

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

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11 **Keywords:** abundance, biodiversity, diversity profile, ecosystem function, Hill number, rarity

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 hypothesized that  
20 Hill numbers that emphasize rare species more than richness does may distinguish large, complex,  
21 and presumably higher-functioning assemblages from smaller and simpler ones. In this study, we  
22 tested 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 does 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 biodiversity  
38 gradients poorly, because species composition and abundance can change dramatically with little to  
39 no change in observed species richness [8–10]. Therefore, other metrics of biodiversity may provide  
40 improved clarity about the linkages between biodiversity and ecosystem function (BEF) outside  
41 experimental contexts.

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, richness was  
52 considered a good proxy for functional diversity and redundancy, which were considered the key  
53 mechanisms through which biodiversity maintains ecosystem function [12–14]. However, the choice  
54 of richness may not have been based on theoretical expectation that richness, rather than other  
55 abundance-weighted diversity measures, best described functionally important biodiversity  
56 gradients.

57

58 Using species richness as the key biodiversity measure poses methodological problems for BEF  
59 research, especially when community properties other than richness vary, as in naturalistic systems.  
60 Species richness is not only sensitive to the extent and depth of sampling, but also to the distribution

61 of relative abundances in the sampled assemblage. To illustrate this, consider the difficulty of  
62 accurately measuring species richness in a community with one hyper-dominant species and many  
63 very rare species, versus measuring richness in a community in which abundance is evenly  
64 distributed. Richness, like other diversity measures, summarizes the distribution of relative  
65 abundances in an assemblage, and when estimated from data, cannot be independent from that  
66 distribution, even if such a measure were desirable [6,15]. However, different diversity measures vary  
67 in the extent to which they emphasize rare vs. common species, with species richness heavily  
68 emphasizing rare species. A unified family of diversity measures, known as “Hill numbers” or “Hill  
69 diversities,” summarizes a distribution of relative abundances as the abundance-weighted,  
70 generalized mean rarity [16–18]. Hill numbers are governed by a scaling parameter,  $\ell$ , that scales  
71 species rarity when computing the mean, and higher values of  $\ell$  afford more leverage, or emphasis, to  
72 rare species, while lower values emphasize common species more [18].

73  
74 The Hill diversity of an assemblage is not a single value, but rather a spectrum that varies  
75 continuously across  $\ell$  [6,16] (Figure 1), raising the question of how ecosystem function relates to  
76 biodiversity measures with different emphasis on common vs. rare species. While several recent  
77 studies have compared whether richness ( $\ell = 1$ ), exponentiated Shannon ( $\ell = 0$ ), or inverse Simpson ( $\ell$   
78 = -1) best explains ecosystem function [19–22], there has been no examination of how Hill numbers  
79 relate to ecosystem function across a wide range of  $\ell$  values. This is a striking knowledge gap because,  
80 although nearly all studies of the relationship between biodiversity and ecosystem function have used  
81 species richness as a measure of diversity [3], other diversity measures could both better describe  
82 variation in biodiversity, and also have stronger links to ecosystem functioning. Furthermore, Hill  
83 diversities with  $\ell > 1$ , which emphasize rare species even more than richness does, have scarcely been  
84 studied at all, not to mention in relationship to ecosystem function. Thus, biodiversity-function  
85 studies may be *underestimating* the importance of biodiversity for function by not considering Hill  
86 diversities with different emphases on rare and common species via different values of the scaling  
87 parameter  $\ell$ .

88  
89 Despite clear declines in richness at the global scale, local changes in biodiversity and their  
90 connection to function are likely better captured by measuring total abundance and species’ relative  
91 abundances [8,23], for at least three reasons. First, as already discussed, observed richness is a poor

92 predictor of true richness [24], and good estimators of true richness based only on species frequencies  
93 in samples may never exist [25]. Thus, even if underlying variation in species richness correlates  
94 strongly with, or even drives, ecosystem function, estimating richness from samples could severely  
95 obscure the underlying pattern. Second, although observed richness does increase with observed  
96 abundance, to the extent that abundance *per se* drives function, Hill diversities that better reflect  
97 abundance (i.e., when  $\ell \gg 1$ ) should be stronger correlates of function than richness ( $\ell = 1$ ) is. Third, if  
98 diversity effects on function are mediated by positive species interactions [3,26–28], more probable  
99 and stronger between equally abundant species [29,30], Hill diversities that better reflect the  
100 probability of interspecific encounter (e.g. Hill-Simpson diversity, at  $\ell = -1$  [31]) might explain function  
101 better than richness does.

102

103 Here, we ask how biodiversity-ecosystem function correlations in observational datasets change in  
104 sign and magnitude across a wide range of values of the scaling parameter  $\ell$ . In natural communities,  
105 classic BEF mechanisms such as selection and complementarity co-occur with other sources of  
106 variation in function, such as abundance, evenness, demography, and environment [32,33].

107 Researchers variously use mathematical partitions [34] or regression and path analysis [32,35] to  
108 partially account for subsets of these factors, depending on their system knowledge, assumptions,  
109 and preferred study focus. To focus on what different diversity scaling factors reveal, we keep  
110 analyses simple and general by presenting the overall correlation between total function and diversity  
111 across natural communities, which represents the net effects of many factors. In the context of these  
112 multiple correlations, we analyze ecosystem functions that can be expressed as the product of mean  
113 per-capita function and total abundance, which works well for many functions [36,37]. As a first step  
114 towards a more granular approach, we also present separate correlations between diversity and total  
115 abundance [38] and between diversity and per-capita function, which captures selection effects due  
116 to shifts in community composition, together with complementarity effects on individual-level  
117 function. We explore whether diversity measures other than richness can better explain BEF patterns  
118 and potentially help identify BEF mechanisms in natural systems.

