

1 **Manuscript type:** Statistical report

2 **Running head:** Correcting γ -dependence for β -metrics

3 **Title:** Undersampling correction methods to control γ -dependence for comparing β -diversity
4 between regions

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21

22 **Abstract**

23 Measures of β -diversity are known to be highly constrained by the variation in γ -diversity across
24 regions (i.e., γ -dependence), making it challenging to infer underlying ecological processes.

25 Undersampling correction methods have attempted to estimate the actual β -diversity in order to
26 minimize the effects of γ -dependence arising from the problem of incomplete sampling.

27 However, no study has systematically tested their effectiveness in removing γ -dependence, and
28 examined how well undersampling-corrected β -metrics reflect true β -diversity patterns that

29 respond to ecological gradients. Here, we conduct these tests by comparing two undersampling
30 correction methods with the widely used individual-based null model approach, using both

31 empirical data and simulated communities along a known ecological gradient across a wide
32 range of γ -diversity and sample sizes. We found that undersampling correction methods using

33 diversity accumulation curves were generally more effective than the null model approach in
34 removing γ -dependence. In particular, the undersampling-corrected β -Shannon diversity index

35 was most independent on γ -diversity and was the most reflective of the true β -diversity pattern
36 along the ecological gradient. Moreover, the null model-corrected Jaccard-Chao index removed

37 γ -dependence more effectively than either approach alone. Our validation of undersampling
38 correction methods as effective tools for accommodating γ -dependence greatly facilitates the

39 comparison of β -diversity across regions.

40 **Key words:** beta-diversity (β) metrics, diversity accumulation curve, ecological processes,

41 undersampling, null model

42 **INTRODUCTION**

43 β -diversity is defined as the difference in species composition across space (Anderson *et al.*
44 2011). Importantly, analyzing differences in β -diversity across regions allows ecologists to test
45 hypotheses regarding the processes driving patterns of biodiversity (Anderson *et al.* 2011; Mori
46 *et al.* 2018). Recently, researchers have become increasingly aware of the influence of variation
47 in γ -diversity (i.e., the total species richness in a region) on measures of β -diversity (i.e.,
48 γ -dependence) (Kraft *et al.* 2011; Myers and LaManna 2016). Typically, the more species that are
49 present in a community, the larger the sample size needed to adequately describe the diversity of
50 the community (Colwell and Coddington 1994; Chao and Jost 2012). As a result, measures of
51 β -diversity across species-poor communities may be relatively free of γ -dependence, since small
52 samples will capture most of the true composition. In contrast, small samples from species-rich
53 communities will likely encompass only a tiny fraction of the true composition, leading to severe
54 undersampling and inflated β -diversity (Condit *et al.* 2005; Tuomisto and Ruokolainen 2012).
55 Therefore, γ -dependence is expected to be ubiquitous and particularly problematic when
56 comparing β -diversity among high- and low-diversity regions (Kraft *et al.* 2011; Tuomisto and
57 Ruokolainen 2012).
58 Properly accounting for the γ -dependence of β -diversity metrics is important, since γ -dependence
59 can lead to spurious interpretations regarding the ecological mechanisms driving community
60 assembly and dynamics (Myers and LaManna 2016). An individual-based randomization null

61 model approach has been widely used for the correction of γ -dependence (Chase and Myers 2011;
62 Kraft *et al.* 2011; Xu *et al.* 2015; Myers and LaManna 2016). However, its effectiveness in
63 removing γ -dependence has been questioned (Qian *et al.* 2013; Bennett and Gilbert 2016; Ulrich
64 *et al.* 2017). Alternatively, another approach for minimizing the effects of γ -dependence is to
65 simply use β -diversity metrics that explicitly account for undersampling (Colwell and
66 Coddington 1994; Chao and Jost 2012; Marcon *et al.* 2012; Tuomisto and Ruokolainen 2012).
67 For example, estimators have been developed to adjust the Jaccard and Sørensen indices based
68 on the degree of undersampling in the data (Chao *et al.* 2005). Species accumulation curves have
69 been applied to rarefy and extrapolate species richness with respect to sample size (Colwell *et al.*,
70 2012); these methods have been recently extended to diversity accumulation curves to obtain
71 asymptotic estimations of the real β -diversity (Chao *et al.* 2013; 2014).
72 There is a long history documenting the effects of undersampling on β -diversity (Wolda 1981;
73 Colwell and Coddington 1994; Tuomisto and Ruokolainen 2012; Beck *et al.* 2013), which
74 revealed the necessity for combining undersampling correction methods to facilitate the
75 comparison of β -diversity across regions. However, no study has examined whether β -diversity
76 metrics incorporated with specific undersampling correction methods could effectively remove
77 γ -dependence. While previous studies have examined the robustness of β -metrics to
78 γ -dependence by testing whether metrics can identify simple unstructured communities randomly
79 sampled from species pools of different sizes (e.g. Kraft *et al.* 2011; Bennett and Gilbert 2016;
80 Ulrich *et al.* 2017), this method may not reflect natural communities that are likely structured by

81 ecological gradients. Therefore, a rigorous assessment of the ability of β -diversity measures to
82 reveal true β -diversity patterns in response to ecological gradients is needed.

83 We compared the effectiveness—in terms of the magnitude of independence on γ -diversity and
84 sample size—of two undersampling correction methods to the null model approach in
85 conjunction with two major classes of commonly used β -diversity metrics. To do this, we used
86 both Gentry’s global forest dataset and simulated metacommunities with variable degrees of
87 stochastic and deterministic responses to a known ecological gradient, as well as a wide range of
88 sample sizes and γ -diversities. Using these data, we asked the following questions: (1) Are
89 β -metrics that incorporate undersampling correction methods able to effectively remove
90 γ -dependence compared with similar uncorrected β -metrics? (2) Do β -metrics with
91 undersampling correction methods reflect real β -diversity patterns caused by underlying
92 ecological processes? and (3) Do undersampling correction methods outperform null model
93 approaches in removing γ -dependence and reflecting ecological gradients? We expect that results
94 from this study will lead to useful insights regarding the most appropriate β -diversity metrics to
95 use across different communities around the globe.

96

97 **METHODS**

98 **Abundance-based β -metrics**

99 We selected five commonly used abundance-based β -metrics, representing two general
100 approaches to measure β -diversity (Anderson *et al.* 2011): classical metrics calculated using

101 α -diversity and γ -diversity, and multivariate metrics based on summary statistics of pairwise
102 dissimilarity among samples (Baselga 2010; Legendre and De Caceres 2013). Although these
103 two classes of metrics emphasize different facets of β -diversity, they capture Whittaker's original
104 measures of β -diversity as variation in species composition along environmental or spatial
105 gradients (Anderson *et al.* 2011; Legendre and De Caceres 2013).

