or individuals) present in the  
130 community. Pollination was measured as the typical number of pollen grains deposited during a  
131 single visit of a bee taxon to the focal plant species, multiplied, at each site, by bee species's  
132 abundance to calculate total pollen deposition of one species to the focal plant there. Reef fish  
133 biomass was measured by visually estimating individual fish body lengths during dive surveys, which  
134 were then used to calculate biomass using species-specific allometric equations. Tropical tree  
135 biomass was measured by converting observed individual diameter at breast height into biomass  
136 estimates using taxon-specific allometric equations that included information about wood density  
137 [42,43]. In total, we used 39 community datasets, each consisting of one function measured across a  
138 collection of assemblages.

139

140 *Which value of  $\ell$  produces the strongest biodiversity- ecosystem function correlations?*

141 We compute Hill diversity as a function of species relative abundances,  $p_1, p_2, \dots, p_S$ , and a scaling  
142 factor,  $\ell$ , using the formula

143

144

$$D = \left( \sum_{i=1}^S p_i \left( \frac{1}{p_i} \right)^\ell \right)^{1/\ell}$$

145 or its limit as  $\ell$  approaches 0 [16,44] . We used observed species abundances to calculate species  
146 diversities at each site as the Hill diversity along a wide range of  $\ell$  values (from -10 to +10 at intervals  
147 of 0.05) (figure S1). We calculated total function as the sum of species' functions at each site. We  
148 computed the correlation between the natural logarithm of each diversity and the natural logarithm  
149 of total function, across all sites in the community dataset (hereafter, the "BEF correlation"). To  
150 identify the  $\ell$  value that produced the strongest BEF correlation in each community dataset, we

151 plotted the correlation against the scaling factor  $\ell$ . We identified the single  $\ell$  value with the largest  
152 absolute correlation (i.e., largest R-squared for the relationship between log diversity and log  
153 function).

154

155 *How do biodiversity-ecosystem function correlations change in sign and strength over a wide range of*  
156 *Hill diversities?*

157 To determine not only which  $\ell$  value produced the strongest BEF correlation across community  
158 datasets, but also to see how adjusting the Hill diversity scaling parameter affects BEF relationships  
159 more comprehensively, we plotted the BEF correlation against the Hill diversity scaling factor  $\ell$  for  
160 each community dataset. We examined curves to identify patterns in the sign and strength of the BEF  
161 correlation along the spectrum of emphasis on common and rare species.

162

163 *What is the role of absolute abundance in shaping BEF correlations?*

164 To begin to separate effects of total and relative abundance on BEF correlations across the Hill  
165 diversity spectrum, we looked separately at the relationships between diversity and two  
166 complementary components of total function, namely total abundance and mean per-capita function.  
167 We used the same graphical approach we used to assess the sign and strength of the BEF correlation  
168 across the Hill diversity spectrum. For each community dataset, we found the correlation between the  
169 natural logarithm of Hill diversity at each site and either the natural logarithm of total abundance at  
170 each site), or the natural logarithm of mean per-capita function at each site, and plotted these  
171 correlations against the Hill diversity scaling parameter  $\ell$ . Although on the logarithmic scale,  
172 abundance and mean per-capita function combine additively to create total function, the BEF  
173 correlation does not additively decompose into abundance by biodiversity and per-capita function by  
174 biodiversity correlations, as there is also covariance between abundance and per-capita function.  
175 Nevertheless, by partitioning total function into additive components and examining how each of  
176 these relates to biodiversity gradients across the Hill spectrum, we can better characterize the role of  
177 total abundance in generating patterns in the BEF correlation itself.

178

## 179 **Results**

180 *Which value of  $\ell$  produces the strongest biodiversity- ecosystem function correlations?*

181 For most datasets, the strongest biodiversity-ecosystem correlations were located at or just above  
182 richness ( $\ell = 1$ ), with a mode at  $\ell = 1.5$  (figure 2). A substantial minority (11 of 39 datasets) had  
183 strongest BEF correlations at values of  $\ell > 5$ , including a peak at  $\ell = 10$ , the largest value of  $\ell$  we  
184 considered. There were a few outliers: Two tree carbon storage datasets had their strongest BEF  
185 correlations near inverse Simpson ( $\ell = -1$ ) and Shannon ( $\ell = 0$ ) diversities, and a single fish dataset had  
186 a strongest BEF correlation at  $\ell = -10$ , the smallest value of  $\ell$  we considered (figure 2).