119

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

- 121 1) Which values of the Hill diversity scaling factor  $\ell$  produce the strongest biodiversity-  
122 ecosystem function correlations?

- 123 2) How do biodiversity-ecosystem function correlations change in sign and strength over a wide  
124 range of values of the Hill diversity scaling factor  $\ell$ ?
- 125 3) What is the role of absolute abundance in shaping BEF correlations over the Hill diversity  
126 spectrum?

127

## 128 **Materials and Methods**

129 To find how biodiversity-ecosystem function correlations change with different diversity scaling, we  
130 used previously published community datasets that recorded both the abundance and function of  
131 species at multiple sites. We chose datasets of disparate ecosystem functions and spatial scales:  
132 pollination by wild bee visitors to a landscape-scale array of three plant species [39,40], reef fish  
133 biomass from dive surveys replicated within 32 globally distributed geographic regions [41,42], and  
134 above-ground tree biomass in census plots replicated within four tropical forests [43,44] (Table 1). In  
135 each system, total function of a community can be estimated as the summed contribution across  
136 species (or individuals) present in the community. Pollination was measured as the product of first,  
137 the typical number of pollen grains deposited during a single visit of a focal bee taxon to the focal  
138 plant species, and second, the number of observed visits to the focal plant species by the focal bee  
139 taxon. Reef fish biomass was measured by visually estimating individual fish body lengths during dive  
140 surveys, which were then used to calculate biomass using species-specific allometric equations.  
141 Tropical tree biomass was measured by converting observed individual diameter at breast height into  
142 biomass estimates using taxon-specific allometric equations that included information about wood  
143 density [45,46]. In total, we used 39 community datasets, each consisting of one function measured  
144 across a collection of assemblages.

145

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

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

149

150

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

151 or its limit as  $\ell$  approaches zero (exponential Shannon entropy) [18,47]. Historically, it has been more  
152 common to express Hill diversity with a scaling parameter “ $a$ ” or “ $q$ ”, equal to  $1-\ell$  [6,16,48]. We used  
153 the expression above (with the scaling parameter  $\ell$ , instead), to highlight that this expression is a  
154 specific example of the more general weighted power mean [17,18]. This  $\ell$  formulation’s biggest  
155 advantage over the  $q$ -formulation is that it clarifies the differences between weights (abundances)  
156 and the rarity scaling controlled by the parameter  $\ell$  [18]. Furthermore, because the equations for  
157 richness, Hill Shannon, and Hill-Simpson diversities straddle  $\ell = 0$ , this formulation may support the  
158 intuition that the spectrum of Hill diversity measures can extend in either direction (Figure 1), either  
159 further emphasizing common species (as  $\ell$  gets increasingly negative) or further emphasizing rare  
160 ones (as  $\ell$  gets increasingly positive).

161  
162 We used observed species abundances to calculate species diversities at each site as the Hill diversity  
163 along a wide range of  $\ell$  values (from -10 to +10 at intervals of 0.05) (Figure S1). We calculated total  
164 function as the sum of species’ functions at each site. We computed the correlation between the  
165 natural logarithm of each diversity and the natural logarithm of total function, across all sites in the  
166 community dataset (hereafter, the “BEF correlation”). We focused on the logarithms of function, and  
167 later, abundance variables because  $\log(\text{total function}) = \log(\text{abundance}) + \log(\text{per capita function})$ ,  
168 and we also log-transformed diversity because we anticipated that across the wide array of  
169 ecosystems considered, multiplicative, rather than additive, differences in diversity would be most  
170 comparable. To identify the  $\ell$  value that produced the strongest BEF correlation in each community  
171 dataset, we plotted the correlation against the scaling factor  $\ell$ . We identified the single  $\ell$  value with  
172 the largest absolute correlation (i.e., largest R-squared for the relationship between  $\log(\text{diversity})$  and  
173  $\log(\text{function})$ ).

174  
175 *How do biodiversity-ecosystem function correlations change in sign and strength over a wide range of*  
176 *values of the Hill diversity scaling factor  $\ell$ ?*

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

182

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

184 To begin to separate effects of total and relative abundance on BEF correlations across the Hill  
185 diversity spectrum, we looked separately at the relationships between diversity and two  
186 complementary components of total function, namely total abundance and mean per-capita function.  
187 We used the same graphical approach we described above, regarding the sign and strength of the BEF  
188 correlation across the Hill diversity spectrum. For each community dataset, we found the correlation  
189 between the natural logarithm of Hill diversity at each site and either the natural logarithm of total  
190 abundance at each site, or the natural logarithm of mean per-capita function at each site, and plotted  
191 these correlations against the Hill diversity scaling parameter  $\ell$ . Although on the logarithmic scale,  
192 abundance and mean per-capita function combine additively to create total function, the BEF  
193 correlation does not additively decompose into abundance by biodiversity and per-capita function by  
194 biodiversity correlations, as there is also covariance between abundance and per-capita function.  
195 Acknowledging this caveat, we suggest that by partitioning total function into additive components  
196 and examining how each of these relates to biodiversity gradients across the Hill spectrum, we can  
197 better characterize the role of total abundance in generating patterns in the BEF correlation itself.

