

1 In press, **Ecology**, “Concepts and Synthesis” section

2
3 ***Partitioning diversity into independent alpha and beta***
4 ***components***

5
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8
9 **Abstract**

10
11 Existing general definitions of beta diversity often produce a beta with a hidden
12 dependence on alpha. Such a beta cannot be used to compare regions that differ in alpha
13 diversity. To avoid misinterpretation, existing definitions of alpha and beta must be
14 replaced by a definition which partitions diversity into independent alpha and beta
15 components. The unique such definition is derived here. When these new alpha and beta
16 components are transformed into their numbers equivalents (effective numbers of
17 elements), Whittaker’s multiplicative law ($\alpha \cdot \beta = \gamma$) is necessarily true for
18 all indices. The new beta gives the effective number of distinct communities. The most
19 popular similarity and overlap measures of ecology (Jaccard, Sorensen, Horn, and
20 Morisita-Horn indices) are monotonic transformations of the new beta diversity. Shannon
21 measures follow deductively from this formalism and do not need to be borrowed from
22 information theory; they are shown to be the only standard diversity measures which can
23 be decomposed into meaningful independent alpha and beta components when
24 community weights are unequal.

25
26 **Keywords:** Diversity, alpha, beta, gamma, Shannon, partition, independent, Horn,
27 Morisita-Horn

28
29
30 **1. Introduction**

31
32 Alpha, beta, and gamma diversities are among the fundamental descriptive variables of
33 ecology and conservation biology, but their quantitative definition has been controversial.
34 Traditionally alpha, beta, and gamma diversities have been related either by the additive
35 definition $H_\alpha + H_\beta = H_\gamma$ or the multiplicative definition $H_\alpha \cdot H_\beta = H_\gamma$. However, when these
36 definitions are applied to most diversity indices, they produce a beta which depends on
37 alpha. This hidden dependence on alpha can lead to spurious results when researchers
38 compare beta values of regions with different alpha diversities.

39
40 For example, suppose an ecologist applies the additive definition of beta to the Gini-
41 Simpson index (Lande 1996, Veech et al. 2002, Keylock 2005) to calculate the beta
42 diversity of two samples of flowering plants from the antarctic tundra. The only
43 flowering plants in Antarctica are *Colobanthus quitensis* and *Deschampsia antarctica*. In
44 the first tundra sample (a 50 hectare plot) the proportions might be 60% *C. quitensis*,
45 40% *D. antarctica*. In the second tundra sample (another 50 ha plot), the proportions

46 might be 80% *C. quitensis* and 20% *D. antarctica*. Ecologists would agree that these
47 samples, which share all their species and differ only slightly in species frequencies,
48 should exhibit a relatively low beta diversity. The beta diversity is 0.021 according to the
49 additive definition used with the Gini-Simpson index.

50
51 Now the same ecologist wants to compare this beta diversity to the beta diversity of the
52 trees >1cm diameter of two tropical rainforest 50 ha plots, one from Panama (Barro
53 Colorado Island; Condit et al.2005) and one from Malaysia (Pasoh; He 2005 and pers.
54 com., Gimaret-Carpentier et al.1998). These rainforest plots are on different continents
55 and share no species of trees, and ecologists would agree that these samples should
56 exhibit considerably higher beta diversity (as this term is used in theoretical discussions)
57 than the homogeneous antarctic samples. However, the alpha Gini-Simpson index is
58 0.9721 and the gamma Gini-Simpson index is 0.9861; the beta diversity is $0.9861 -$
59 $0.9721 = 0.014$. This value of beta is 33% *lower* than the antarctic beta diversity. The
60 additive beta definition fails to rank these data sets correctly because the beta it produces
61 is confounded with alpha. (When diversity is high, Gini-Simpson alpha and gamma both
62 approach unity. Therefore if beta is defined as gamma minus alpha, beta must approach
63 zero whenever alpha diversity is high, regardless of the turnover between samples.) The
64 multiplicative definition also fails for many indices, for the same reason.

65
66 If beta diversity is to behave as ecologists expect, we must develop a new general
67 expression relating alpha, beta, and gamma, and the new expression must ensure that beta
68 is free to vary independently of alpha. In fact, this requirement and ecologists' other
69 requirements for an intuitive measure of beta are sufficiently strong that they can be taken
70 as axioms, and a new general mathematical expression relating alpha, beta, and gamma
71 can be logically derived from these axioms. This approach ensures that beta behaves as
72 ecologists expect and measures what ecologists really want to measure. By removing the
73 hidden alpha dependence often produced by the old definitions of beta, the new
74 expression opens the way for researchers to focus on biologically meaningful aspects of
75 beta. The new method of partitioning, derived directly from biologists' requirements,
76 gives results that agree with standard practice in information theory and physics, and
77 leads to a unified mathematical framework not only for diversity measures but also for
78 ecology's most popular similarity and overlap measures. The Sorensen, Jaccard,
79 Morisita-Horn, and Horn indices all turn out to be simple monotonic transformations of
80 the new beta diversity.

81

82

83 **2. Basic properties of intuitive alpha and beta**

84

85 There is general agreement that alpha and beta should have the following properties,
86 which I take as axioms in the derivations which follow:

87

88 **1. Alpha and beta should be free to vary independently; a high value of the alpha**
89 **component should not, by itself, force the beta component to be high (or low), and**
90 **vice versa.** Alpha and beta decompose regional diversity into two *orthogonal*
91 components: a measure of average single-location (or single-community) diversity and a

92 measure of the relative change in species composition between locations (or
93 communities). Since these components measure completely different aspects of regional
94 diversity, they must be free to vary independently; alpha should not put mathematical
95 constraints on the possible values of beta, and vice-versa. If beta depended on alpha, it
96 would be impossible to compare beta diversities of regions whose alpha diversities
97 differed. Wilson and Shmida (1984) were the first to make this an explicit requirement
98 for beta.

99

100 **2. A given number should denote the same amount of diversity or uncertainty**
101 **whether it comes from the alpha component, the beta component, or the gamma**
102 **component, so that a diversity index could be meaningfully partitioned into within-**
103 **community and among-community components.** Lande (1996) made explicit this
104 useful property of beta, which is closely related to Property 1.

105

106 **3. Alpha is some type of average of the diversity indices of the communities or**
107 **samples that make up the region.** To avoid imposing any preconceptions on the kind of
108 average to use, I make only the minimal assumption that if the diversity index has the
109 same value H_0 for all communities in a region, then alpha must also equal H_0 .

110

111 **4. Gamma must be completely determined by alpha and beta.** I make no assumption
112 about *how* alpha and beta determine gamma.