187

188 *How do biodiversity-ecosystem function correlations change in sign and strength over a wide range of*  
189 *Hill diversities?*

190 Across all ecosystem functions, we found common patterns in the relationship between the BEF  
191 correlation and the Hill diversity scaling parameter,  $\ell$ . When  $\ell$  is  $< 1$ , the diversity-function correlation  
192 is typically weak and may be positive or negative (figure 3). Near  $\ell = 1$ , the diversity-function  
193 correlation rapidly increases, although a substantial minority of community datasets first show a  
194 sharp negative turn in the relationship near Hill-Simpson and Hill-Shannon diversities (figure 3 b-d).  
195 Across all the datasets we considered, the mean correlation between  $\ln(\text{diversity})$  and  $\ln(\text{total}$   
196  $\text{function})$  was not significantly different from zero for either Hill-Simpson or Hill-Shannon diversity  
197 ( $p > 0.28$  for two-sided Student's t-test, with no correction for multiple tests). By richness ( $\ell = 1$ ), almost  
198 all datasets showed positive diversity-function correlations, with the mean  $R^2 = 0.381$ . For most  
199 datasets, the strongest correlations are located near richness, with a mode near  $\ell = 1.5$ , where the  
200 mean  $R^2$  was 0.445, after which the diversity-function correlation slowly declines as  $\ell$  values continue  
201 to increase (figure 3). A substantial minority of datasets showed continually stronger relationships as  $\ell$   
202 increased (some profiles in figure 3 b, c), leading to highest  $R^2$  values at or near the maximum  $\ell$  we  
203 considered ( $\ell = 10$ ).

204

205 This study was not designed to contrast trends between ecosystem functions, but it is important to  
206 note that the relationship between the BEF correlation, and the emphasis the diversity metric puts on  
207 rare vs. common species (i.e., the value of  $\ell$ ), did not appear uniform. For the three bee community  
208 datasets, total pollen deposition and bee diversity were positively correlated at every value of  $\ell$ .  
209 Correlation strength peaked at richness ( $\ell = 1$ ) or just beyond ( $\ell = 2$ ), but remained relatively strong  
210 across all higher values of  $\ell$  (figure 3a). For the 32 reef fish community datasets, total fish biomass and

211 fish diversity tended to be weakly and often negatively correlated at low  $\ell$  values. Correlation strength  
212 tended to peak either slightly above richness at  $\ell = 1.5$ , or grow with  $\ell$  for an observed peak near  
213 the maximum value considered ( $\ell = 10$ ). (figure 2, figure 3 b, c). When considering either very high or  
214 very low  $\ell$  values, note that at either end of the Hill number spectrum, diversities rapidly converged  
215 towards their maximum or minimum asymptote. Thus, large changes in the BEF correlation rarely  
216 occurred outside a fairly narrow range between  $\ell = -2$  and 2. Finally, the four tropical tree community  
217 datasets showed generally weak correlations. In two tree datasets, BEF correlation strength peaked at  
218 intermediate  $\ell$  values where the BEF correlation was strongly negative (figure 3 d). In another (Barro  
219 Colorado Island) diversity-function correlation was negative even at high  $\ell$  values (figure 3 d, orange  
220 line), but modestly positive for negative  $\ell$  values.

221

222 *What is the role of absolute abundance in shaping BEF correlations?*

223 As expected, the relationship between diversity and abundance was mostly similar to the relationship  
224 between diversity and function, as total abundance underlies function in our datasets. This can be  
225 seen in the similar shape of the curves showing the correlation between  $\ln(\text{diversity})$  and either  
226  $\ln(\text{function})$  (figure 3) or  $\ln(\text{abundance})$  (figure 4 a-d), as the sign and strength of correlation typically  
227 moved in similar ways across the  $\ell$  spectrum. In almost all cases, the correlation between  $\ln(\text{diversity})$   
228 and  $\ln(\text{abundance})$  was very strong (and in many cases approached unity), for large, positive values of  
229 the Hill diversity scaling parameter  $\ell$ . As previously remarked, this result is a mathematical  
230 inevitability when datasets contain very rare species/singletons. Additionally, across datasets, we  
231 found that the rise towards the high correlation observed for large  $\ell$  values typically occurred in the  
232 range of  $\ell$  values typically considered by ecologists (-1 to 1), likely reflecting biological and sampling  
233 linkages between abundance and diversity; the correlation frequently saturated once  $\ell$  was greater  
234 than two. While for some community datasets, diversity was largely independent of abundance for  
235 negative  $\ell$  values, we also saw community datasets in which  $\ln(\text{abundance})$  and  $\ln(\text{diversity})$  had  
236 modest to strong negative correlation across negative  $\ell$  values. Because Hill diversities typically  
237 change little with  $\ell$  below around -2 [6], this result implies that in these systems, total abundance and  
238 the degree of dominance are positively linked [45].