198

## 199 **Results**

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

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

207

208 *How do biodiversity-ecosystem function correlations change in sign and strength over a wide range of*  
209 *values of the Hill diversity scaling factor  $\ell$ ?*

210 Across all ecosystem functions, we found common patterns in the relationship between the BEF  
211 correlation and the Hill diversity scaling parameter,  $\ell$ . When  $\ell$  was  $< 1$ , the diversity-function  
212 correlation was typically weak and could be positive or negative (Figure 3). Near  $\ell = 1$ , the diversity-

213 function correlation rapidly increased, although a substantial minority of community datasets first  
214 showed a sharp negative turn in the relationship near Hill-Simpson and Hill-Shannon diversities  
215 (Figure 3 b-d). Across all the datasets we considered, the mean correlation between  $\log(\text{diversity})$  and  
216  $\log(\text{total function})$  was not significantly different from zero for either Hill-Simpson or Hill-Shannon  
217 diversity ( $p > 0.28$  for two-sided Student's t-test, with no correction for multiple tests). At richness ( $\ell =$   
218 1), almost all datasets showed positive diversity-function correlations, with the mean  $R^2 = 0.381$ . For  
219 most datasets, the strongest correlations were located near richness, with a mode near  $\ell = 1.5$ , where  
220 the mean  $R^2$  was 0.445, after which the diversity-function correlation slowly declined as  $\ell$  values  
221 continued to increase (Figure 3). A substantial minority of datasets showed continually stronger  
222 relationships as  $\ell$  increased (some profiles in Figure 3 b, c), leading to highest  $R^2$  values at or near the  
223 maximum  $\ell$  we considered ( $\ell = 10$ ).

224

225 This study was not designed to contrast trends between ecosystem functions, but it is important to  
226 note that the relationship between the BEF correlation, and the emphasis the diversity metric puts on  
227 rare vs. common species (i.e., the value of  $\ell$ ), did not appear uniform across systems. For the three bee  
228 community datasets, total pollen deposition and bee diversity were positively correlated at every  
229 value of  $\ell$ . Correlation strength peaked at richness ( $\ell = 1$ ) or just beyond ( $\ell = 2$ ), but remained relatively  
230 strong across all higher values of  $\ell$  (Figure 3a). For the 32 reef fish community datasets, total fish  
231 biomass and fish diversity tended to be weakly and often negatively correlated at low  $\ell$  values.  
232 Correlation strength tended to peak either slightly above richness at  $\ell = 1.5$ , or grow with  $\ell$  for an  
233 observed peak near the maximum value considered ( $\ell = 10$ ) (Figure 2, Figure 3 b, c). When considering  
234 either very high or very low  $\ell$  values, note that at either end of the Hill number spectrum, diversities  
235 rapidly converged towards their maximum or minimum asymptote. Thus, large changes in the BEF  
236 correlation rarely occurred outside a fairly narrow range between  $\ell = -2$  and 2. Finally, the four tropical  
237 tree community datasets showed generally weak correlations. In two tree datasets, BEF correlation  
238 strength peaked at intermediate  $\ell$  values where the BEF correlation was strongly negative (Figure 3 d).  
239 In another (Barro Colorado Island) diversity-function correlation was negative even at high  $\ell$  values  
240 (Figure 3 d, orange line), but modestly positive for negative  $\ell$  values.

241

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

243 As expected, the relationship between diversity and abundance was mostly similar to the relationship  
244 between diversity and function, as total abundance underlies function in our datasets. This can be  
245 seen in the similar shape of the curves showing the correlation between  $\log(\text{diversity})$  and either  
246  $\log(\text{function})$  (Figure 3) or  $\log(\text{abundance})$  (Figure 4 a-d), as the sign and strength of correlation  
247 typically moved in similar ways across the  $\ell$  spectrum. In almost all cases, the correlation between  
248  $\log(\text{diversity})$  and  $\log(\text{abundance})$  was very strong (and in many cases approached unity), for large,  
249 positive values of the Hill diversity scaling parameter  $\ell$ . As previously remarked, this result is a  
250 mathematical inevitability when datasets contain very rare species/singletons. Additionally, across  
251 datasets, we found that the rise towards the high correlation observed for large  $\ell$  values typically  
252 occurred in the range of  $\ell$  values typically considered by ecologists (-1 to 1), likely reflecting biological  
253 and sampling linkages between abundance and diversity; the correlation frequently saturated once  $\ell$   
254 was greater than two. While for some community datasets, diversity was largely independent of  
255 abundance for negative  $\ell$  values, we also saw community datasets in which  $\log(\text{abundance})$  and  
256  $\log(\text{diversity})$  had modest to strong negative correlation across negative  $\ell$  values. Because Hill  
257 diversities typically change little with  $\ell$  below -2 [6], this result implies that in these systems, total  
258 abundance and the degree of dominance were positively linked [49].

259  
260 While the curves in Figures 3 a-d and 4 a-d show strong resemblance, for some community datasets  
261 the BEF and diversity-abundance relationships diverged, implying those BEF relationships resulted  
262 from processes other than abundance. For example, correlations between abundance and diversity  
263 were always strongly positive for the reef fish data for large, positive  $\ell$  values, but in some reef fish  
264 community datasets, correlations between diversity and function were only weakly positive at higher  
265  $\ell$  values (Figure 4 b, c). Such divergences between the diversity-function and diversity-abundance  
266 curves could be due to strong and/or countervailing relationships between mean per-capita function  
267 and diversity, which also showed some overall patterns across community datasets (Figure 4 e-h). In  
268 general, Hill diversities with negative  $\ell$  values were positively related to per-capita function,  
269 suggestive of a positive relationship between evenness and mean per-capita function. This pattern  
270 was not ubiquitous, however, with notable exceptions in both tree and bee community datasets  
271 (Figure 4 e, h). We found that the correlation between diversity and mean per-capita function often  
272 exhibited a positive peak at intermediate  $\ell$  values, a pattern particularly pronounced in the reef fish  
273 community datasets (Figure 4 f, g). Finally, there was a tendency towards a negative correlation

274 between  $\log(\text{diversity})$  and  $\log(\text{mean per-capita function})$  for larger, positive values of  $\ell$  (when  
275 diversity becomes largely synonymous with abundance), though the strength of this relationship was  
276 variable.