113

114 **5. Alpha can never be greater than gamma.** Lande (1996), following Lewontin (1972),
115 pointed out that the partitioning of gamma into alpha and beta only makes sense if alpha
116 were always less than or equal to gamma for a given diversity index. From the viewpoint
117 of information theory, this property is a reasonable one. Most diversity indices may be
118 considered generalized measures of uncertainty (Taneja 1989, Keylock 2005), and alpha
119 may be considered the conditional uncertainty in species identity given that we know the
120 location sampled. Gamma is the uncertainty in species identity when we do not know the
121 location sampled. Knowledge can never increase uncertainty, so alpha can never be
122 greater than gamma.

123

124 These five relatively uncontroversial properties are strong enough to completely
125 determine the new general index-independent expression which defines beta. This in turn
126 permits the derivation of explicit expressions for alpha and beta for almost any diversity
127 index. To develop this new picture of alpha and beta diversity, it is necessary to deal with
128 diversity indices in a more general way than is customary. The next section provides the
129 vocabulary and tools needed for this.

130

131

132 **3. The “numbers equivalents” of diversity indices**

133

134 The mathematical tool that permits the derivation of a general definition of beta is the
135 concept of the “numbers equivalent” or “effective number of elements” of a diversity
136 index. The concept is often used in economics (where the term originated; Adelman
137 1969, Patil and Taillee 1982) and physics (where it is called the “number of states”), but

138 since it is unfamiliar to many ecologists it will be briefly reviewed here.

139

140 The numbers equivalent of a diversity index is the number of equally-likely elements
 141 needed to produce the given value of the diversity index. Hill (1973) and Jost (2006)
 142 showed that the notion of diversity in ecology corresponds not to the value of the
 143 diversity index itself but to its numbers equivalent. (The derivations in the following
 144 sections do not depend on this interpretation of the numbers equivalent as the true
 145 diversity; the skeptical reader may treat numbers equivalents merely as useful
 146 mathematical tools for deriving the alpha, beta, and gamma components of traditional
 147 diversity indices.)

148

149 To see the contrast between a raw index and its numbers equivalent, suppose a continent
 150 with 30 million equally common species is hit by a plague that kills half the species. How
 151 do some popular diversity indices judge this drop in diversity? Species richness drops
 152 from thirty million to fifteen million; according to this index the post-plague continent
 153 has half the diversity it had before the plague. This accords well with our biological
 154 intuition about the magnitude of the drop. However, the Shannon entropy only drops
 155 from 17.2 to 16.5; according to this index the plague caused a drop of only 4% in the
 156 “diversity” of the continent. This does not agree well with our intuition that the loss of
 157 half the species and half the individuals is a large drop in diversity. The Gini-Simpson
 158 index drops from 0.99999997 to 0.99999993; if this index is equated with “diversity”, the
 159 continent has lost practically no “diversity” when half its species and individuals
 160 disappeared.

161

162 Converting the diversity indices in the preceding paragraph to their numbers equivalents
 163 makes them all behave as biologists would intuitively expect of a diversity. (See Table 1
 164 for the conversion formulas.) Species richness is its own numbers equivalent, so the
 165 numbers equivalent of species richness drops by 50% when the plague kills half the
 166 continent’s species. The Shannon entropy is converted to its numbers equivalent by
 167 taking its exponential (MacArthur 1965); this gives a post-plague to pre-plague diversity
 168 ratio of $\exp(16.5)/\exp(17.2)$ which is exactly 50%, compared to the counterintuitive drop
 169 of 4% shown by the raw index. The Gini-Simpson index is converted to its numbers
 170 equivalent by subtracting from unity and taking the reciprocal (Jost 2006); this gives a
 171 post-plague to pre-plague diversity ratio of $[1/(1 - 0.99999993)]/[1/(1 - 0.99999997)] =$
 172 50% , again the intuitive number rather than the 0.000003% shown by the ratio of the raw
 173 indices. This example does not depend on all the species being equally common; if these
 174 30 million species had any smoothly varying frequency distribution, and half the species
 175 were randomly deleted, the numbers equivalents of these diversity indices would still
 176 drop by approximately half.

177

178 **Table 1.** Conversion of common indices to true diversities (modified from Jost 2006).

179

180

Index H:	Diversity in terms of H:	Diversity in terms of p_i :
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182

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183	Species richness $H \equiv \sum_{i=1}^S p_i^0$	H	$\sum_{i=1}^S p_i^0$
184			
185	Shannon entropy $H \equiv -\sum_{i=1}^S p_i \ln p_i$	$\exp(H)$	$\exp(-\sum_{i=1}^S p_i \ln p_i)$
186			
187	Simpson concentration $H \equiv \sum_{i=1}^S p_i^2$	1/H	$1/\sum_{i=1}^S p_i^2$
188			
189			
190	Gini-Simpson index $H \equiv 1 - \sum_{i=1}^S p_i^2$	1/(1-H)	$1/\sum_{i=1}^S p_i^2$
191			
192	HCDT entropy $H \equiv (1 - \sum_{i=1}^S p_i^q)/(q-1)$	$[(1 - (q-1)H)]^{1/(1-q)}$	$(\sum_{i=1}^S p_i^q)^{1/(1-q)}$
193			
194	Renyi entropy $H \equiv (-\ln \sum_{i=1}^S p_i^q)/(q-1)$	$\exp(H)$	$(\sum_{i=1}^S p_i^q)^{1/(1-q)}$

195
196

197 The numbers equivalents of all standard diversity indices behave in this intuitive way
 198 because they all have the “doubling” property (Hill 1973): if two equally large,
 199 completely distinct communities (no shared species) each have diversity X, and if these
 200 communities are combined, then the diversity of the combined communities should be
 201 2X. This natural semi-additive property is at the core of the intuitive ecological concept
 202 of diversity. Most raw diversity indices do not obey this property, but their numbers
 203 equivalents do. It is also this property which makes ratios of numbers equivalents behave
 204 reasonably (in sharp contrast to ratios of most raw diversity indices; see Jost 2006).