106 In the two classes of β -metrics, we first excluded β -metrics that were mathematically dependent
107 on γ -diversity (Chao *et al.* 2012), because the information these metrics contain about γ -diversity
108 may result in correlations with β -diversity (Tuomisto 2010; Chao *et al.* 2012; Marcon *et al.* 2012;
109 Legendre and De Caceres 2013). Next, we focused on abundance-based β -diversity metrics,
110 since the γ -dependence of incidence-based β metrics (metrics based on species presence-absence
111 data) have been explored in previous studies (Bennett and Gilbert 2016), and accurate
112 undersampling correction is difficult to obtain based on incidence data alone (Chao *et al.* 2006).

113 Therefore, of the classical metrics, we considered the β -Shannon diversity and the normalized
114 divergence indices (Jost 2007; Marcon *et al.* 2012; Chao and Chiu 2016). These two metrics
115 quantify β -diversity as the effective number of compositionally distinct sampling units, which is
116 equal to the “true β -diversity” defined by Jost (2007) and Tuomisto (2010, see more details in
117 *Appendix 2*). Multivariate metrics have been shown to be more robust to γ -dependence than
118 classical metrics (Condit *et al.* 2005; Bennett and Gilbert 2016; Marion *et al.* 2017), and we were
119 especially interested in comparing β -diversity across multiple communities; thus we chose to
120 examine the widely-used Jaccard, Hellinger, and Bray-Curtis pairwise dissimilarity indices, and

121 transformed pairwise dissimilarity matrices into the total variance of community compositional
122 heterogeneity (Legendre and De Caceres 2013. See details in *Appendix 1*).
123 For classical metrics, we assayed the effectiveness of undersampling correction methods by
124 comparing the undersampling-corrected β -Shannon diversity (Chao *et al.* 2013; 2014) to the raw
125 normalized divergence index (Chao and Chiu 2016). We conducted this comparison because the
126 β -Shannon diversity and the normalized divergence index are exactly identical ($q = 1$) given true
127 species richness and species abundances (Chao *et al.* 2019). For the multivariate metrics, we
128 compared the total variance of the undersampling-corrected Jaccard-Chao distance matrix (Chao
129 *et al.* 2005) to the total variance of the Hellinger and Bray-Curtis distance matrices.

130 **Undersampling correction methods and the null model approach**

131 For multivariate metrics, Chao *et al.* (2005) proposed the undersampling-corrected Jaccard index
132 (Jaccard-Chao), which estimates the relative abundances of undetected shared species (see more
133 details in Appendix 2). Classical metrics are calculated based on γ - and α -diversity, and observed
134 diversity at both α - and γ -scales are constrained by undersampling bias (Chao *et al.* 2013; 2014).
135 Chao *et al.* (2013; 2014) extended the species accumulation curve (Colwell *et al.* 2012) to the
136 diversity accumulation curve, which corrects for the γ -dependence of β -Shannon diversity by
137 asymptotically estimating both true α - and γ -Shannon diversity (${}^1\hat{D}(\infty)$) of samples in a region
138 (See details of ${}^1\hat{D}(\infty)$ in *Appendix 2*).
139 As a comparison, we also examined the effectiveness of the randomization null model by
140 calculating all five null model-corrected β -diversity measures (β -deviations) (Chase and Myers

141 2011; Kraft *et al.* 2011) (see more details of null model approach in Appendix 2).

142 **Simulated metacommunities and empirical data**

143 We applied a niche-based competition model to create a total of 16200 metacommunities. These
144 metacommunities were produced under 324 simulation scenarios with nine levels of niche
145 strength from neutral to niche-structured, in combination with six levels of γ -diversity (50, 100,
146 150, 200, 300, and 400 species) and six different sample sizes (50, 100, 150, 200, 250, and 300
147 individuals per community) (See more details in *Appendix 3*), and each scenario was executed
148 for 50 replicates. We set the metacommunity scale as the γ -scale, and each community as the α -
149 scale.

150 We also downloaded Gentry's global forest dataset from SALVIAS (www.salvias.net). The dataset
151 consists of 197 sampling plots distributed from temperate to tropical forests around the world
152 (Phillips and Miller 2002). Within each plot, ten 0.01 ha (2 m \times 50 m) subplots were surveyed,
153 where all woody individuals with a diameter of breast height (DBH) ≥ 2.5 cm were identified and
154 recorded. We set the plot scale (i.e., all ten subplots) as the γ -scale, and each subplot as α -scale.

155 **Statistical analyses**

156 To compare the performance of β -metrics, we regressed the raw and undersampling-corrected
157 β -diversity metrics and their β -deviations against γ -diversity and sample size using multiple
158 linear regression. All variables were standardized before being included in the model. To assess
159 whether β -diversity metrics and their β -deviations were able to distinguish β -diversity created by
160 different simulated niche strength scenarios, we examined the significance of differences in

161 β -diversity among niche-strength scenarios. Finally, we performed an analysis of variance
162 (ANOVA) to analyze the differences of β -diversity among niche strength scenarios, followed by
163 a multiple comparisons based on Tukey's honestly significant difference (HSD) test (Tukey
164 1949). All statistical analyses were performed in R, version 3.4.1 (R Core Team 2019). The
165 Shannon diversity index and all undersampling corrections were implemented using the
166 "entropart" package (Marcon and Hérault 2015). The Hellinger, Bray-Curtis, and Jaccard-Chao
167 indices were calculated in "vegan" package (Oksanen *et al.* 2015).

168

169 **RESULTS**

170 **The effectiveness of undersampling correction methods in correcting γ -dependence**

171 Metrics for comparing β -diversity among regions are not expected to display systematic changes
172 with γ -diversity and sample size. Using simulated data, we found the corrected β -Shannon
173 diversity to be relatively insensitive to changes in γ -diversity and sample size (Fig. 1a and *Table*
174 *S1*), as the Jaccard-chao index showed much less dependence (Fig. 1d). In contrast, the
175 normalized divergence, Hellinger, and Bray-Curtis indices were strongly dependent on both (Fig.
176 1b-c, e and *Table S1*). In general, results of Gentry's datasets confirmed the results of the
177 simulation experiment (*Table S3*), except that the Jaccard-Chao index had a much stronger
178 γ -dependence than in simulated communities (*Table S1* and *S3*).

179 **Variation of β -metrics along a niche strength gradient**

180 Metrics for comparing β -diversity among regions should ideally detect the variation of

181 β -diversity across niche strength scenarios regardless of γ -diversity and sample size. Only the
182 corrected β -Shannon diversity clearly distinguished all niche strength scenarios (Fig. 2a). In
183 contrast, the Hellinger, Bray-Curtis, Jaccard-Chao, and normalized divergence indices only
184 roughly detected the differences in β -diversity between strongly niche-structured scenarios and
185 others; they were unable to distinguish between neutrally-structured metacommunities and those
186 with low and moderate niche-strength (Figs. 2b-2e, the left six groups), nor between the three
187 strongest niche-structured communities.