239

240 While the curves in figures 3 a-d and 4 a-d show strong resemblance, for some community datasets  
241 the BEF and diversity-abundance relationships diverge, implying those BEF relationships result from



242 processes other than abundance. For example, correlations between abundance and diversity were  
243 always strongly positive for the reef fish data for large, positive  $\ell$  values, but in some reef fish  
244 community datasets, correlations between diversity and function were only weakly positive at higher  
245  $\ell$  values (figure 4 b, c). Such divergences between the diversity-function and diversity-abundance  
246 curves could be due to strong and/or countervailing relationships between mean per-capita function  
247 and diversity, which also showed some overall patterns across community datasets (figure 4 e-h). In  
248 general, Hill diversities with negative  $\ell$  values were positively related to per-capita function,  
249 suggestive of a positive relationship between evenness and mean per-capita function. This pattern  
250 was not ubiquitous, however, with notable exceptions in both tree and bee community datasets  
251 (figure 4 e, h). We found that the correlation between diversity and mean per-capita function often  
252 exhibited a positive peak at intermediate  $\ell$  values, a pattern particularly pronounced in the reef fish  
253 community datasets (figure 4 f, g). Finally, there was a tendency towards a negative correlation  
254 between  $\ln(\text{diversity})$  and  $\ln(\text{mean per-capita function})$  at for larger, positive values of  $\ell$  (when  
255 diversity becomes largely synonymous with abundance), though the strength of this relationship was  
256 variable.

257

## 258 **Discussion**

259 We explored which Hill diversities best predicted ecosystem function, and were surprised to find that  
260 diversities near richness ( $1 < \ell < 2$ ) often performed the best (figure 2). This result was unexpected  
261 based on three assumptions we described in the introduction: first, observed richness is not a robust  
262 biodiversity measure; second, if abundance drives function, Hill diversities with high  $\ell$  should be more  
263 predictive; third, if positive species interactions (e.g., complementarity [46]) drive function,  $\ell$  values  
264 that emphasize the probability of interspecific encounter ( $-1 \leq \ell < 1$ ) should be more predictive. The  
265 disconnect between observed and true richness is not, practically speaking, a resolvable problem and  
266 thus we cannot evaluate how much this first issue is affecting our results [22]. In the following  
267 paragraphs, we first interpret the unexplored meaning of Hill diversity when  $\ell > 1$  and then explore the  
268 latter two points, namely: how do Hill diversities near richness outperform Hill diversities with higher  $\ell$   
269 that better reflect abundance, and why we might have found such low predictive power for Hill  
270 diversities that should capture the effects of (potentially positive) species interactions. To better  
271 ground our discussion, we use an admittedly imprecise simplification and refer to  $\ell$  values as falling

272 within the “evenness range” ( $-1 \leq \ell < 1$ ), the “rare emphasis range” ( $1 < \ell < 2$ , justification follows), or  
273 the “abundance range” ( $\ell > 2$ ).

274

275 Before we can fully understand our results, we must interpret Hill diversities with  $\ell > 1$ , which have  
276 seen little attention. Traditionally used Hill diversities with  $\ell < 1$  reach their maximum possible value,  
277 species richness, when species all have the same abundance. However, Hill diversities with  $\ell > 1$ ,  
278 which strongly emphasize rare species, increase with heterogeneity (rather than homogeneity) in  
279 species abundance. By emphasizing rare species even *more* than richness does, these diversities may  
280 reflect two essential features of community size: the total number of species and the total number of  
281 individuals. As these features are not practically separable and both apparently drive function, it may  
282 be advantageous to measure them jointly. Arguably, observed richness does this [31], but our results  
283 show that  $\ell$  values in the rare emphasis range, which are relatively more sensitive to abundance than  
284 richness is, yield measures of diversity that better predict function. Beyond the rare emphasis range,  
285 Hill diversity quickly converges on abundance (at least in most observational data). This results in a  
286 slight decline in Hill diversity’s ability to predict ecosystem function for larger  $\ell$  values (figures 2-3).

287

288 Hill diversities in the evenness range ( $-1 \leq \ell < 1$ ) should capture the effects of species interactions by  
289 emphasizing the probability of interspecific encounter, but these diversities were poor predictors of  
290 function. This was unexpected because a consistent BEF finding, including in real-world systems, has  
291 been that function increases with evenness [47–50], which increases Hill diversity for  $\ell < 1$  [51–53].  
292 Additionally, in the evenness range, sample Hill diversities have relatively good statistical properties  
293 as estimators of true diversity, and asymptotic estimators [54] can further improve the situation,  
294 largely avoiding the robustness issues we highlight with species richness. Instead, the observed weak  
295 predictive power of Hill diversities with  $\ell$  values in the evenness range is because functions analyzed  
296 here are the product of two components, abundance and per-capita function, which each showed  
297 different responses to increasing  $\ell$ . Abundance-diversity relationships often mirrored function-  
298 diversity correlations (compare figure 3 with the top row of figure 4). In other words, across the  $\ell$   
299 spectrum, Hill diversities had nearly the same relationship with abundance and with function,  
300 underlining the necessity of accounting for the role of total abundance in BEF research [55]. However,  
301 Hill diversities in the evenness range deviated from this pattern, instead exhibiting often strong,  
302 countervailing relationships with abundance and per-capita function (figure 4).