205

206 Some new notation and definitions are needed to work efficiently with numbers
 207 equivalents. Almost all diversity indices used in the sciences -- species richness,
 208 Shannon entropy, exponential of Shannon entropy, Simpson concentration, inverse
 209 Simpson concentration, the Gini-Simpson index, Renyi entropies (Renyi 1970), Tsallis
 210 entropies (Keylock 2005), the Berger-Parker index, the Hurlbert-Smith-Grassle index for

211 $m = 2$ (Smith and Grassle 1977), and others-- are functions of the basic sum $\sum_{i=1}^S p_i^q$, with

212 q a non-negative integer, or limits of such functions as q approaches unity. All such
 213 measures will be called “standard diversity indices” and will be symbolized by the letter

214 H; the results of this paper apply to all such measures. The sums $\sum_{i=1}^S p_i^q$ which are at the

215 heart of these measures will be symbolized by ${}^q\lambda$:

216
$${}^q\lambda = \sum_{i=1}^S p_i^q, \quad (1)$$

217 a generalization of the notation for Simpson concentration $\lambda = \sum_{i=1}^S p_i^2$. (In this notation

218 Simpson concentration is ${}^2\lambda$.)

219

220 Every diversity measure H has a numbers equivalent, which will be symbolized qD or
 221 ${}^qD(H)$ or $D({}^q\lambda)$. There is an unexpected unity underlying all standard diversity indices;
 222 their numbers equivalents are all given by a single formula:

223
$${}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)} = ({}^q\lambda)^{1/(1-q)}. \quad (2)$$

224 This expression was first discovered by Hill (1973) in connection with the Renyi
 225 entropies; Jost (2006) showed that it gives the numbers equivalents of all standard
 226 diversity indices. It is this unity which permits the derivation of general index-
 227 independent formulas involving diversity. The number q, the value of the exponent in the
 228 basic sum underlying a diversity index, is called the “order” of the diversity measure.
 229 Species richness is a diversity index of order zero, Shannon entropy is a diversity index
 230 of order one, and all Simpson measures are diversity indices of order two. The order q
 231 determines a diversity measure’s sensitivity to rare or common species (Keylock 2005);
 232 orders higher than 1 are disproportionately sensitive to the most common species, while
 233 orders lower than 1 are disproportionately sensitive to the rare species. The critical point
 234 that weighs all species by their frequency, without favoring either common or rare
 235 species, occurs when $q = 1$; Eq. 2 is undefined at $q = 1$ but its limit exists and equals

236
$${}^1D = \exp\left(-\sum_{i=1}^S p_i \ln p_i\right) \quad (3)$$

237 which is the exponential of Shannon entropy. This special quality of Shannon measures
 238 gives them a privileged place as measures of complexity and diversity in all of the
 239 sciences. It is striking that Shannon measures do not need to be borrowed from
 240 information theory but arise naturally from this formalism of numbers equivalents.

241

242 It is important to distinguish a diversity index H from its numbers equivalent qD . Since
 243 the numbers equivalent of an index, not the index itself, has the properties biologists
 244 expect of a true diversity, the numbers equivalent qD of a diversity index of order q will
 245 be called the *true diversity* of order q. All diversity indices of a given order q have the
 246 same true diversity qD .

247

248 The alpha, beta, and gamma components of a diversity index, H_α , H_β and H_γ , can be
 249 individually converted to true alpha, beta, and gamma diversities by taking their numbers
 250 equivalents ${}^qD(H_\alpha)$, ${}^qD(H_\beta)$, and ${}^qD(H_\gamma)$. The reverse transformation from true alpha and
 251 beta diversities to alpha and beta components of particular indices is also sometimes
 252 useful. Any general expression based on the properties of numbers equivalents can be
 253 transformed into index-specific relations by simple algebra using the transformations in
 254 Table 1. The derivations in the following sections are based on this idea.

255

256 **4. Decomposing a diversity index into independent components**

257

258 Numbers equivalents permit the decomposition of any diversity index H into two
 259 independent components, which we may symbolize as H_A and H_B . These components
 260 may be alpha and beta diversity, or they may be any other pair of orthogonal qualities,
 261 like evenness and richness (Buzas and Hayek 1996). Suppose H_A has a numbers
 262 equivalent of x equally likely outcomes, and orthogonal H_B has a numbers equivalent of y
 263 equally likely outcomes. Then if H_A and H_B are independent and completely determine
 264 the total diversity, the diversity index of the combined system must have a numbers
 265 equivalent of exactly xy equally likely outcomes; if it did not, some other factor besides
 266 those measured by H_A and H_B would be present, contrary to our assumption that those
 267 two components completely determined the total diversity. Thus:

$$268 \quad D(H_A) \cdot D(H_B) = D(H_{tot}). \quad (4)$$

269

270 Working backwards from this simple mathematical relation between numbers
 271 equivalents, we can discover the correct decomposition of any standard diversity index
 272 into two independent components. The numbers equivalent of the Gini-Simpson index is

$$273 \quad {}^qD(H) = 1/(1 - H) \quad (5)$$

274 (Table 1) so Eq. 4 becomes

$$275 \quad 1/(1-H_A) \cdot 1/(1-H_B) = 1/(1-H_{tot}) \quad (6)$$

276 Simplifying yields

$$277 \quad H_{tot} = H_A + H_B - H_A \cdot H_B \text{ or } H_B = (H_{tot} - H_A)/(1 - H_A) \quad (7)$$

278 This, not the additive rule, defines the relationship between independent components of
 279 the Gini-Simpson index (Fig. 1). This is a well known equation in information theory
 280 (Aczel and Daroczy 1975) and physics (Tsallis and Brigatti 2004; see Keylock 2005).

281

282 The same technique yields the decomposition of any other standard diversity index into
 283 two independent components, H_A and H_B . The results for some common indices are:

284

$$285 \quad \text{Species richness: } H_A \cdot H_B = H_{tot} \quad (8a-g)$$

$$286 \quad \text{Shannon entropy: } H_A + H_B = H_{tot}$$

$$287 \quad \text{Exponential of Shannon entropy: } H_A \cdot H_B = H_{tot}$$

$$288 \quad \text{Gini-Simpson index: } H_A + H_B - (H_A \cdot H_B) = H_{tot}.$$

$$289 \quad \text{Simpson concentration: } H_A \cdot H_B = H_{tot}$$

$$290 \quad \text{HCDDT entropies: } H_A + H_B - (q-1) \cdot (H_A) \cdot (H_B) = H_{tot}$$

$$291 \quad \text{Renyi entropies: } H_A + H_B = H_{tot}$$

292

293 Many of the above results are known in ecology, information theory, or physics, though
 294 they have never before been derived in a unified way. Equation 8a is Whittaker's original
 295 definition of beta; 8b follows from Shannon's (1948) information theory; 8c was
 296 proposed in ecology by MacArthur (1965); 8e was introduced by Olszewski (2004) in the
 297 context of beta diversity and by Buzas and Hayek (1996) in the context of
 298 richness/evenness; 8f and 8g are well known in generalized information theory. The
 299 derivation of these formulas is unique; no other decomposition of these indices can yield
 300 independent components. The decomposition varies between indices, so there is no
 301 universal multiplicative or additive rule at the level of individual indices. This explains
 302 why the traditional additive and multiplicative definitions have both been popular; each

303 does work well for certain indices. The universal rule only appears at the level of the true
 304 diversities (${}^qD_{\text{tot}} = {}^qD_A \cdot {}^qD_B$), showing that these are actually the more useful quantities
 305 for diversity analysis.