188 **The performance of β -metrics with a null model approach**

189 Using simulated data, the null model approach generally reduced the dependence of γ -diversity
190 and sample size for all β -metrics tested (Fig. S1). The β -deviations of the corrected β -Shannon
191 diversity and Jaccard-Chao index were only slightly sensitive to γ -diversity and sample size (Fig.
192 S1, Table S2). Compared to the raw normalized divergence, the sensitivities of the β -deviations
193 of the Hellinger and Bray-Curtis indices to γ -diversity and sample size were greatly reduced,
194 albeit non-zero (Fig. S1, Table S2). Results of empirical data showed very similar results to the
195 simulated data (Table S4), except the β -deviation of the normalized divergence index showed
196 greater γ -dependence (Table S3 and S4).

197 The β -deviations of the raw metrics and the Jaccard-Chao index showed some ability to
198 distinguish between niche strength scenarios; however, these β -deviations were incapable of
199 discriminating between neutrally- and weakly niche-structured metacommunities (Figs.
200 S2b-S2e).

201 **DISCUSSION**

202 We found that the undersampling correction method using the diversity accumulation curve
203 (Chao *et al.* 2014) was most successful at correcting γ -dependence for the β -Shannon diversity
204 and distinguishing β -diversity patterns generated from simulated ecological gradients. As a result,
205 undersampling correction methods using diversity accumulation curves are more promising tools
206 for correcting γ -dependence than current null model approaches. This increased performance is
207 likely because the undersampling correction method approximates the true β -diversity using
208 diversity accumulation curve to separately estimate mathematically independent true α - and
209 γ -diversity (Marcon *et al.* 2012; Chao *et al.* 2014). This avoids the interdependence of β - and
210 γ -diversity (Bennett and Gilbert 2016; Ulrich *et al.* 2017), and the problem of removing a real
211 trend by preserving species abundance distribution in the randomization process of the null
212 model approach (Qian *et al.* 2013; Xu *et al.* 2015). On the other hand, it is worth noting that the
213 effectiveness of specific undersampling correction methods may not be adequate to accurately
214 estimate the true diversity when sample sizes are extremely small (Chao *et al.* 2005; Chao *et al.*
215 2014). For example, Jaccard-Chao failed in reducing undersampling bias in Gentry's data caused
216 by severe sampling at both α and γ scales in Gentry's dataset with an average of 34 individual
217 trees in each subplot (Tuomisto and Ruokolainen 2012).

218 Multivariate metrics were shown to be more robust to γ -dependence than classical measures
219 because the mean α -diversity and the total diversity of each sample pair for pairwise metrics do
220 not increase with the number of sampling units (Bennett and Gilbert 2016; Marion *et al.* 2017).

221 However, our results show that multivariate metrics still suffer from γ -dependence, perhaps
222 because same-sized plots share a smaller fraction of species in higher diversity areas (Condit *et*
223 *al.* 2005).

224 β -deviations have become a popular method for comparing β -diversity among regions. However,
225 β -deviations of raw metrics also retained a degree of γ -dependence (Bennett and Gilbert 2016;
226 Ulrich *et al.* 2017), and failed to discern the β -diversity pattern along a known ecological
227 gradient (Bennett and Gilbert 2016). However, the null model approach can be integrated with a
228 wider range of β -metrics and may be more useful than undersampling correction methods when
229 the undersampling of community data is not severe (Chase and Myers 2011; Tucker *et al.* 2016).
230 Moreover, the β -deviation of the Jaccard-Chao index greatly outperformed either approach alone,
231 suggesting a complementary way to combine approaches.

232 Our results illustrate the importance of testing the robustness of β -metrics to γ -dependence with
233 simulated communities along a known gradient, as it is inadequate to examine the robustness
234 using unstructured communities randomly sampled from species pools of different sizes. In this
235 study, we found that all β -deviations of raw metrics could identify neutrally structured
236 communities ($\beta_{dev} \approx 0$, Fig. S2), but were unable to discern the variation of β -diversity along an
237 ecological gradient.

238 Taken together, we found that the undersampling correction methods using diversity
239 accumulation curves were more effective at removing γ -dependence than commonly used null
240 model approaches; in particular, the corrected β -Shannon diversity performed best. Meanwhile,

241 the null model-corrected Jaccard-Chao index may exemplify a complementary way to combine a
242 null model approach with a less effective undersampling correction method. These tools allow
243 for comparison of β -diversity along broad biogeographic or disturbance gradients with changing
244 γ -diversity. However, the reliability of different β -metrics at comparing compositional
245 differences between regions depends on other ecosystem characteristics such as species
246 abundance distribution and intraspecific aggregation (Chao and Jost 2012; Beck *et al.* 2013).
247 Other approaches remain to be examined with respect to correcting γ -dependence in future
248 studies. For example, the Simpson dissimilarity index (β_{sim}) is supposed to quantify β -diversity
249 due to true spatial turnover of species among sites without the influence of γ -diversity (Baselga
250 2010).

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257

258 **Data Availability**

259 The data and associated R code supporting the findings of this study have been uploaded as part
260 of the electronic supplementary material.

261 **Literature Cited**

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345 distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients.
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347

348 **Figure Legends:**

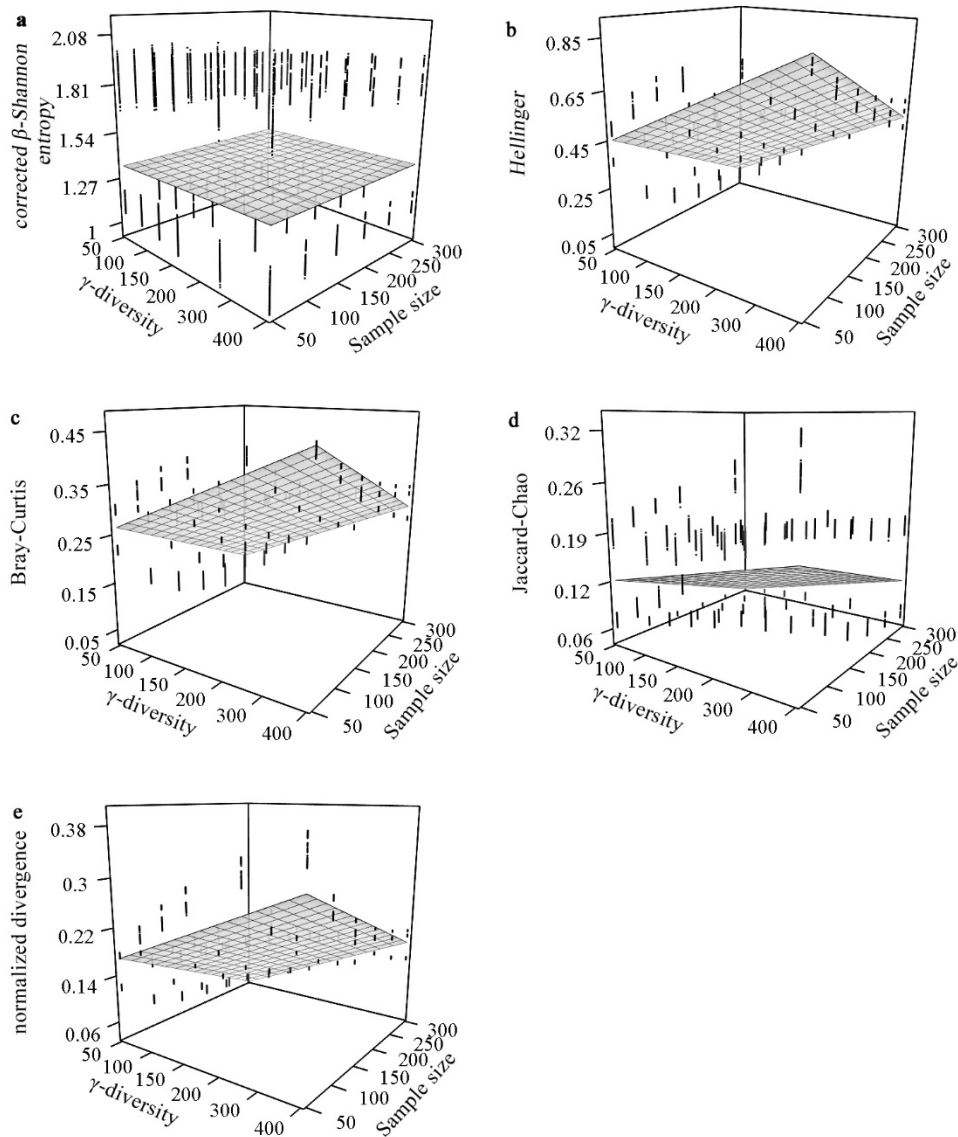
349 **Figure 1.** The sensitivity of raw and undersampling corrected β -diversity metrics to γ -diversity
350 and sample size. β -diversity was measured by a) corrected β -Shannon diversity, b) Hellinger, c)
351 Bray-Curtis, d) Jaccard-Chao index, and e) the normalized divergence index. In each panel, the
352 surface of γ -diversity and sample size was fitted using multiple linear regression (detailed model
353 parameters are listed in *Table S1*).