303

304 The relationship between diversity and per-capita function differed from the diversity-abundance  
305 relationship, with correlation coefficients for per-capita function generally decreasing with increases  
306 in  $\ell$ , but often showing a positive peak in the evenness range (figure 4). Positive species interactions,  
307 including those that increase per-capita function, are expected to predict total function [46,56]. Our  
308 results partly support these expectations, as Hill diversities in the evenness range, which should track  
309 the probability of interspecific encounter, were positively associated with per-capita function, even as  
310 they tended to be negatively associated with abundance. As we increased  $\ell$ , the correlation between  
311 Hill diversity and per-capita function disappeared near richness ( $\ell = 1$ ), also pushing against  
312 expectations that richness best captures function-relevant biodiversity gradients. In the rare emphasis  
313 and abundance ranges, we typically found a negative correlation between Hill diversity and per-capita  
314 function. This likely reflects spatial constraints and/or fundamental tradeoffs between having many,  
315 smaller-bodied individuals versus fewer larger ones [57,58]. This scenario is particularly easy to  
316 imagine for trees crowding in fixed-area plots, which physically and energetically prohibit arbitrarily  
317 large numbers of the largest trees. Similar energetic and spatial constraints limit the number of very  
318 large fish that might be seen in a single dive. Thus, we suspect that one reason we see a decline in the  
319 correlation between mean per-capita function and diversity with increasing  $\ell$  in the fish and tree  
320 datasets is decreases in per-capita function due to crowding.

321

322 Although Hill diversities in the rare emphasis range were most often the best predictor of total  
323 function, Hill diversities with  $\ell$  values in the abundance range also predicted function well, and should  
324 not be discounted. Hill diversities in the abundance range were the *best* predictor of function in a  
325 substantial minority of datasets (Fig. 2), and for nearly all datasets were *strong* predictors of function  
326 (Fig. 3, far right of x-axes). This was expected because of a general link between higher abundance and  
327 higher function [55,59–63]. Even as Hill diversities in the “abundance” range were strong predictors of  
328 function, we also note that abundance can relate to Hill diversity across the full spectrum of  $\ell$  values.  
329 For example, if high-abundance sites tend to be dominated by many individuals of one or a few  
330 species [45], Hill diversities that emphasize the most common species will decrease with abundance.  
331 Thus, we should not expect that strong effects of abundance on function are captured exclusively at  
332 high values of  $\ell$ .

333

334 The predictive power of power of Hill diversity changed nonlinearly with increases in  $\ell$ , as multiple  
335 facets of community structure (e.g., richness, abundance, evenness) affect function simultaneously. If  
336 we had found a monotonic strengthening of BEF relationships with increasing  $\ell$ , we would argue that  
337 Hill “diversities” with large positive scaling parameters were simply abundance metrics masquerading  
338 as measures of diversity. Instead, we found, across a variety of regions, taxa, and ecosystem functions,  
339 intermediate, positive  $\ell$  values in the “rare emphasis” range tended to produce the strongest BEF  
340 relationships (Fig. 3). All Hill diversities with positive  $\ell$  values (including richness) tend to increase with  
341 both abundance and richness, which we argue can be a useful property, especially for BEF research.  
342 Because the goal of summarizing species’ abundances with diversity metrics is to distill complex,  
343 multivariate information [15], this claim is not radical. In fact, Hill diversities that emphasize rare  
344 species more than richness does can reflect intuitive notions of diversity, which include both high  
345 density and high compositional variation [64]. Our study points to the need for further theoretical  
346 work to explicate the meaning of these seldom-used Hill diversities in the rare emphasis range, and  
347 their linkages to ecosystem function.