306

307

308 **5. Alpha and beta**

309

310 The previous section showed how to decompose any diversity measure into two
 311 independent components. Thus, if alpha and beta are to be independent (Property 1 of
 312 Section 2) the numbers equivalents of the alpha, beta, and gamma components of a
 313 diversity index must be related by

$$314 \quad \mathbf{D(H}_\gamma) = \mathbf{D(H}_\alpha) \cdot \mathbf{D(H}_\beta). \quad (9)$$

315 This is Whittaker's law, here shown to be valid for the numbers equivalents of any
 316 diversity index. True beta diversity (the numbers equivalent of the beta component of any
 317 diversity index) thus has a uniform interpretation regardless of the diversity index used: it
 318 is the effective number of distinct communities or samples in the region.

319 Under what circumstances can these components H_α and H_β satisfy all the requirements
 320 for an intuitive alpha and beta, Properties 1-5 of Section 2? Let us set aside Property 5
 321 (Lande's requirement that alpha never exceed gamma) for the moment. Properties 1-4 are
 322 strong enough not only to give the decomposition equation above but also to give an
 323 explicit expression for the alpha and beta components of any standard diversity index.

324 For $q \neq 1$,

$$325 \quad H_\alpha \equiv H({}^q\lambda_\alpha) = H\left\{ [w_1^q (\sum_{i=1}^S p_{i1}^q) + w_2^q (\sum_{i=1}^S p_{i2}^q) + \dots] / [w_1^q + w_2^q + \dots] \right\} \quad (10)$$

326

327 [Digital Appendix Proof 1]. The true alpha diversity of order q is the numbers equivalent
 328 of that alpha component:

$$329 \quad {}^qD_\alpha \equiv D({}^q\lambda_\alpha) = \left\{ [w_1^q (\sum_{i=1}^S p_{i1}^q) + w_2^q (\sum_{i=1}^S p_{i2}^q) + \dots] / [w_1^q + w_2^q + \dots] \right\}^{1/(1-q)} \quad (11a)$$

330 This is undefined at $q = 1$ but the limit as q approaches 1 exists and equals:

$$331 \quad {}^1D_\alpha = \exp[-w_1 \sum_{i=1}^S (p_{i1} \ln p_{i1}) + - w_2 \sum_{i=1}^S (p_{i2} \ln p_{i2}) + \dots] \quad (11b)$$

332 which is the exponential of the standard alpha Shannon entropy.

333

334 For any standard diversity index, alpha must take this form, and beta must be given by
 335 Eq. 9, if they are to satisfy Properties 1-4. Now let us turn to Property 5, the requirement
 336 that alpha must never exceed gamma. The general expressions for alpha, Eqs. 11 and 12,
 337 are only consistent with Property 5 for certain combinations of q (the order of the
 338 diversity index) and w_j (the statistical weights of the communities or samples). For other
 339 values of these variables, alpha may exceed gamma. This means that under some
 340 conditions, some diversity indices cannot be decomposed into independent alpha and beta
 341 components satisfying all of Properties 1-5. Property 5 acts as a filter on the permissible
 342 diversity indices for a given application. There are two distinct cases, which are treated
 343 separately:

344

345 ***Case 1: Alpha and beta when community weights are all equal***

346

347 Biologists often compare communities in the abstract, using alpha and beta and
 348 associated similarity measures to quantify differences in species compositions. In these
 349 kinds of comparisons the actual sizes of the communities are immaterial; the only things
 350 that matter are the species frequencies, and the community weights are therefore all taken
 351 to be equal. Weights will also be equal when some ecological dimension is divided into
 352 equal parts (each part contributing equally to the total pooled population), and in some
 353 other applications.

354

355 When the N community weights w_j are all equal, $w_j = 1/N$ and the alpha component of
 356 any diversity index (for $q \neq 1$), Eq. 10, simplifies to

$$357 \quad H_\alpha = H[(1/N)(\sum_{i=1}^S p_{i1}^q + \sum_{i=1}^S p_{i2}^q + \dots + \sum_{i=1}^S p_{iN}^q)] = H[(1/N)({}^q\lambda_1 + {}^q\lambda_2 + \dots + {}^q\lambda_N)] \quad (12)$$

358 and the true alpha diversity of order q (for $q \neq 1$), Eq. 11a, simplifies to

$$359 \quad {}^qD_\alpha \equiv D({}^q\lambda_\alpha) = \{[1/N][(\sum_{i=1}^S p_{i1}^q) + (\sum_{i=1}^S p_{i2}^q) + \dots + (\sum_{i=1}^S p_{iN}^q)]\}^{1/(1-q)}. \quad (13)$$

360 For $q=1$ (Shannon measures) the traditional definitions are correct. The alpha Shannon
 361 entropy is the average of the Shannon entropies of the samples, and the true alpha
 362 diversity of order 1 (the numbers equivalent of Shannon alpha entropy) is for this case

$$363 \quad {}^1D_\alpha = \exp\{-1/N[(\sum_{i=1}^S (p_{i1} \ln p_{i1})) + \sum_{i=1}^S (p_{i2} \ln p_{i2}) + \dots + \sum_{i=1}^S (p_{iN} \ln p_{iN})]\}. \quad (14)$$

364

365 When community weights are equal, Eqs. 13 and 14 for alpha always satisfy Property 5,
 366 Lande's condition that alpha never exceed gamma [Proof 2.] Therefore in this case ($w_j =$
 367 $1/N$) there is no restriction on the allowable values of q, and all standard diversity indices
 368 are valid.

369

370 Equation 12 differs slightly from the traditional definition of alpha. The alpha component
 371 of a diversity index is not the average of the diversity indices of the individual
 372 communities, as previously thought. Rather, we must average the basic sums ${}^q\lambda$ of the
 373 individual communities, and then calculate the diversity index of that average. For
 374 indices that are linear in the ${}^q\lambda$ (e. g. the Gini-Simpson index or species richness), the end
 375 result is the same as the traditional definition. For nonlinear diversity indices such as the
 376 Renyi entropy, however, the difference is important. As in all these new results, there is
 377 no choice about it; the new expression follows mathematically from the conditions on
 378 beta given in Section 2, and the traditional definition of alpha is logically inconsistent
 379 with these principles.

380

381 The true alpha diversities are the numbers equivalents of the alpha components of these
 382 indices. The numbers equivalents of all alpha diversities of a given order q are equal; this
 383 was not true under the traditional definition of alpha. This leads to the surprising
 384 simplification discussed in Section 6.