354

355 **Figure 2.** The variation of β -diversity metrics along a niche strength gradient. From left to right,
356 metacommunities varied from stochastically-structured to niche-structured; a) corrected
357 β -Shannon diversity, b) Hellinger, c) Bray-Curtis, d) Jaccard-Chao, and e) normalized
358 divergence indices. Different letters annotated in each panel indicate significantly different mean
359 values of different ecological scenarios.

360 Figure 1

361



362

363 **Figure 1.** The sensitivity of raw and undersampling corrected β -diversity metrics to γ -diversity

364 and sample size. β -diversity was measured by a) corrected β -Shannon diversity, b) Hellinger, c)

365 Bray-Curtis, d) Jaccard-Chao index, and e) the normalized divergence index. In each panel, the

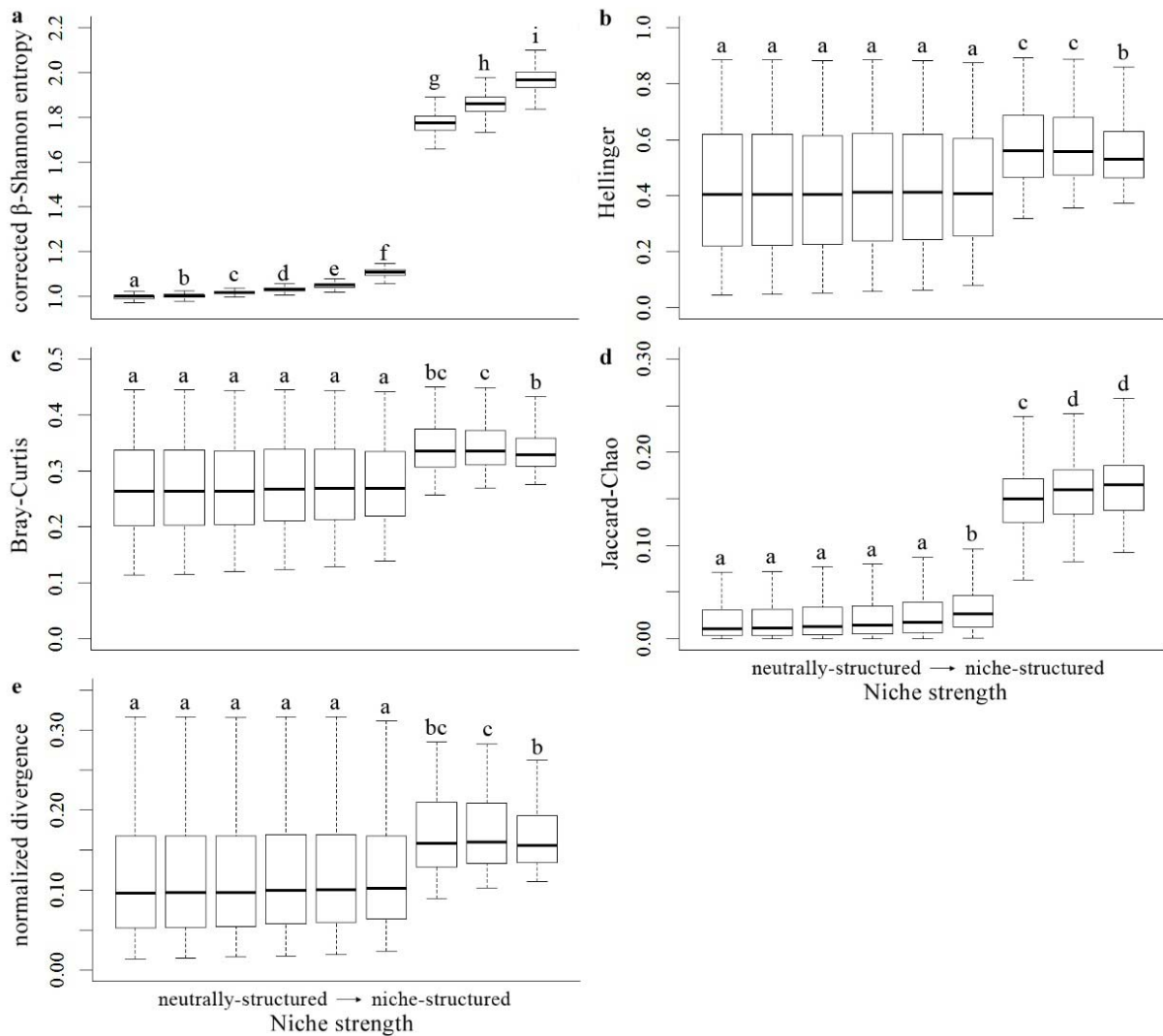
366 surface of γ -diversity and sample size was fitted using multiple linear regression (detailed model

367 parameters are listed in *Table S1*).

368

369

370 Figure 2.



371

372 **Figure 2.** The variation of β -diversity metrics along a niche strength gradient. From left to right,
373 metacommunities varied from stochastically-structured to niche-structured; a) corrected
374 β -Shannon diversity, b) Hellinger, c) Bray-Curtis, d) Jaccard-Chao, and e) normalized
375 divergence indices. Different letters annotated in each panel indicate significantly different mean
376 values of different ecological scenarios.