277

## 278 **Discussion**

279 Diversities near richness ( $1 < \ell < 2$ ) often had strong positive correlations with ecosystem function  
280 (Figure 2), echoing a large body of research emphasizing the importance of richness in BEF  
281 relationships [3]. However, this was not a foregone conclusion, because most empirical BEF work does  
282 not consider other portions of the diversity spectrum [8], and because much of the theoretical and  
283 empirical work is grounded in closed communities where richness has a clear interpretation. We were  
284 surprised by the consistent performance of richness, because of three concerns we described in the  
285 introduction: first, observed richness is not a robust biodiversity measure in observational data;  
286 second, Hill diversities with high  $\ell$  should better explain function in systems with highly variable total  
287 abundance; third,  $\ell$  values that emphasize the probability of interspecific encounter ( $-1 \leq \ell < 1$ ) might  
288 better explain function if species interactions are very important. The disconnect between observed  
289 and true richness is not, practically speaking, a resolvable problem and thus we cannot evaluate how  
290 much this first issue is affecting our results [25]. In the following paragraphs, we explore the latter two  
291 points, namely: how do Hill diversities near richness outperform Hill diversities with higher  $\ell$  that  
292 better reflect abundance, and why we might have found such low explanatory power for Hill  
293 diversities that should capture the effects of (potentially positive) species interactions. Although all  
294 the information about relative abundances is contained in any continuous interval along the Hill  
295 diversity spectrum, at different values of  $\ell$ , different aspects of the abundance distribution are  
296 emphasized. To better ground our discussion, we use an admittedly imprecise simplification, and  
297 refer to  $\ell$  values as falling within the “inverse dominance range” ( $\ell < 1$ ), the “evenness emphasis  
298 range” ( $-1 \leq \ell < 1$ ), the “rare emphasis range” ( $1 \leq \ell < 2$ , justification follows), or the “abundance  
299 emphasis range” ( $\ell > 2$ ).

300

301 As  $\ell$  values increase, empirical diversities values are increasingly dependent on total abundance, since  
302 the abundance of the rarest species is typically at the lower bound set by the detection threshold (for  
303 count data, one). Hill diversities in the “rare emphasis range,” like richness itself, are affected by  
304 abundance as well as diversity *per se*. This is reasonably viewed as a sampling nuisance [6,24]. But

305 viewed in another light, measures that combine abundance, relative abundance, and richness  
306 components could predict function well because, owing partly to their sampling properties, they  
307 describe salient biodiversity gradients. In fact, our results showed that  $\ell$  values in the rare emphasis  
308 range that, compared to richness, are relatively more sensitive to abundance tended to better explain  
309 function. Rare-emphasis Hill diversities increase with richness, abundance, and often also dominance.  
310 As a result, they might vary with the importance of sampling effects whereby higher-functioning  
311 (likely, highly abundant) species are more likely to occur in species-rich assemblages (a kind of  
312 selection effect) [34,50,51]. We found that rare-emphasis Hill diversities tended to explain function  
313 best, with  $1 < \ell < 2$  performing better than richness,  $\ell = 1$ , but because they still reflect compositional  
314 heterogeneity, also better than abundance alone (Figures 2-3).

315  
316 Hill diversities in the evenness emphasis range ( $-1 \leq \ell < 1$ ) should capture the effects of species  
317 interactions by emphasizing the probability of interspecific encounter, but these diversities explained  
318 function poorly. This was partly unexpected because in several observational datasets, function  
319 increases with evenness [52–55], which increases Hill diversity for  $\ell < 1$  [56–58]. Additionally, in the  
320 evenness emphasis range, sample Hill diversities have relatively good statistical properties as  
321 estimators of true diversity, and asymptotic estimators [24] can further improve the situation, largely  
322 avoiding the robustness issues we highlight with species richness. Instead, the observed weak  
323 explanatory power of Hill diversities with  $\ell$  values in the evenness emphasis range is because  
324 functions analyzed here are the product of two components, abundance and per-capita function,  
325 which each showed different responses to increasing  $\ell$ . Abundance-diversity relationships often  
326 followed function-diversity correlations (compare Figure 3 with the top row of Figure 4). In other  
327 words, across the  $\ell$  spectrum, Hill diversities had nearly the same relationship with abundance and  
328 with function, underlining the necessity of accounting for the role of total abundance in BEF research  
329 [59]. However, Hill diversities in the evenness emphasis range deviated from this pattern, instead  
330 exhibiting often strong, countervailing relationships with abundance and per-capita function (Figure  
331 4). This fits with previous BEF literature, which anticipates a variety of mechanisms linking evenness  
332 and ecosystem function, without a clear prediction for when the net result is positive or negative [60–  
333 63].