385

Jost: Partitioning diversity

386 The beta components of some common diversity indices are (from Eq. 8a-g):

387 Species richness: $H_\beta = H_\gamma / H_\alpha$ (15a-g)

388 Shannon entropy: $H_\beta = H_\gamma - H_\alpha$

389 Exponential of Shannon entropy: $H_\beta = H_\gamma / H_\alpha$

390 Gini-Simpson index: $H_\beta = (H_\gamma - H_\alpha) / (1 - H_\alpha)$.

391 Simpson concentration: $H_\beta = H_\gamma / H_\alpha$

392 HCDT entropies: $H_\beta = (H_\gamma - H_\alpha) / (1 - (q-1)(H_\alpha))$

393 Renyi entropies: $H_\beta = H_\gamma - H_\alpha$

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395 The true beta diversities are the numbers equivalents of these components. The true beta

396 diversities can also be calculated directly from the generalized Whittaker's law, by

397 converting the diversity index's gamma and alpha components to numbers equivalents

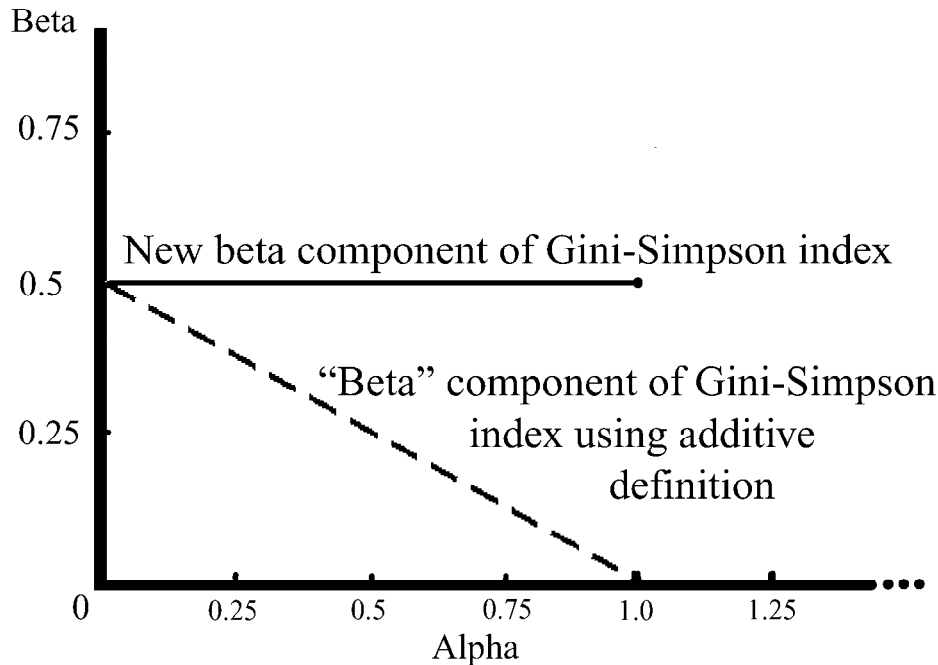
398 (true diversities) and dividing, as Whittaker (1972) and MacArthur (1965) suggested for

399 species richness and Shannon entropy.

400

401 Figure 1

Beta vs. Alpha



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Figure 1. Beta versus alpha for two equally-weighted communities with no species in common. The additive definition $H_\gamma = H_\alpha + H_\beta$ yields a beta component which is strongly dependent on the alpha component when it is applied to the Gini-Simpson index. The new beta component derived here for the Gini-Simpson index, defined by the relation $H_\gamma = H_\alpha + H_\beta - H_\alpha H_\beta$, is independent of alpha. (Modified from Jost 2006.)

Case 2: Alpha and beta when community weights may be unequal

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425

Ecologists commonly need to calculate the alpha and beta diversity of a landscape. The community or sample weights will usually be unequal in this application. In this kind of application the unequal sizes of the different communities play an essential role in the outcome; for a given set of distinct communities, beta diversity is smallest when one community dominates the landscape, and largest when all communities share the landscape equally. When weights may be unequal, most diversity indices cannot be decomposed into independent alpha and beta components which satisfy Lande’s condition that alpha never exceed gamma (Property 5 above). If alpha is not to exceed gamma when weights are unequal, only two values of q are permissible, $q = 0$ and $q = 1$. [Proof 3.]

When $q = 0$, the diversity index is species richness or its monotonic transformations. Its alpha diversity (Eq. 11a) reduces to ${}^0D_\alpha = (1/N)(S_1 + S_2 + \dots S_N)$, which is always less than or equal to the gamma diversity S_{tot} . However, this expression weighs each

426 community equally regardless of its true weight, so it is not a satisfactory measure when
427 community weights are important.

428

429 When $q = 1$, the diversity index is Shannon entropy (or any monotonic transformation of
430 it). This always satisfies Lande's condition that alpha not exceed gamma, because it is a
431 concave function (Lande 1996). Its numbers equivalent, the true alpha diversity, is given
432 by Eq. 11b, the exponential of the traditional alpha Shannon entropy. Therefore, when
433 weights may be unequal, *Shannon measures ($q = 1$) are the only diversity measures that*
434 *can be decomposed into independent alpha and beta components satisfying Properties 1-*
435 *5 above.* "One expects that deductions made from any other information measure, if
436 carried far enough, will eventually lead to contradictions" (Jaynes 1957).

437

438

439 **6. Traditional diversity indices are superfluous**

440

441 Jost (2006) showed that for diversity analyses of single communities, most traditional
442 diversity indices are superfluous. Their numbers equivalents are the biologically
443 meaningful entities, and these could be expressed more simply and directly in terms of q
444 and the basic sums ${}^q\lambda$, rather than calculating indices and then converting these to their
445 numbers equivalents. This conclusion can now be extended to multiple-community
446 diversity analyses when the communities have equal weights (the only case for which
447 there is a choice of diversity measures other than Shannon measures). In fact the
448 unifying mathematics works even when weights are unequal, but non-Shannon measures
449 are prohibited in this case because alpha could exceed gamma.

450

451 The new expression for true alpha diversity, Eq. 11 (the numbers equivalent of the
452 properly-defined alpha component of a diversity index), is a function only of the species
453 frequencies, the community weights, and the exponent q ; for a given value of q it is
454 independent of the diversity index used. The same applies to true gamma diversity (the
455 numbers equivalent of the diversity index of the pooled samples), and since true beta
456 diversity (the numbers equivalent of the beta component of a diversity index) equals true
457 gamma diversity divided by true alpha diversity for all standard diversity indices, true
458 beta diversity also depends only on the species frequencies, the community weights, and
459 q . Diversity indices are therefore superfluous; for a given value of q , all standard
460 diversity indices give the same final numbers equivalents. For example the Gini-Simpson
461 index, the Simpson concentration, the inverse Simpson concentration, the Renyi entropy
462 of degree 2, and the Hurlbert-Smith-Grassle index with $m = 2$ all give exactly the same
463 true alpha, beta, and gamma diversities for any given set of communities. These indices
464 can therefore be bypassed and the final numbers equivalents can be formulated more
465 simply in terms of q and the sums ${}^q\lambda$. For the purpose of calculating true alpha, beta, and
466 gamma diversities (numbers equivalents), indices add nothing except unnecessary
467 calculations.