348  
349 By considering Hill diversities over a wide range of  $\ell$ , we place ourselves at odds with the convention  
350 that Hill diversities should be considered only when  $\ell \leq 1$  [6,14,15,65,66]. The most compelling  
351 argument for that restricted range of scaling parameters is presented by Patil and Taillie, who argued  
352 that diversity should not decrease when abundance is shifted from more to less abundant species,  
353 including to species with zero abundance, a variation on Dalton’s “principle of transfers” [15,67]. This  
354 diversity property does not hold for Hill diversity when  $\ell > 1$ , which has species richness as its  
355 minimum, occurring in the perfectly even community, and increases (given richness and abundance)  
356 as some species get progressively rarer. A more pragmatic argument comes from Chao et al., who  
357 noted that estimating the relative abundance of rare species is an increasing problem for diversity  
358 measures as  $\ell$  increases; they therefore suggest using only more estimable Hill diversities with  $\ell \leq 1$  [6].  
359 However, theoretical work suggests that even richness ( $\ell = 1$ ) is poorly estimated [22], and by this logic  
360 should not be used either. Finally, and most generally, diversity measures have traditionally been  
361 considered separate from abundance/density measures (but see [68,69]), whereas with increasing  $\ell$   
362 values, observed diversity and observed abundance tend to be more strongly correlated (and in fact  
363 approach a correlation of one in our datasets). Despite these arguments, our results show that Hill  
364 diversities with  $\ell > 1$  are meaningful ecological diversity measures, at least in the sense that they

365 convey more information about function than do more widely-used Hill numbers. Choosing to exclude  
366 these Hill diversities might be desirable for some conceptualizations of diversity, but we are opening  
367 the narrower question of which Hill diversities—with their variable emphasis on richness, abundance,  
368 evenness, and dominance—best predict ecosystem function. In this pursuit, allowing diversity metrics  
369 to highlight absolute abundance is valuable.

370

371 As global changes lead to shifting species abundances, ecologists must continue to describe and  
372 predict how these shifts impact ecosystems and the way they function. Yet, understanding the  
373 separate and combined roles of total and relative abundance in mediating ecosystem function  
374 remains a difficult challenge, in large part because total abundance is inextricably linked to diversity  
375 measures. It is mathematically linked for large, positive  $\ell$  values. It is practically constrained by  
376 sampling effects for  $\ell$  closer to 1 (i.e., near species richness). As  $\ell$  becomes negative, Hill diversities  
377 may lose their dependence on total abundance [21]. However, in the majority of community datasets,  
378 we saw at least weak negative correlations between negative- $\ell$  Hill diversities and observed  
379 abundances, likely due to increasing dominance in more abundant systems [45]. Overall, this suggests  
380 that in observational contexts, simple partitioning of abundance and diversity effects may not be  
381 tractable, at least not in a satisfying manner [31,36]. Since no single-best diversity measure is likely to  
382 emerge for all BEF studies, we encourage researchers to be open-minded towards Hill diversities  
383 across a wide spectrum of  $\ell$  values and their potential links to mechanisms underlying BEF  
384 relationships.

385

### 386 **Competing Interests**

387 *We have no competing interests.*

388

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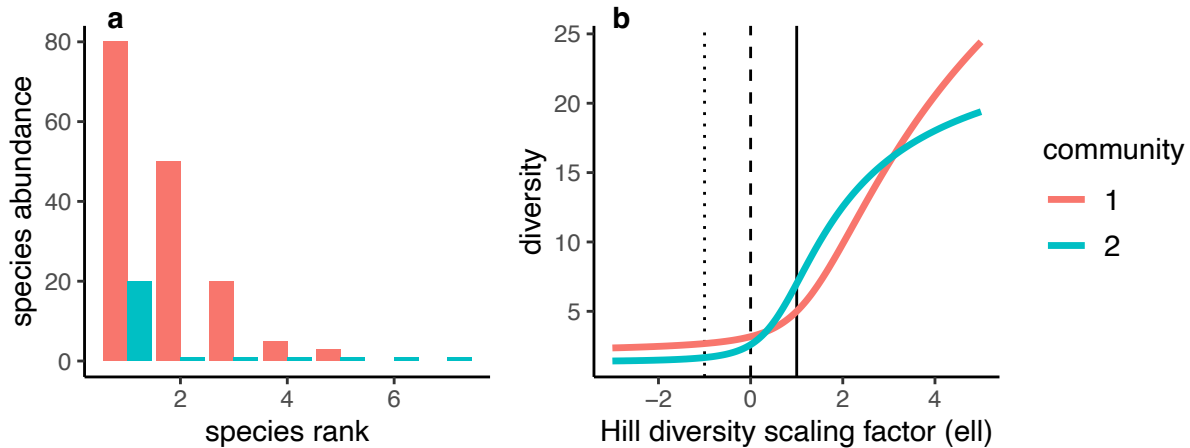
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567 **Table 1. To learn how biodiversity-ecosystem function correlations are affected by different Hill**  
568 **diversity scaling factors, we gathered published, observational community datasets on three**  
569 **ecosystem functions.** These were subdivided into a total of 39 community datasets, each including  
570 observations of species' identities, abundances, and functions across replicated sites.