377 **Table S1.** The sensitivity of different β -metrics to γ -diversity and sample size based on simulated
 378 data. The standardized coefficients are standardized regression coefficients of multiple linear
 379 regression models.

β-metrics	explanatory variables	Standardized coefficients	Standard Error	t value	P(> t)	R-square	AIC
corrected	γ -diversity	0.017	0.0079	2.17	0.030		
β-Shannon diversity	sample size	0.012	0.0079	1.49	0.14	0.00043	45973.65
Hellinger	γ -diversity	0.67	0.0036	184.3	<0.001	0.79	20779.97
	sample size	-0.59	0.0036	-163.1	<0.001		
Bray-Curtis	γ -diversity	0.63	0.0042	152.35	<0.001	0.72	25379.46
	sample size	-0.56	0.0042	-135.6	<0.001		
Jaccard-Chao	γ -diversity	0.31	0.0067	45.88	<0.001	0.26	41039.71
	sample size	-0.41	0.0067	-60.61	<0.001		
normalized	γ -diversity	0.63	0.0038	165.51	<0.001	0.77	22494.81
divergence	sample size	-0.61	0.0038	-159.6	<0.001		

380

381

382 **Table S2.** The sensitivity of different β -deviations (the deviation between the observed and
 383 null-expected β -diversity) to γ -diversity and sample size based on simulated communities. In
 384 each model, explanatory variables include γ -diversity and sample size. The standardized
 385 coefficients are standardized regression coefficients of multiple linear regression models.

β -deviations	explanatory variables	Standardized coefficients	Standard Error	t value	P(> t)	R-square	AIC
corrected	γ -diversity	0.031	0.0079	3.98	<0.001		
	sample size	-0.026	0.0079	-3.27	0.0011	0.0016	45977.76
β-Shannon diversity	γ -diversity	-0.282	0.0073	38.63	<0.001		
	sample size	0.239	0.0073	32.70	<0.001	0.14	43600.11
Hellinger	γ -diversity	-0.286	0.0073	39.27	<0.001		
	sample size	0.242	0.0073	33.24	<0.001	0.14	43526.36
Bray-Curtis	γ -diversity	0.047	0.0079	5.98	<0.001		
	sample size	-0.014	0.0079	-1.80	0.073	0.0024	45941.74
Jaccard-Chao	γ -diversity	-0.185	0.0076	24.32	<0.001		
	sample size	0.170	0.0076	22.39	<0.001	0.063	44921.34
normalized divergence	γ -diversity						
	sample size						

386 **Table S3.** The sensitivity of β -metrics to γ -diversity and sample size based on
 387 Gentry's global forest dataset. The standardized coefficients are standardized
 388 regression coefficients of multiple linear regression models.

β-metrics	explanatory variables	Standardized coefficients	Standard Error	t value	P(> t)	R-square	AIC
corrected	γ -diversity	0.44	0.079	5.66	<0.001		
β-Shannon diversity	sample size	-0.094	0.079	-1.20	0.23	0.16	531.53
Hellinger	γ -diversity	1.00	0.043	23.00	<0.001	0.74	298.28
	sample size	-0.34	0.043	-7.74	<0.001		
Bray-Curtis	γ -diversity	0.96	0.049	19.55	<0.001	0.67	345.05
	sample size	-0.34	0.049	-7.00	<0.001		
Jaccard-Chao	γ -diversity	0.95	0.052	18.15	<0.001	0.63	370.60
	sample size	-0.52	0.052	-9.88	<0.001		
normalized divergence	γ -diversity	-0.36	0.063	-5.71	<0.001	0.46	443.35
	sample size	-0.41	0.063	-6.60	<0.001		

389

390

391 **Table S4.** The sensitivity of different β -deviations (the deviation between the
 392 observed and null-expected β -diversity) to γ -diversity and sample size based on
 393 Gentry's global forest dataset. The standardized coefficients are standardized
 394 regression coefficients of multiple linear regression models.

β-deviations	explanatory variables	Standardized coefficients	Standard error	t value	P(> t)	R-square	AIC
corrected	γ -diversity	0.15	0.084	1.79	0.074		
β-Shannon diversity	sample size	0.040	0.084	0.48	0.63	0.031	559.80
Hellinger	γ -diversity	-0.69	0.070	-9.87	<0.001	0.34	484.81
	sample size	0.30	0.070	4.31	<0.001		
Bray-Curtis	γ -diversity	-0.73	0.067	-10.83	<0.001	0.38	471.48
	sample size	0.31	0.067	4.65	<0.001		
Jaccard-Chao	γ -diversity	-0.20	0.085	-2.41	0.017	0.029	560.22
	sample size	0.10	0.085	1.19	0.23		
normalized	γ -diversity	-1.03	0.0031	-33.22	<0.001	0.87	166.51
divergence	sample size	0.22	0.0031	7.06	<0.001		

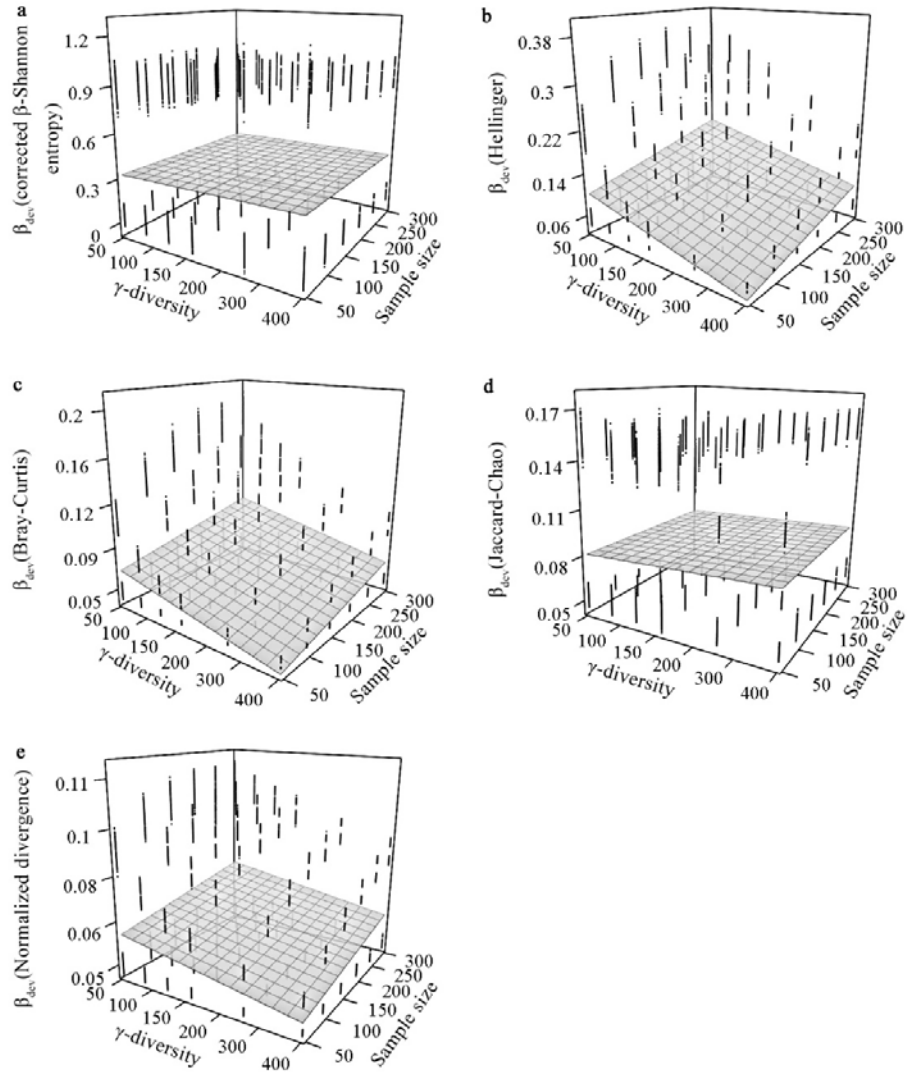
395

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397

398

399 Fig. S1



400

401 **Figure S1.** The sensitivity of β -deviation (β_{dev}) to γ -diversity and sample size.