334

335 The relationship between diversity and per-capita function differed from the diversity-abundance  
336 relationship, with correlation coefficients for per-capita function generally decreasing with increases  
337 in  $\ell$ , but often showing a positive peak in the evenness emphasis range (Figure 4). Positive species  
338 interactions, including those that increase per-capita function, are expected to explain total function  
339 [51,64,65]. Our results partly support these expectations, as Hill diversities in the evenness emphasis  
340 range, which should track the probability of interspecific encounter, were positively associated with  
341 per-capita function, even as they tended to be negatively associated with abundance. As we increased  
342  $\ell$ , the correlation between Hill diversity and per-capita function disappeared near richness ( $\ell = 1$ ), also  
343 pushing against expectations that richness best captures function-relevant biodiversity gradients. In  
344 the rare emphasis and abundance emphasis ranges, we typically found a negative correlation  
345 between Hill diversity and per-capita function. Recent work highlighting the functional contribution of  
346 rare species to ecosystem function led us to suspect the opposite might occur [40,66–68]. The  
347 observed negative correlation likely reflects spatial constraints and/or fundamental tradeoffs  
348 between having many, smaller-bodied individuals versus fewer larger ones [69,70]. This scenario is  
349 particularly easy to imagine for trees crowding in fixed-area plots, which physically and energetically  
350 prohibit arbitrarily large numbers of the largest trees. Similar energetic and spatial constraints limit  
351 the number of very large fish that might be seen in a single dive. Thus, we suspect that one reason we  
352 saw a decline in the correlation between mean per-capita function and diversity with increasing  $\ell$  in  
353 the fish and tree datasets is decreases in per-capita function due to crowding.

354  
355 Even as Hill diversities in the rare emphasis range most often explained total function best, Hill  
356 diversities with  $\ell$  values in the abundance emphasis range also explained function well, and should  
357 not be discounted. Hill diversities in the abundance emphasis range were the *best* predictor of  
358 function in a substantial minority of datasets (Fig. 2), and for nearly all datasets were *strong* predictors  
359 of function (Fig. 3, far right of x-axes). This was expected because of a general link between higher  
360 abundance and higher function [38,59,71–74]. Even as Hill diversities in the “abundance emphasis”  
361 range related strongly to function, we also note that abundance (like evenness) can relate to Hill  
362 diversity across the full spectrum of  $\ell$  values. For example, if high-abundance sites tend to be  
363 dominated by many individuals of one or a few species [49], Hill diversities that emphasize inverse  
364 dominance will decrease with abundance. Thus, we should not expect that strong effects of  
365 abundance on function are captured exclusively at high values of  $\ell$ .

366

367 The explanatory power of Hill diversity changed nonlinearly with increases in  $\ell$ , as multiple facets of  
368 community structure (e.g., richness, abundance, evenness) affect function simultaneously. If we had  
369 found a monotonic strengthening of BEF relationships with increasing  $\ell$ , we would argue that Hill  
370 “diversities” with large positive scaling parameters were simply abundance metrics masquerading as  
371 measures of diversity. Instead, we found, across a variety of regions, taxa, and ecosystem functions,  
372 intermediate, positive  $\ell$  values in the “rare emphasis” range tended to produce the strongest BEF  
373 relationships (Fig. 3). All Hill diversities with positive  $\ell$  values (including richness) tend to increase with  
374 both abundance and richness, which we argue can be a useful property, especially for BEF research.  
375 Because the goal of summarizing species’ abundances with diversity metrics is to distill complex,  
376 multivariate information [17], this claim is not radical. In fact, Hill diversities that emphasize rare  
377 species more than richness does can reflect intuitive notions of diversity, which include both high  
378 density and high compositional variation [75]. Our study points to the need for further theoretical  
379 work to explicate the meaning of these seldom-used Hill diversities in the rare emphasis range, and  
380 their linkages to ecosystem function.

381

382 By considering Hill diversities over a wide range of  $\ell$ , we place ourselves at odds with the convention  
383 that Hill diversities should be considered only when  $\ell \leq 1$  [6,16,17,48,76]. The most compelling  
384 argument for that restricted range of scaling parameters is presented by Patil and Taillie, who argued  
385 that diversity should not decrease when abundance is shifted from more to less abundant species,  
386 including to species with zero abundance, a variation on Dalton’s “principle of transfers” [17,77]. This  
387 diversity property does not hold for Hill diversity when  $\ell > 1$ , which has species richness as its  
388 minimum, occurring in the perfectly even community, and increases (given richness and abundance)  
389 as some species get progressively rarer. A more pragmatic argument comes from Chao et al., who  
390 noted that estimating the relative abundance of rare species is an increasing problem for diversity  
391 measures as  $\ell$  increases; they therefore suggest using only more estimable Hill diversities with  $\ell \leq 1$  [6].  
392 However, theoretical work suggests that even richness ( $\ell = 1$ ) is poorly estimated [24,25], and by this  
393 logic should not be used either. Finally, and most generally, diversity measures have traditionally  
394 been considered separate from abundance/density measures (but see [78,79]), whereas with  
395 increasing  $\ell$  values, observed diversity and observed abundance tend to be more strongly correlated  
396 (and in fact approach a correlation of one in our datasets). Despite these arguments, our results show

397 that Hill diversities with  $\ell > 1$  are meaningful ecological diversity measures, at least in the sense that  
398 they convey more information about function than do more widely-used Hill numbers. Choosing to  
399 exclude these Hill diversities might be desirable for some conceptualizations of diversity, but we are  
400 opening the narrower question of which Hill diversities—with their variable emphasis on richness,  
401 abundance, evenness, and dominance—best explain ecosystem function. In this pursuit, allowing  
402 diversity metrics to highlight absolute abundance is valuable.