Ecosystem function	Citation	Datasets	Replication	Max extent (km)
Rate of wild bee pollen deposition	Genung et al. 2022	Landscape array of 3 plant species	Each plant species present at 25 sites	35
Fish biomass	Lefcheck et al. 2021	32 globally distributed ecoregions (16 temperate, 16 tropical)	11-186 sites (median 59)	17 - 4,677
Above-ground carbon storage	Condit et al. 2000, Cavanaugh et al. 2014	Tree species ID and estimated biomass at four globally distributed tropical forests	50 1-Ha subplots from the 50-Ha BCI census; sets of six 1-Ha plots in three tropical regions.	1 (Condit et al.); 32-681 (Cavanaugh et al.)

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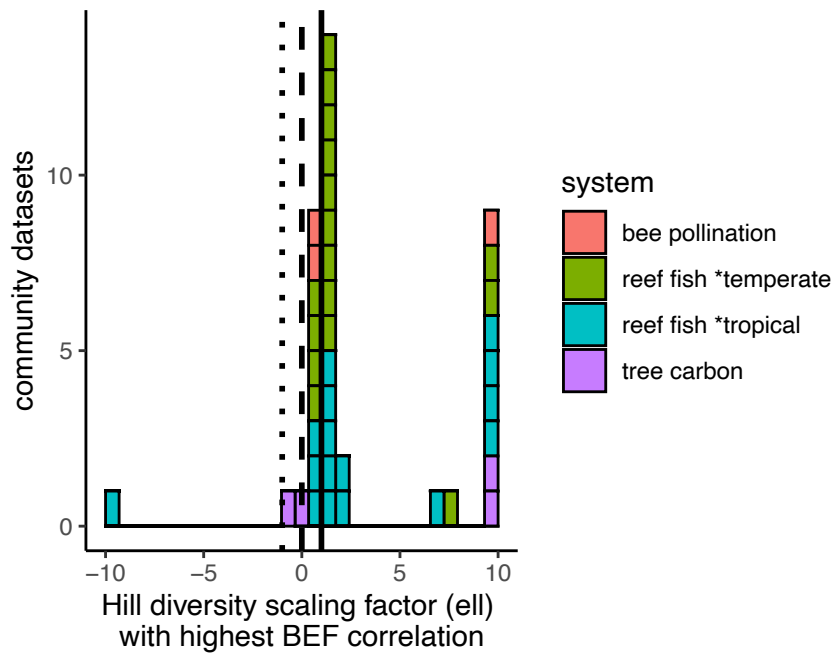
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594 **Fig 1. Two hypothetical communities with (a) different species abundance distributions have (b)**

595 **different diversity profiles.** At large negative  $ell$  values, each diversity profile converges on the  
596 inverse proportional abundance of the one most abundant species in the assemblage (inverse  
597 dominance). As  $ell$  values are more positive, each diversity profile converges on the inverse  
598 proportional abundance of the one least abundant species in the assemblage (equal to total  
599 abundance when the least abundant species is a singleton). Because singletons are ubiquitous in  
600 observational data, sample Hill diversities converge on observed abundance with increasingly large,  
601 positive values of  $ell$ . In the example, the red community is more even and more abundant, so its  
602 diversity is higher compared to the blue community at both ends of the diversity spectrum. However,  
603 the blue community has more species, and therefore is more diverse around richness ( $ell = 1$ , solid  
604 vertical). Other commonly used diversities are inverse Simpson (dotted) and exponentiated Shannon  
605 (dashed).