402 β -diversity was measured by a) corrected β -Shannon diversity, b) Hellinger, c)

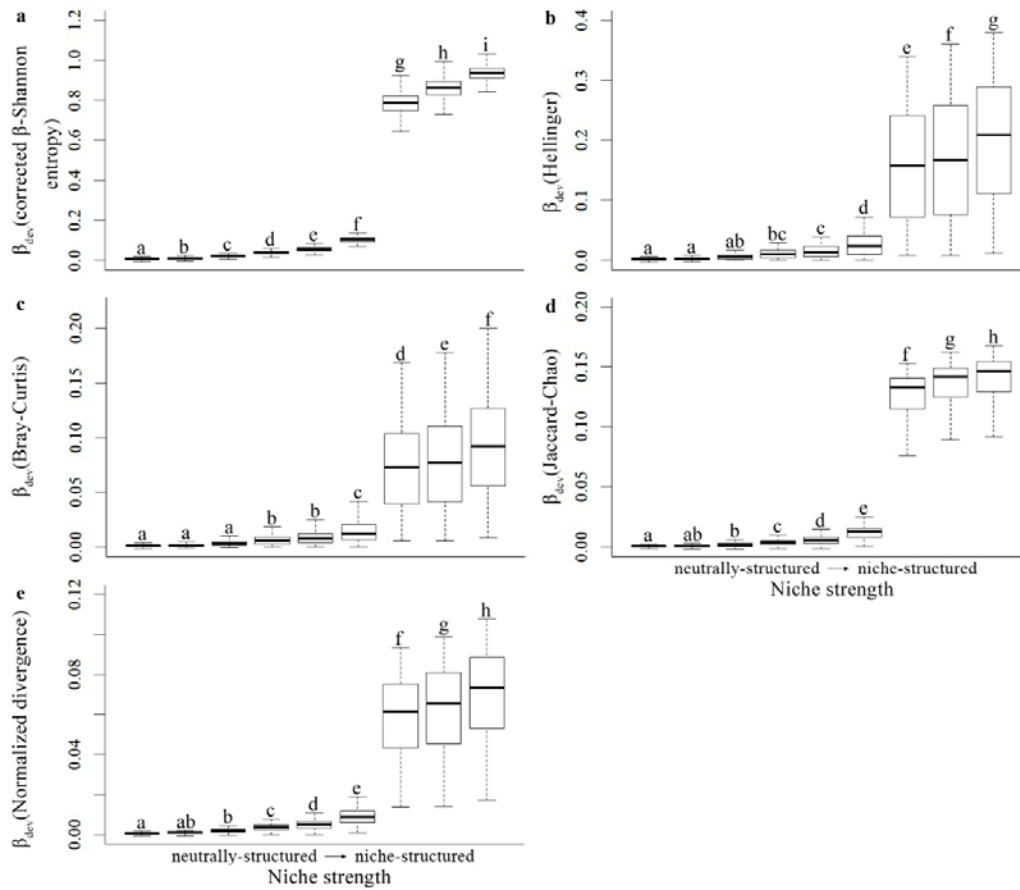
403 Bray-Curtis, d) Jaccard-Chao, and e) the normalized divergence indices. In each panel,

404 the surface of γ -diversity and sample size was fitted using multiple linear regression

405 (detailed model parameters given in *Table S2*).

406

407 Fig. S2



408

409 **Figure S2.** The variation of β -deviations (β_{dev}) along a niche strength gradient. From
410 left to right, metacommunities varied from stochastically to niche-structured; a)
411 corrected β -Shannon diversity, b) Hellinger, c) Bray-Curtis, d) Jaccard-Chao, and e)
412 the normalized divergence indices. The different letters annotated in each panel
413 indicate significantly different mean values of different ecological scenarios.

414 **Supporting information**

415

416 **Appendix 1. Five abundance-based β -metrics and their properties**

417 1) *Corrected β -Shannon diversity* (Jost 2007). β -Shannon diversity partitions

418 γ -diversity into mathematically independent α - and β -diversity components as

419 follows:

420
$${}^q D_\alpha = \left(\frac{1}{N} \sum_{i=1}^S p_{i1}^q + \frac{1}{N} \sum_{i=1}^S p_{i2}^q + \dots + \frac{1}{N} \sum_{i=1}^S p_{iN}^q \right)^{1/(1-q)} \quad (1)$$

421
$${}^q D_\gamma = \left\{ \sum_{i=1}^S \left[\frac{1}{N} (p_{i1} + p_{i2} + \dots + p_{iN}) \right]^q \right\}^{1/(1-q)} \quad (2)$$

422
$${}^q D_\beta = {}^q D_\gamma / {}^q D_\alpha \quad (3)$$

423 where ${}^q D_\alpha$, ${}^q D_\beta$, and ${}^q D_\gamma$ are the q -th order α , β , and γ diversity, respectively; p_i is

424 the proportional abundance of species I ; S and N are the total number of species and

425 the total number of local communities (or plots), respectively, in the regional

426 community. β -Shannon diversity is a standard abundance-sensitive measure that

427 weights species in proportion to abundance according to diversity order q ; when $q = 0$,

428 D is equivalent to species richness. For increasing q , abundant species are given

429 progressively more weight. Here we took $q = 1$ to weight all species by their

430 abundance, without favoring either common or rare species. β -Shannon diversity

431 quantifies β -diversity as the effective number of equally large and completely distinct

432 communities, ranging from 1 to N (N is the number of local communities) (Jost 2007;

433 Tuomisto 2010). We also incorporated undersampling correction methods with

434 β -Shannon diversity for correcting γ -dependence (Chao *et al.* 2013; 2014).