403

404 Our correlational analyses of observational data do not consider confounding variables, which may  
405 obscure links between biodiversity and ecosystem function, across the Hill diversity spectrum.  
406 Experimental and statistical approaches to better account for environmental drivers of diversity  
407 and/or function and more rigorously trace causal pathways (e.g., [35,80]) will be useful in validating  
408 and extending our findings [81]. One obvious effect of ignoring confounding variables is that the BEF  
409 correlations we found are likely to be low, as the confounding variables add noise that is not  
410 accounted for. Future work linking environmental gradients and other confounding variables to  
411 particular regions of the Hill diversity spectrum (e.g., regions emphasizing inverse dominance,  
412 evenness, rare species, or total abundance) may also clarify mechanisms underlying BEF  
413 relationships.

414

415 As global changes lead to shifting species abundances, ecologists must continue to describe and  
416 predict how these shifts impact ecosystems and the way they function. Yet, understanding the  
417 separate and combined roles of total and relative abundance in mediating ecosystem function  
418 remains a difficult challenge, in large part because total abundance is inextricably linked to diversity  
419 measures. It is mathematically linked for large, positive  $\ell$  values. It is practically constrained by  
420 sampling effects for  $\ell$  closer to 1 (i.e., near species richness). As  $\ell$  becomes negative, Hill diversities  
421 may lose their dependence on total abundance [24]. However, in the majority of community datasets,  
422 we saw at least weak negative correlations between negative- $\ell$  Hill diversities and observed  
423 abundances, likely due to increasing dominance in more abundant systems [49]. Overall, this suggests  
424 that in observational contexts, simple partitioning of abundance and diversity effects may not be  
425 tractable, at least not in a satisfying manner [50,82]. Since no single-best diversity measure is likely to  
426 emerge for all BEF studies, we encourage researchers to be open-minded towards Hill diversities

427 across a wide spectrum of  $\ell$  values and their potential links to mechanisms underlying BEF  
428 relationships.

429

### 430 **Competing Interests**

431 *We have no competing interests.*

432

### 433 **Acknowledgements**

434 We thank Rachael Winfree for key discussions that sparked this work, Jonathan Dushoff for providing  
435 insight on Hill numbers, and participants in the Hakai Synthesizing Biodiversity Seminar Series for  
436 useful feedback on preliminary results. Mary O'Connor and two anonymous reviewers provided  
437 helpful feedback on an earlier draft of this manuscript. We gratefully acknowledge all data collectors  
438 and data holders. Data for three tropical forests (Pasoh, Indonesia; Yasuní, Ecuador; and Volcán Barva,  
439 Costa Rica) were originally made available to us by the Tropical Ecology Assessment and Monitoring  
440 (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden,  
441 the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these  
442 institutions, the Gordon and Betty Moore Foundation, and other donors.

443

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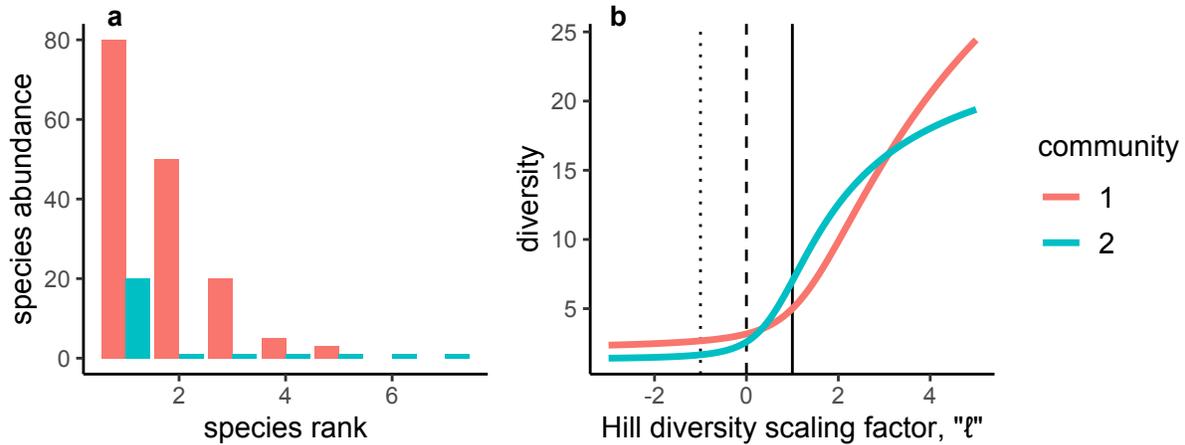
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643 **Table 1. To learn how biodiversity-ecosystem function correlations are affected by different Hill**  
644 **diversity scaling factors, we gathered published, observational community datasets on three**  
645 **ecosystem functions.** These were subdivided into a total of 39 community datasets, each including  
646 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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670 **Figure 1. Two hypothetical communities with (a) different species abundance distributions have**

671 **(b) different diversity profiles.** At large negative  $\ell$  values, each diversity profile converges on the

672 inverse proportional abundance of the one most abundant species in the assemblage (inverse

673 dominance). As  $\ell$  values are more positive, each diversity profile converges on the inverse

674 proportional abundance of the one least abundant species in the assemblage (equal to total

675 abundance when the least abundant species is a singleton). Because singletons are ubiquitous in

676 observational data, sample Hill diversities converge on observed abundance with increasingly large,

677 positive values of  $\ell$ . In the example, the red community is more even and more abundant, so its

678 diversity is higher compared to the blue community at both ends of the diversity spectrum. However,

679 the blue community has more species, and therefore is more diverse around richness ( $\ell = 1$ , solid

680 vertical). Other commonly used diversities are inverse Simpson (dotted,  $\ell = -1$ ) and exponentiated

681 Shannon (dashed,  $\ell = 0$ ). In the diversity literature, it has been less common to explore the right side of

682 this spectrum (i.e.,  $\ell > 1$ )