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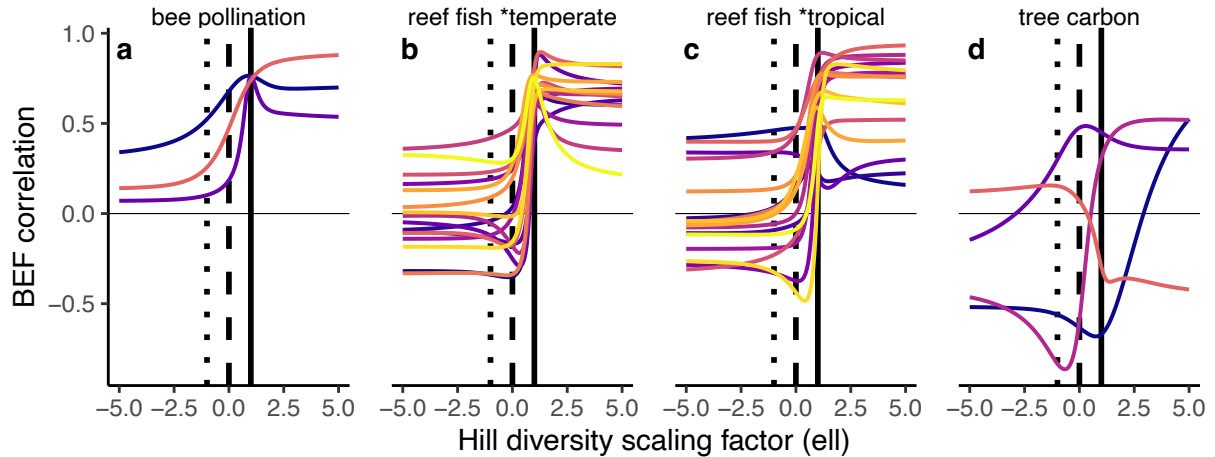
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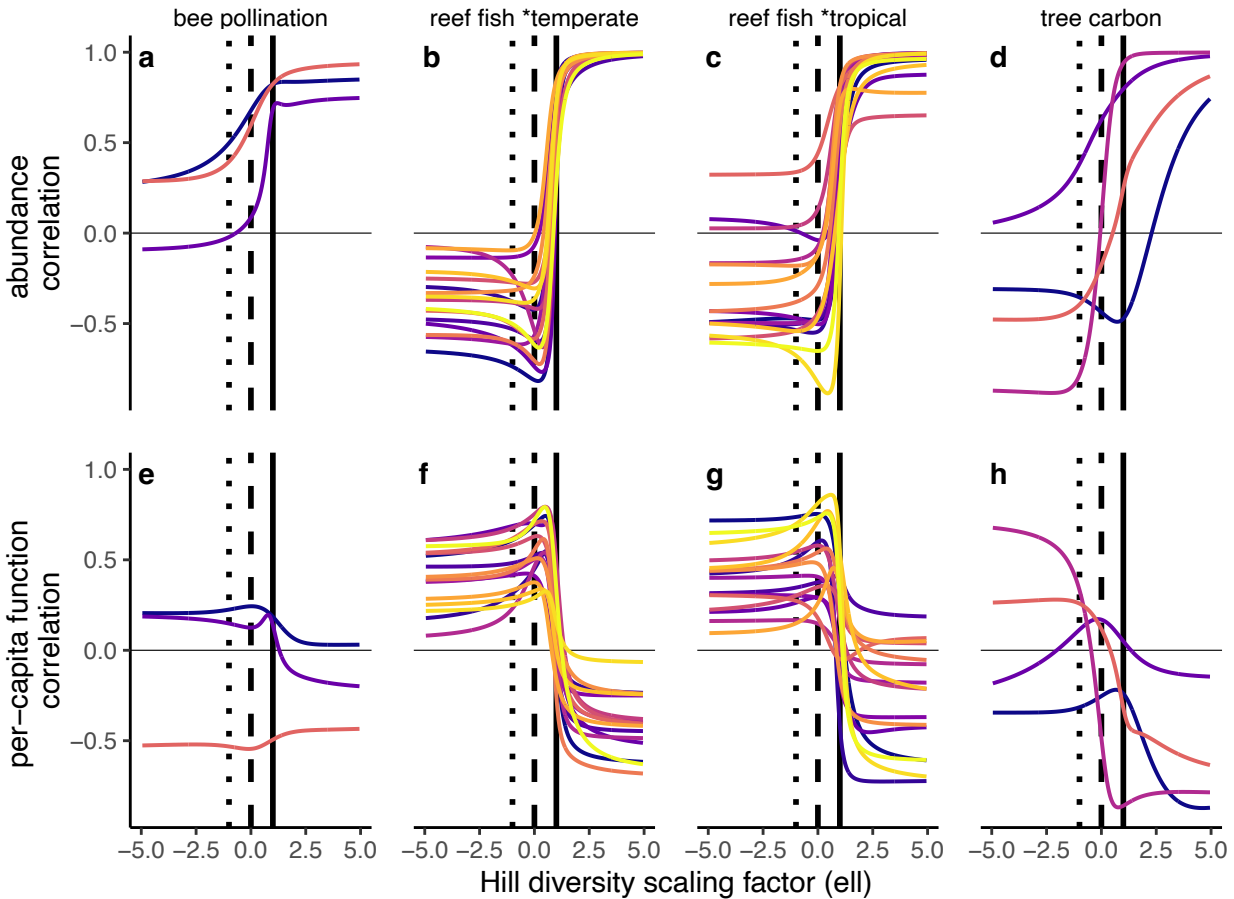
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**Figure 2. Across 39 observed biodiversity-ecosystem function (BEF) correlations calculated using a wide range of diversity scaling factors, the BEF relationships with the highest  $r^2$  were typically found using diversities near richness (vertical solid line; modal  $\ell = 1.5$ ). The highest BEF  $r^2$  value for a community dataset was rarely found using diversities that emphasize the relative abundance of common species, including exponentiated Shannon (dashed line) and inverse Simpson (dotted line). Correlations were calculated between log diversity and log ecosystem function at a site (total above-ground carbon in tropical forest plots, rate of pollen grain deposition by wild bees, or total biomass of reef fish encountered in fixed-effort dive surveys in temperate and tropical regions).**