435 2) *Normalized divergence* (Chao and Chiu 2016). The normalized divergence unifies
 436 two major measures of β -diversity: the total variance of community species
 437 abundance matrix and diversity decomposition. The formulae are as follows:

$$438 \quad {}^q D_\gamma = \begin{cases} \left[\sum_{i=1}^S \left(\frac{z_{i+}}{z_{++}} \right)^q \right]^{1/(1-q)} & q \geq 0, q \neq 1, \\ \exp \left[- \sum_{i=1}^S \left(\frac{z_{i+}}{z_{++}} \right) \log \left(\frac{z_{i+}}{z_{++}} \right) \right] & q = 1; \end{cases} \quad (4)$$

$$439 \quad {}^q D_\alpha = \begin{cases} \frac{1}{N} \left[\sum_{i=1}^S \left(\frac{z_{i1}}{z_{++}} \right)^q + \left(\frac{z_{i2}}{z_{++}} \right)^q + \dots + \left(\frac{z_{iN}}{z_{++}} \right)^q \right]^{1/(1-q)} & q \geq 0, q \neq 1 \\ \exp \left\{ - \left[\sum_{i=1}^S \left(\frac{z_{i1}}{z_{++}} \right) + \sum_{i=1}^S \left(\frac{z_{i2}}{z_{++}} \right) + \dots + \sum_{i=1}^S \left(\frac{z_{iN}}{z_{++}} \right) \right] - \log N \right\} & q = 1; \end{cases} \quad (5)$$

440 where z_i is the abundance of the i -th species in a local community, z_{i+} and z_{++} are the
 441 total abundances of the i -th species and of all species, respectively, in the regional
 442 community (Chao and Chiu 2016). Normalized divergence is calculated as the ratio
 443 of ${}^q D_\gamma$ (equation 8) and ${}^q D_\alpha$ (equation 9). Focusing on abundance-based measures,
 444 we took the value of diversity order $q=1$ for equal weight of rare and common species
 445 in this study, which is identical to β -Shannon diversity given true species richness and
 446 species abundance (Chao *et al.* 2019). Theoretically, normalized divergence uses a
 447 novel normalization method to transform the maximum value for completely distinct
 448 communities to 1, and removes these mathematical constraints by α , γ , and total
 449 abundance (Chao and Chiu 2016). However, it remains untested whether normalized
 450 divergence is robust to undersampling bias in empirical studies.

451 3) *Jaccard-Chao* (Chao *et al.*, 2006). Jaccard-Chao, D_J , is an abundance-based
 452 version of the classic Jaccard index. The equation for D_J takes the form:

$$453 \quad D_J = \frac{uv}{u+v-uv} \quad (6)$$

454 where U and V are the total relative abundances of individuals belonging to the shared
455 species between two communities in community 1 and 2, respectively. Importantly,
456 this index is mathematically independent of γ -diversity (Property 7 and 10 in Table 2
457 of Legendre and De Caceres 2013). Moreover, Jaccard-Chao corrects undersampling
458 by incorporating undetected species into U , V —significantly reducing undersampling
459 bias (Chao *et al.* 2005) (See more details regarding undersampling correction method
460 for Jaccard-Chao in Appendix 2).

461 4) *Bray-Curtis* (Bray and Curtis 1957) and *Hellinger* (Rao 1995; Chao *et al.* 2015).
462 The abundance-based Hellinger (D_H) and Bray-Curtis (D_{BC}) indices are widely used
463 pairwise dissimilarity measures of β -diversity. They are calculated as:

$$464 \quad D_H = \sqrt{\sum_{i=1}^S \left(\sqrt{\frac{z_{1i}}{z_{1+}}} - \sqrt{\frac{z_{2i}}{z_{2+}}} \right)^2} \quad (7)$$

$$465 \quad D_{BC} = \frac{\sum_{i=1}^S |z_{1i} - z_{2i}|}{z_{1+} + z_{2+}} \quad (8)$$

466 where z_{1i} and z_{2i} are the abundances of i -th species in community 1 and 2, while z_{1+}
467 and z_{2+} are total abundances of community 1 and 2, respectively. The multivariate
468 pairwise dissimilarity metrics, based on distance or dissimilarity matrices, quantify
469 the average compositional dissimilarity across all pairs of samples in the study area.
470 Moreover, both the Hellinger and the Bray-Curtis indices have the desirable property
471 of being mathematically unrelated to γ -diversity (Table 6.2 in Jost *et al.* 2011;
472 Property 7 and 10 in Table 2 of Legendre and De Caceres 2013). However, no
473 undersampling correction methods are incorporated into either of the two metrics.
474 We were especially interested in comparing β -diversity across multiple communities.
475 Thus, we transformed the pairwise dissimilarity matrices quantified by Jaccard-Chao,

476 Hellinger, and Bray-Curtis distance matrices into the total variance of community
477 compositional heterogeneity as:

$$478 \quad BD_{total} = \frac{1}{N} \sum_{h=1}^{N-1} \sum_{i=1}^N D_{hi}^2 \quad (9)$$

479 where D_{hi} is the pairwise dissimilarity value of i -th and h -th position in the
480 subdiagonal dissimilarity matrix (Legendre and De Caceres 2013). The total variance
481 of the transformed data matrix is mathematically unrelated to γ -diversity and total
482 abundance (Legendre and De Caceres 2013; Chao and Chiu 2016).

483

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520

521 **Appendix 2. Undersampling correction methods and the null model approach**

522

523 **Undersampling correction method for β -Shannon diversity**

524 Chao *et al.* (2013; 2014) extended the species accumulation curve (Colwell *et al.* 2012)

525 to the diversity accumulation curve, which corrects for the γ -dependence of

526 β -diversity by asymptotically estimating the true α - and γ -Shannon diversity (${}^1\hat{D}(\infty)$)

527 of samples in a region. The ${}^1\hat{D}(\infty)$ ($q=1$, q is the diversity order) is calculated as:

528
$${}^1\hat{D}(\infty) = \exp[\hat{H}(\infty)] \quad (1)$$

529 $\hat{H}(\infty)$ is a nearly unbiased estimator of Shannon entropy (Chao *et al.* 2013):

$$\hat{H}(\infty) = \sum_{k=1}^{n-1} \frac{1}{k} \sum_{1 \leq X_i \leq n-1} \frac{X_i}{n} \frac{\binom{n-X_i}{k}}{\binom{n-1}{k}} + \frac{f_1}{n} (1-A)^{-n+1} \left\{ -\log(A) - \sum_{r=1}^{n-1} \frac{1}{r} (1-A)^r \right\}$$

530 (2)

531 where X_i is the species frequency of species i , k is the size of a random sample from

532 the observed community, f_1 is the number of singletons (i.e., species represented by

533 only one individual in the observed sample), and f_2 is the number of doubletons (i.e.,

534 species represented by only two individuals in the observed sample). A is the

535 estimated mean relative frequency of the singletons in the sample:

536
$$A = 2f_2 / [(n-1)f_1 + 2f_2] \quad (3)$$

537

538 **Undersampling correction method for Jaccard-Chao**

539 Chao *et al.* (2005) also proposed the undersampling-corrected Jaccard index

540 (Jaccard-Chao), which estimates the relative abundances of undetected shared species.