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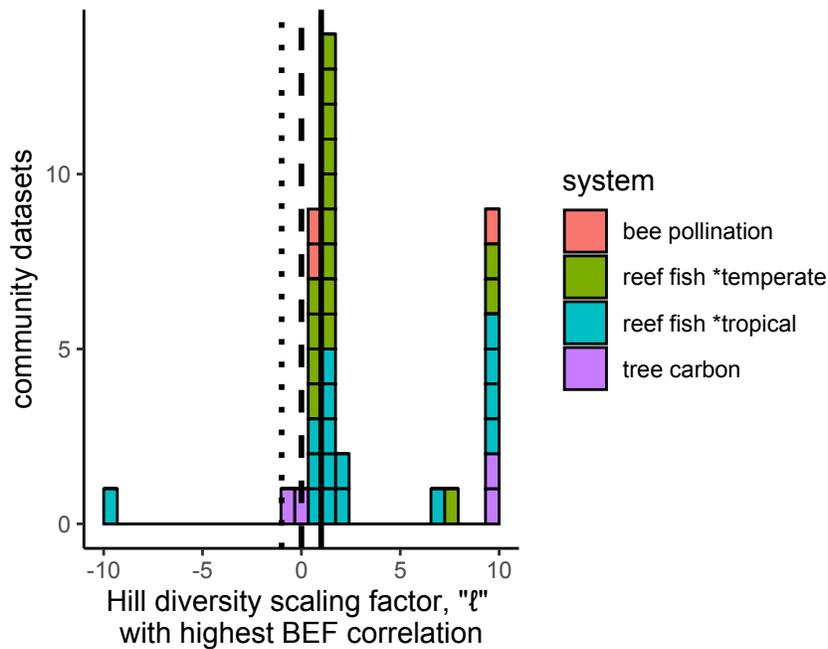
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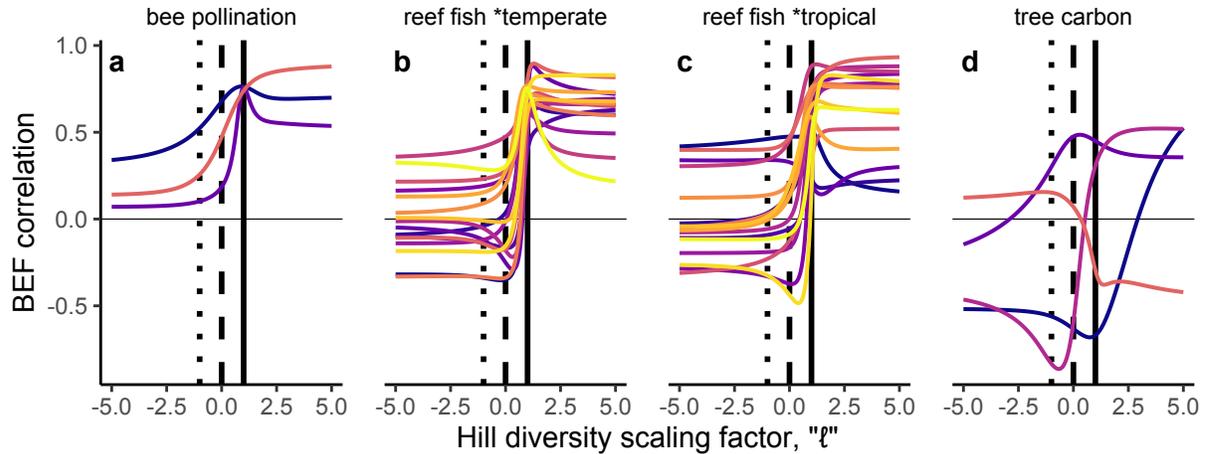
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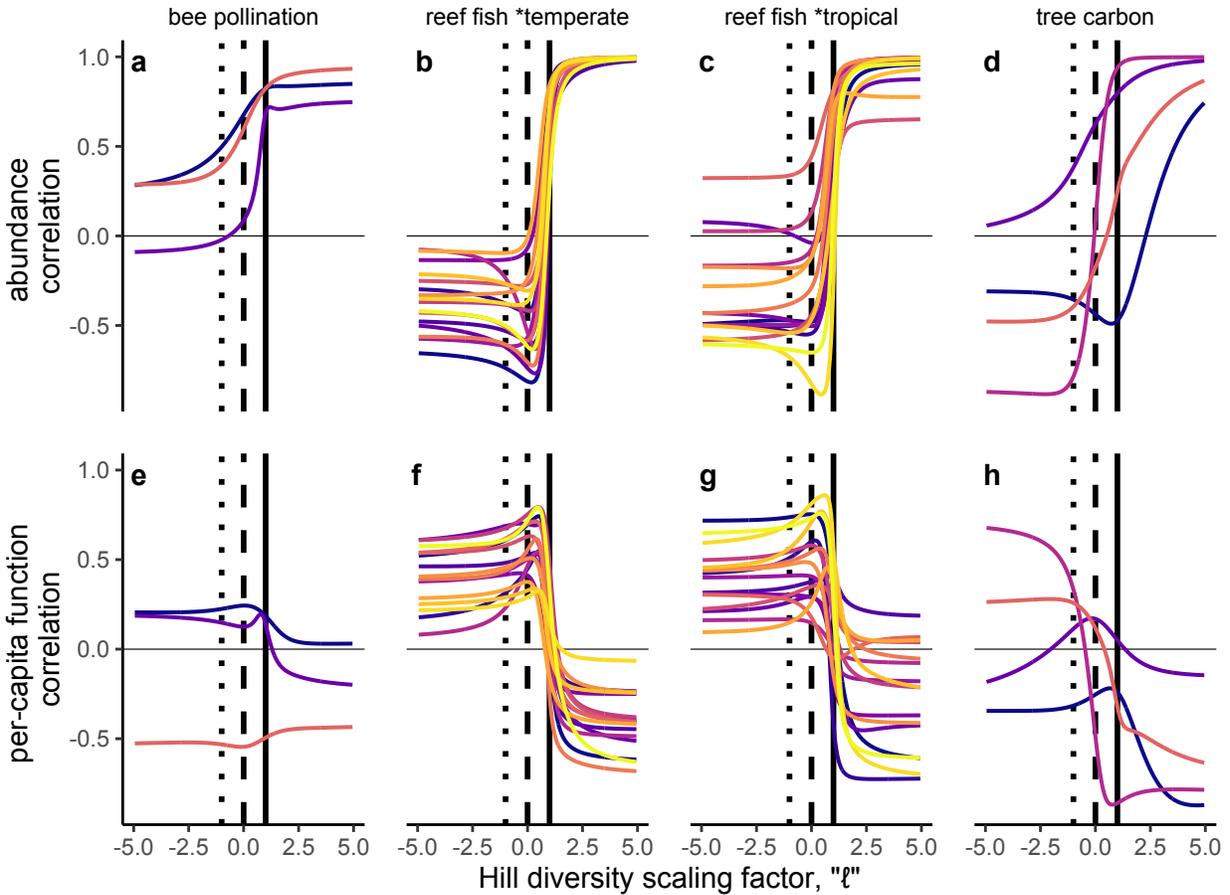
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**Figure 2. Across 39 observed biodiversity-ecosystem function (BEF) correlations calculated using a wide range of diversity scaling factors, the BEF relationships with the highest  $R^2$  were typically found using diversities near richness (vertical 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).