468

469 In the index-free description of diversity, with all community weights equal (the only
470 case in which non-Shannon measures are valid), for $q \neq 1$ the alpha sum ${}^q\lambda_\alpha$ is the mean

471 of the individual community sums, $\sum_{j=1}^N (1/N)^q \lambda_j$. The gamma sum ${}^q\lambda_\gamma$ is calculated from

472 the pooled samples (as $\sum_{i=1}^S [((1/N)(p_{i1} + p_{i2} + \dots + p_{iN})^q]$). These are transformed into true

473 alpha, beta, and gamma diversities of order q (for $q \neq 1$) using Eq. 2, and Whittaker's
 474 law is used to find the true beta diversity:

475 **Alpha diversity of order q:** ${}^qD_\alpha = {}^q\lambda_\alpha^{1/(1-q)}$ (16a-c)

476 **Gamma diversity of order q:** ${}^qD_\gamma = {}^q\lambda_\gamma^{1/(1-q)}$

477 **Beta diversity of order q:** ${}^qD_\beta = {}^qD_\gamma / {}^qD_\alpha = ({}^q\lambda_\gamma / {}^q\lambda_\alpha)^{1/(1-q)} \equiv {}^q\lambda_\beta^{1/(1-q)}$.

478 These are undefined when $q = 1$, but their limits exist as q approaches 1, yielding the
 479 exponential of Shannon alpha, beta, and gamma entropies. The index-free description of
 480 diversity is therefore continuous in q. In fact the precursors to Eq. 16a-c are all
 481 mathematically valid even when weights are unequal, and their limits as q approaches
 482 unity give (see Eq. 11b):

483 ${}^1D_\alpha = \exp[-w_1 \sum_{i=1}^S (p_{i1} \ln p_{i1}) + -w_2 \sum_{i=1}^S (p_{i2} \ln p_{i2}) + \dots]$ (17a-c)

484 ${}^1D_\gamma = \exp[\sum_{i=1}^S -(w_1 p_{i1} + w_2 p_{i2} + \dots) \ln(w_1 p_{i1} + w_2 p_{i2} + \dots)]$

485 ${}^1D_\beta = {}^1D_\gamma / {}^1D_\alpha$

487 It is remarkable that all of Shannon's information functions come out of this theory
 488 automatically without reference to information theory. As shown earlier, these Shannon
 489 measures, Eqs.15a-c, are the only meaningful diversity measures (the only ones satisfying
 490 the properties of Section 2) when community weights are unequal.

491
 492

493 7. Relation between the new beta diversity and indices of community 494 similarity and overlap

495

496 Beta diversity is inversely related to most concepts of community similarity. Suppose we
 497 are comparing the compositional similarity of a set of N communities. The sizes of the
 498 communities are irrelevant to this comparison and so their statistical weights are taken to
 499 be equal. If the equally weighted communities have a high compositional similarity, then
 500 the set of communities must have a low beta diversity. Conversely if the communities
 501 have low similarity, their beta diversity must be high. The relation can be made rigorous:
 502 if conclusions based on a similarity, overlap, or homogeneity measure are to be logically
 503 consistent with (not contradict) conclusions based on a given diversity measure, then the
 504 similarity measure must be a monotonic transformation of the diversity measure's beta
 505 diversity. [Proof 4.] Different kinds of transformations of beta diversity will illuminate
 506 different aspects of its behavior. Each transformation generates an infinite family of
 507 similarity measures parameterized by q, which controls the sensitivity of the measures to
 508 rare or common species. The most popular similarity and overlap measures of ecology
 509 are in fact transformations of the new beta diversity ${}^qD_\beta$.

510

511 The true beta diversity of order 1, the numbers equivalent of beta Shannon entropy, can
 512 be transformed into MacArthur's (1965) homogeneity measure:

513
$$M = 1/ {}^1D_\beta = \exp(H_{\alpha \text{ Shannon}})/\exp(H_{\gamma \text{ Shannon}}). \quad (18)$$

514 It answers the question, "What proportion of total diversity is found within the average
515 community or sample?" For N equally-weighted communities, it can be generalized to
516 other values of q:

517
$$M = 1/ {}^qD_\beta \quad (19)$$

518 which ranges from 1/N (when all communities are completely distinct) to unity (when all
519 communities are identical).

520

521 The lower limit of this simple homogeneity measure depends on the number of samples
522 or communities. It would be easier to interpret and more useful in comparisons if its
523 lower limit were zero. For N equally weighted communities the measure

524
$${}^qS = (1/{}^qD_\beta - 1/N) / (1-1/N) \quad (20)$$

525 is the simplest linear transformation of $1/{}^qD_\beta$ which has this property. It is zero when all
526 N communities in the region are completely distinct from each other, and is unity when
527 all N communities are identical in species composition. It is linear in the proportion of
528 regional diversity contained in the average community. Jost (2006) shows that when this
529 measure is applied to a pair of equally-weighted communities, it produces the Jaccard
530 index when $q = 0$, and the Morisita-Horn index when $q = 2$. Equation 20 may be
531 considered the generalization of these similarity measures to N communities and to
532 arbitrary values of q.

533

534 Shannon measures (and only Shannon measures) are valid not only when statistical
535 weights are equal but also when they are unequal, and in that case MacArthur's measure,
536 Eq. 18, is still a valid measure of regional homogeneity. Its minimum value is

537
$$1/ \exp[- \sum_{j=1}^N (w_j \ln w_j)] \equiv 1/{}^1D_w \quad (21)$$

538 which is the reciprocal of the numbers equivalent of the Shannon entropy of the weights.
539 It takes this value when all communities are completely distinct. Its maximum value is
540 unity when all communities are identical. This homogeneity measure can therefore be
541 converted into a relative index of homogeneity that goes from 0 (all communities
542 distinct) to unity (all communities identical), like Eq. 20:

543
$$\text{Relative homogeneity} = (1/{}^1D_\beta - 1/{}^1D_w) / (1-1/{}^1D_w). \quad (22)$$

544 This measure, like Eq. 18, is useful in the interpretation of the results of additive
545 partitioning using Shannon measures.