541 The equation for Jaccard-Chao takes the form:

$$542 \quad D_J = \frac{UV}{U+V-UV} \quad (4)$$

543 where U and V are the total relative abundances of individuals belonging to the shared
544 species between two communities in community 1 and 2, respectively. The

545 Jaccard-Chao index seeks to correct undersampling by incorporating undetected

546 species into U and V (Chao *et al.* 2005). Specifically, the adjustment of U and V are:

$$547 \quad \hat{U} = \sum_{i=1}^{D_{12}} \frac{X_i}{n} + \frac{(m-1)}{m} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{X_i}{n} I(Y_i = 1) \quad (5)$$

$$548 \quad \hat{V} = \sum_{i=1}^{D_{12}} \frac{Y_i}{m} + \frac{(n-1)}{n} \frac{f_{1+}}{2f_{2+}} \sum_{i=1}^{D_{12}} \frac{Y_i}{m} I(X_i = 1) \quad (6)$$

549 where X_i and Y_i are the numbers of individuals for the shared species i in

550 communities 1 and 2, and m and n are the total abundances of all species in

551 communities 1 and 2. D_{12} is the number of shared species that are observed in both

552 communities; f_{+1} and f_{+2} are the observed numbers of shared species that are

553 singletons and doubletons in community 2, while f_{1+} and f_{2+} are the observed

554 numbers of shared species that are singletons and doubletons in community 1. Finally,

555 $I(Y_i=1)$ is an indicator function, such that $I = 1$ when the shared species i is a

556 singleton species in community 2 but may have any abundance greater than 0 in

557 community 1, and $I = 0$ when the shared species i is not a singleton species in

558 community 2; it also works for $I(X_i=1)$.

559

560 **Randomization null model and β -deviation**

561 The individual-based randomization null model approach simulates the effect of

562 γ -dependence on β -diversity by randomly shuffling individual subplots of each plot
563 (or among communities of each metacommunity in simulated data), while preserving
564 the observed γ -diversity, the relative abundance of each species, and the number of
565 stems in each subplot (Chase and Myers 2011; Kraft *et al.* 2011). We used 999
566 randomizations for each analysis. This method results in a β -deviation, indicating the
567 difference in magnitude between the observed and expected β -diversity values (Chase
568 and Myers 2011; Kraft *et al.* 2011). β -deviation values close to zero can be interpreted
569 as stochastic assembly of communities, indicating the absence of deterministic
570 processes, while those deviating from zero indicate that deterministic processes—such
571 as habitat filtering or competitive interactions—cause patches to be more dissimilar
572 than expected by chance (Chase and Myers 2011; Kraft *et al.* 2011).

573

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593

594 **Appendix 3. Simulating metacommunities from strongly deterministic to**
595 **relatively stochastic structure**

596

597 To examine the robustness of β -metrics to γ -dependence in scenarios with strongly
598 deterministic to relatively stochastic structures, we used a niche-based simulation
599 model to generate the simulated metacommunities. The simulation models were
600 constructed as follows:

601 1) We created a landscape of contiguous 20×20 subplots, in which each subplot
602 represents a local community with adult trees selected from the species pool.

603 2) We generated two environmental variables (E) using an unconditional
604 geo-statistical model, which was simply an application of the general Monte Carlo
605 technique whereby values were generated by a particular variogram without
606 constraints of real data (Webster and Oliver 2007). This technique allowed us to
607 generate two environmental variables with known autocorrelation. That is, two
608 arbitrary spherical semivariogram models with different ranges of autocorrelation,
609 sill (sampled variance of a simulated environmental variable), and nugget (the local
610 variation occurring at scales finer than the sampling interval) components to
611 represent two environmental heterogeneity levels (Webster and Oliver 2007). The
612 simulation of the environmental landscape was implemented using the R package
613 'gstat' (Pebesma 2004).

614 3) We created multiple simulation scenarios with the combination of different
615 levels of γ -diversity, sample size, niche breadth (i.e., the environmental range that a

616 particular species can tolerate), and niche position (i.e., the optimal environmental
617 condition for a particular species) (Devictor *et al.* 2010). Subplots contained
618 combinations of six levels of γ -diversity (50, 100, 150, 200, 300, and 400 species)
619 and sample size (50, 100, 150, 200, 250, and 300 individuals). Recruitment dynamics
620 were modeled as a lottery process, with species-specific survival probabilities
621 determined based on niche breadth and niche position. By changing the combination
622 of niche breadth and niche position, we simulated multiple metacomunities that
623 varied in the degree to which deterministic versus stochastic processes were
624 relatively important in response to an environmental gradient.

625 In each scenario, all species were assigned with the same level of niche breadth but
626 different niche positions (Tucker *et al.* 2016). Specifically, niche breadth (σ) was set
627 equal for all species at three arbitrary levels (narrow: $\sigma=0.1$, medium: $\sigma=0.3$, and
628 wide: $\sigma=0.5$) for each species, where higher values confer larger ranges of species'
629 requirements in terms of habitat conditions (Gravel *et al.* 2006). Each species had a
630 unique niche optimum (μ) and niche position, which were set to follow a β
631 distribution that was symmetrically distributed around the mean habitat of the
632 simulated metacommunity (Gravel *et al.* 2006). The β distribution is parameterized
633 by two positive shape parameters, which control the shape of the distribution
634 (skewness and kurtosis), denoted by α and β (not to be confused with α - and
635 β -diversity) (Forbes *et al.* 2011). We set α and β to be equal to maintain symmetric
636 distributions of niche positions. Like niche breadth, the aggregation of niche
637 positions along the environmental axis was set at three levels by varying the kurtosis

638 of the beta distribution (uniform aggregation: 2, moderate aggregation: 6, and high
639 aggregation: 10) of shape parameters (α and β), correspondingly. This resulted in
640 species distributed around the mean environmental habitats of a community with
641 uniform, moderate, and high aggregation. For each scenario, we simulated 50
642 replicates.

643 4) In the simple niche-based competition model, we assumed that each species
644 could reach all suitable subplots, and the interspecific inequality of competitive
645 ability between species was mainly determined by the survival probabilities along the
646 environmental gradient (Gravel *et al.* 2006). The survival rate of species i in each
647 subplot was:

$$648 \quad S_i(E) \propto \exp\left(\frac{-(E-o_i)^2}{2\sigma_i^2}\right) \quad (1)$$

649 where E is the environmental value in each subplot, o_i is the niche position of species
650 i , and σ_i is the fundamental niche breadth of species i .

651 By changing the combination of niche breadth and niche position, we simulated
652 multiple metacomunities that varied in the degree to which deterministic versus
653 stochastic processes influenced the responses to an environmental gradient.

654 Metacomunities derived from deterministic processes arose when species were
655 evenly distributed (i.e., uniform niche position) around the mean habitat condition
656 and had a narrow niche breadth. Under this scenario, species had the largest
657 interspecific differences in survival rate within each habitat, and competitive
658 exclusion was strong. In contrast, stochastically assembled metacomunities arose
659 when species were highly aggregated (i.e., aggregated niche positions) around the

660 mean habitat conditions, and had a wide niche breadth. Under this scenario, all
661 species had roughly the same competitive capability and survival rate across habitats
662 (Gravel *et al.*, 2006).

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