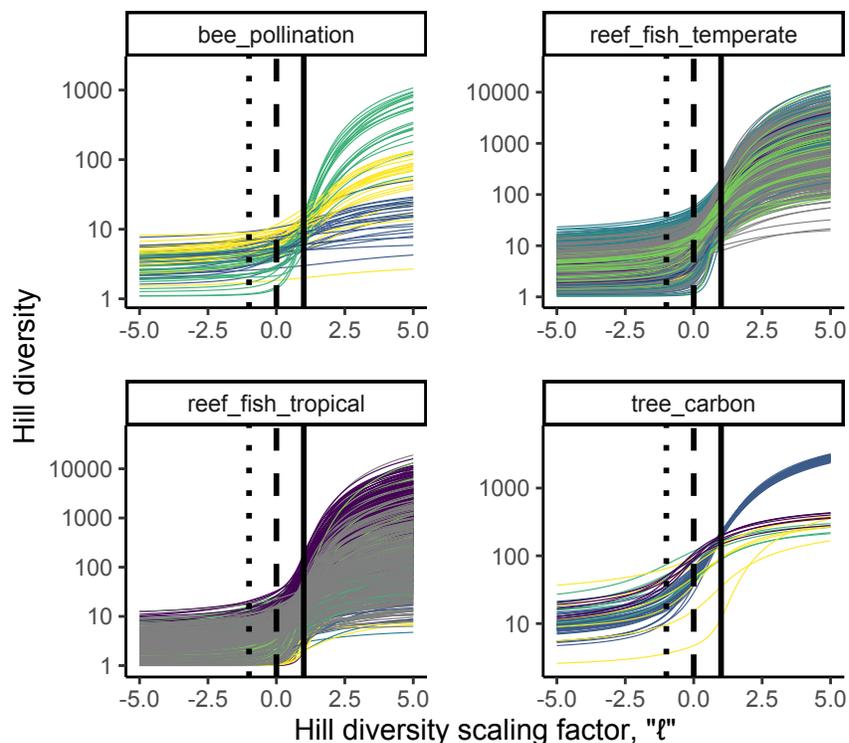
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**Figure 3. Biodiversity-ecosystem function (BEF) correlations across observed communities in a study system vary in magnitude and direction, depending on which scaling factor “ $\ell$ ” is used for calculating species’ diversity.** Ecosystem services 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 0.05 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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**Figure 4. Biodiversity-ecosystem function (BEF) correlation in observational data (Figure 3) can be explained by correlation between total abundance and diversity (first row), correlation between mean per-capita function and diversity (second row), and interactions between these two factors (intractable, not shown).** With a few exceptions, the abundance-diversity correlations roughly match the BEF correlation across the range of  $\ell$  values used to calculate species diversities, while per-capita function-diversity correlations show countervailing trends in magnitude and direction. Compare (a, e) wild bee pollination, reef fish biomass in (b, f) temperate and (c, g) tropical regions, and (d, h) tropical forest above-ground biomass with corresponding panels in Figure 3. 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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 755 **Figure S1. Community datasets (line color) differed in both the shapes of the diversity profiles**  
 756 **(Hill diversity vs.  $\ell$ ) and the degree to which diversity profiles differed between sites.** For  
 757 example, the grey-blue tree\_carbon sites were all 1-Ha subplots from the contiguous BCI 50-Ha forest  
 758 plot, and diversity profiles were very similar between subplots; by contrast the yellow bee\_pollination  
 759 sites (Floral visitors of *Polemonium reptans*) had variable structure with wide variety in richness ( $\ell = 1$ ,  
 760 vertical solid lines), inverse dominance (large negative  $\ell$ ), and abundance (large positive  $\ell$ ). Each curve  
 761 is the diversity profile for a single site; colors indicate a community dataset (set of sites within a region  
 762 at which a single function was measured).

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