546

547 A direct measure of pairwise community overlap is often the most easily interpreted
548 similarity measure. For this purpose the weights of the two communities are irrelevant
549 and are taken to be equal. The new beta diversity can be transformed into such a measure
550 of overlap:

551
$$\text{Overlap (of order } q) \equiv [(1/{}^qD_\beta)^{q-1} - (1/2)^{q-1}] / [1 - (1/2)^{q-1}]. \quad (23)$$

552 Jost (2006) shows that when this measure is applied to a pair of equally weighted
553 communities, it produces the Sørensen index when $q = 0$ and the Morisita-Horn index
554 when $q = 2$. In the limit as q approaches unity it becomes

555
$$\text{Overlap of order } 1 = (\ln 2 - H_{\beta \text{ Shannon}}) / \ln 2 \quad (24)$$

556 which is the Horn index of overlap, the only measure of overlap that does not
557 disproportionately favor either rare or common species. For all values of q, Eq. 23 and 24

558 are true overlap measures in the sense of Wolda (1981): when applied to two
 559 communities each consisting of S equally common species, with C species shared
 560 between the communities, they give C/S , the proportion of a community's species which
 561 are shared.

562
 563 Alternatively, for multiple equally-weighted communities, true beta diversity can be
 564 transformed into the turnover rate per sample (generalizing Harrison et al. 1992) by
 565 taking

$$566 \quad \quad \quad ({}^qD_{\beta}-1)/(N-1). \quad \quad \quad (25)$$

567 where N is the number of samples. This ranges from zero (no turnover between samples)
 568 to unity (each sample is completely different from every other sample).

569
 570 All similarity measures based on the new beta diversity inherit its independence from
 571 alpha, a desirable property (Wolda 1981, Magurran 2004). A very large number of
 572 similarity indices are inconsistent with the beta diversity of any standard diversity index.
 573 These include the Bray-Curtis index (Bray and Curtis 1957), Canberra metric (Lance and
 574 Williams 1967), Renkonen index (Renkonen 1938), and many others. Conclusions based
 575 on such measures can contradict conclusions based on valid diversity indices, and their
 576 possible dependence on alpha make it difficult to disentangle mathematical artifacts from
 577 biologically meaningful effects.

578
 579 Traditional similarity measures have a strong negative bias when sample size is small;
 580 even two samples from the same population will often appear to be dissimilar according
 581 to these measures (Lande 1996). Expressing a similarity measure as a transformation of
 582 beta helps solve this problem, since beta is a simple function of alpha and gamma, and
 583 almost-unbiased estimators of alpha and gamma exist for many diversity measures (e.g.
 584 Chao and Shen 2003).

585
 586

587 **8. Examples**

588

589 *Tundra and rainforest revisited*

590

591 The new measures give very different results than the traditional measures when applied
 592 to the examples of the Introduction. The traditional Gini-Simpson “beta” for the two
 593 intercontinental rainforest samples was $0.9861 - 0.9721 = 0.014$, paradoxically *lower* than
 594 the “beta” diversity of the homogeneous antarctic tundra. This “beta” does not, by itself,
 595 tell the amount of turnover between samples, because of its dependence on alpha (Fig. 1).
 596 Depending on alpha, a “beta” value of 0.014 can mean that the samples are nearly
 597 identical, somewhat similar, or completely different. The similarity measure commonly
 598 used with the additive definition, H_{α}/H_{γ} or $1 - (H_{\beta}/H_{\gamma})$ (Lande 1996), does not resolve this
 599 ambiguity. For the intercontinental rainforest data set, using the Gini-Simpson index, this
 600 “similarity” between samples is 0.99, even though the samples share *no* species. (The
 601 measure would have a value of 1.00 if both communities were identical in species
 602 composition and frequency.) This “similarity” between completely distinct
 603 intercontinental rainforests is even greater than the “similarity” between the

604 homogeneous tundra samples (0.95).

605

606 The new Gini-Simpson beta component is, by Eq. 15d, $(H_\gamma - H_\alpha)/(1 - H_\alpha) = (0.9861 -$
 607 $0.9721)/(1 - 0.9721) = 0.50$. This new beta has a different character than the tradition
 608 “beta”. Using this method (which is standard in most sciences; Aczel and Daroczy 1975,
 609 Tsallis and Brigatti 2004, Keylock 2005) a Gini-Simpson index of 0.5 has the same
 610 absolute and invariable interpretation whether it comes from the alpha, beta, or gamma
 611 component of the index. The interpretation is given by its numbers equivalent, which is
 612 (from Table 1) $1/(1-0.50) = 2.0$. Thus a Gini-Simpson index of 0.50 is always, in any
 613 context, the amount of diversity produced by 2.0 equally-likely, completely distinct
 614 alternatives. In the context of this beta diversity calculation, it correctly indicates that
 615 there are two equally-weighted completely distinct intercontinental rainforest samples in
 616 the data set.

617

618 The calculation of true beta diversity of the rainforest samples using Shannon entropy
 619 (the order 1 diversity measure) is similar to the calculation using the Gini-Simpson index.
 620 The beta component of the Shannon entropy is (by Eq. 15b) $H_\gamma - H_\alpha$, which is 0.6931. A
 621 Shannon entropy of 0.6931 has the same interpretation no matter where it came from. As
 622 always, this interpretation is given by its numbers equivalent, which is (from Table 1)
 623 $\exp(0.6931) = 2.0$. A Shannon entropy of 0.6931 is always the amount of diversity
 624 produced by 2.0 equally-likely, completely distinct alternatives. Here it indicates that
 625 there are two equally-weighted completely distinct intercontinental rainforest samples in
 626 the data set. The agreement with the Gini-Simpson result is not an accident; the numbers
 627 equivalent of the correctly-calculated beta component of any standard diversity index will
 628 be 2.0 for this data set, because the data set consists of two equally large completely
 629 distinct samples.

630

631 In the new approach the antarctic tundra samples always have a lower beta diversity than
 632 the intercontinental rainforest samples, in contrast to the traditional approach which ranks
 633 them in reverse when using the Gini-Simpson index. The new beta component of the
 634 Gini-Simpson index for the antarctic samples is $(0.4199-0.400)/(1-.400) = 0.03$ and its
 635 numbers equivalent, the true beta diversity of order 2, is 1.03. By this measure there are
 636 effectively only 1.03 distinct communities in this data set, meaning that the two samples
 637 are almost identical. The beta Shannon entropy is 0.02 and its numbers equivalent, the
 638 true beta diversity of order 1, is $\exp(.02) = 1.02$. By this measure also the samples are
 639 almost identical. The beta component of species richness is 1.0, which is its own numbers
 640 equivalent. By this measure the communities are truly identical (since they share all
 641 species and this measure ignores frequencies).