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**Figure 3. Biodiversity-ecosystem function (BEF) correlations across observed communities in a study system vary in magnitude and direction, depending on which scaling factor ( $\ell$ ) is used for calculating species' diversity.** Ecosystem services considered here are (a) rate of pollen grain deposition on one of three flower species by wild bees; total biomass of reef fish encountered in fixed-effort dive surveys in (b) temperate and (b) tropical global regions; and (d) total above-ground carbon in tropical forest plots. Correlations are between logged total function at each site, and logged species diversity at a range of  $\ell$  values (at 0.5 intervals) emphasizing the relative abundance of common species' (negative  $\ell$  values) or rare species (positive  $\ell$  values). Vertical lines identify correlations at commonly used diversities: inverse Simpson (dotted), exponential Shannon (dashed), and richness (solid). Colors visually distinguish different community datasets.

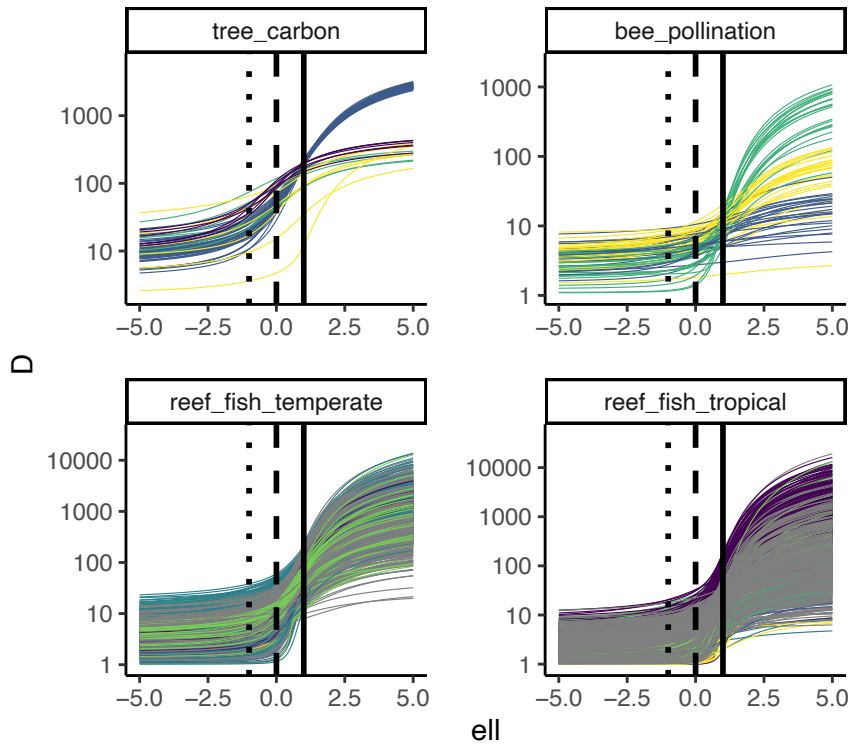


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661 **Figure 4. Biodiversity-ecosystem function (BEF) correlation in observational data (figure 3) can**  
662 **be explained by correlation between total abundance and diversity (first row), correlation**  
663 **between mean per-capita function and diversity (second row), and interactions between these**  
664 **two factors (intractable, not shown).** With a few exceptions, the abundance-diversity correlations  
665 roughly match the BEF correlation across the range of ell values used to calculate species diversities,  
666 while per-capita function-diversity correlations show countervailing trends in magnitude and  
667 direction. Compare (a, e) wild bee pollination, reef fish biomass in (b, f) temperate and (c, g) tropical  
668 regions, and (d, h) tropical forest above-ground biomass with corresponding panels in figure 3.  
669 Vertical lines identify correlations at commonly used diversities: inverse Simpson (dotted),  
670 exponential Shannon (dashed), and richness (solid). Colors visually distinguish different community  
671 datasets.

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678 **Figure S1. Community datasets (line color) differed in both the shapes of the diversity profiles (D**  
679 **vs.  $\ell$ ) and the degree to which diversity profiles differed between sites.** For example, the grey-  
680 blue tree\_carbon sites were all 1-Ha subplots from the contiguous BCI 50-Ha forest plot, and diversity  
681 profiles were very similar between subplots; by contrast the yellow bee\_pollination sites (Floral  
682 visitors of *Polemonium reptans*) had variable structure with wide variety in richness ( $\ell = 1$ , vertical  
683 solid lines), inverse dominance (large negative  $\ell$ ), and abundance (large positive  $\ell$ ). Each curve is  
684 the diversity profile for a single site; colors indicate a community dataset (set of sites within a region  
685 at which a single function was measured).  
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