642

643 As shown in Section 6, traditional diversity indices are superfluous and the true
 644 diversities of any order q can be calculated directly from the basic sums ${}^q\lambda$ (or, for $q=1$,
 645 from Eq. 17a-c). For example, instead of using the Gini-Simpson index to calculate
 646 alpha, beta, and gamma diversities of order 2, we can calculate them more simply as
 647 follows:

648 ${}^2\lambda_1$ (Panamanian rainforest sample) = 0.049171219

649 ${}^2\lambda_2$ (Malaysian rainforest sample) = 0.00656619

650 ${}^2\lambda_\alpha$ (average of the basic sums of the samples) = 0.0278839

651 ${}^2\lambda_\gamma$ (pooled samples) = 0.013941

652 The true beta diversity of order 2 is therefore (Eq. 16c):

653 $({}^q\lambda_\gamma / {}^q\lambda_\alpha)^{1/(1-q)} = (0.013941 / 0.0278839)^{1/(1-2)} = 2.000$

654 in agreement with the Gini-Simpson result. For any data set, all order 2 diversity indices
 655 will always give the same true beta diversity (the numbers equivalent of its beta
 656 component) as this direct index-free calculation. In general the results will depend on the
 657 order q , but if the samples are completely distinct (as in this case), or if they are perfectly
 658 identical, the results will be the same for all q .

659
 660 The similarity measures given in Section 7 are helpful in interpreting the new beta
 661 diversity. For the intercontinental rainforest samples, for any standard diversity index the
 662 proportion of regional diversity contained in the average community (Eq. 19) is 1/2; the
 663 similarity measure Eq. 20 is zero, and the overlap between communities (Eq. 23) is also
 664 zero. The turnover rate per community (Eq. 25) is 1.00 for any index, indicating complete
 665 turnover between communities.

666
 667 These same measures clearly show that the antarctic communities are homogeneous. For
 668 the true diversity of order 2 the beta diversity equals 1.03, so the proportion of regional
 669 diversity contained in the average community (Eq. 19) is 0.97; the similarity measure Eq.
 670 20 is 0.94, and the overlap between communities (Eq. 23) is also 0.94. The community
 671 turnover rate (Eq. 25) is 0.03, indicating that there is almost no turnover between these
 672 communities.

673

674 ***Beta diversity of a landscape, and analysis of heirarchical diversity components***

675

676 In the previous example the statistical weights of the two communities in each data set
 677 were taken to be equal; this meant we could legitimately use the full range of diversity
 678 indices rather than just Shannon measures (Case 1 of Section 5). This is not the case
 679 when calculating the alpha, beta, and gamma diversities of a landscape, where population
 680 density is not uniform, resulting in unequal statistical weights for different samples or
 681 communities (Case 2 of Section 5). The proofs of Sections 4 and 5 show that under these
 682 circumstances only Shannon measures can be decomposed into meaningful independent
 683 alpha and beta components. The additive definition of beta is valid for Shannon entropy
 684 (Eq. 8b), so the standard techniques of additive partitioning can be used with this index
 685 (but only with this index) to study the heirarchical partitioning of diversity (within-
 686 samples, between samples within communities, between communities, etc). One
 687 modification is necessary; the final results need to be converted to their numbers
 688 equivalents, the exponentials of Shannon alpha, beta, and gamma entropies, before they
 689 can be properly interpreted. Thus Lande's similarity or homogeneity measure H_α/H_γ must
 690 be replaced by MacArthur's measure, $\exp(H_\alpha)/\exp(H_\gamma)$; otherwise the "similarity" value
 691 will be inflated as in the intercontinental rainforest example above. MacArthur's measure
 692 correctly gives the proportion of regional diversity contained in the average sample. The
 693 relative homogeneity, Eq. 22, is also useful in analyzing the results. (Alternatively, the
 694 entire partitioning could have been done multiplicatively using the numbers equivalents
 695 from the beginning. The results are the same.)

696

697

698 **9. Conclusions**

699

700 *Limitations of additive partitioning of diversity*

701

702 Additive partitioning of diversity into hierarchical components (Lande 1996; see Veech
703 et al. 2002 for a complete review of its history) is a popular method of diversity analysis,
704 in which beta is compared between different hierarchical levels. However, the technique
705 only makes sense if the beta it produces is independent of alpha; if beta depends on alpha,
706 the beta values between different hierarchical levels cannot be compared with each other
707 (since each level has a higher alpha than the preceding level) nor with the beta values of
708 other ecosystems with different alpha values.

709

710 The proofs of Sections 4 and 5 show that when community statistical weights differ the
711 only index which can be additively partitioned into independent alpha and beta
712 components is the Shannon entropy. The frequently recommended Gini-Simpson index
713 cannot be used; its decomposition into independent alpha and beta components is only
714 possible when the statistical weights of all samples are equal, and even then the
715 decomposition is not additive.

716

717 Also, for many diversity indices (including Shannon entropy and the Gini-Simpson
718 index) the similarity measure used with additive partitioning, H_α/H_γ , necessarily
719 approaches unity for high-diversity ecosystems, regardless of the amount of
720 differentiation between samples. If the Gini-Simpson index is used as the diversity
721 measure, it is mathematically impossible for the “similarity” to be lower than the alpha
722 “diversity”. This happens because H_γ for this index is strictly less than unity; therefore
723 the quotient H_α/H_γ must always be greater than H_α . Since H_α for this index often exceeds
724 0.95 in tropical ecosystems, a set of tropical samples will often have a Gini-Simpson
725 “similarity” greater than 0.95 even if they have nothing in common (i.e. even when they
726 are completely distinct in species composition and frequencies). This measure should not
727 be used to draw conclusions about differences in composition between samples (contrary
728 to the recommendations of Veech et al. 2002 and contrary to the practices of most of the
729 studies cited therein).

730

731 *The importance of numbers equivalents*

732

733 Many biologists think of diversity indices simply as intermediate steps in the calculation
734 of statistical significance. On this view, one measure of diversity is as good as another, as
735 long as it can be used to calculate the statistical significance of the effect under study. A
736 moment's reflection, however, shows that this is not reasonable. A very tiny bias in a coin
737 can be detected at any desired significance level if enough trials are made, but it is still an
738 insignificant bias in practice. The statistical significance of an effect has little to do with
739 the actual magnitude or biological significance of the effect, which is the really important
740 scientific question. We therefore need measures that behave intuitively so that we can
741 judge changes in their magnitudes.

742

743 Ecologists' intuitive theoretical concept of diversity corresponds not to the raw values of
744 diversity indices but to their numbers equivalents (Hill 1973, Peet 1974, Jost 2006).

745 Converting diversity indices to their numbers equivalents allows us to judge changes in
746 their magnitude, because numbers equivalents possess the "doubling" property (Section 3)
747 that characterizes our intuitive concept of diversity. When alpha, beta, and gamma are
748 expressed as numbers equivalents, their magnitudes have simple intuitive interpretations
749 in terms of the number of equally common species or the number of distinct equally large
750 communities; it is easy to visualize these and easy to judge the importance of changes in
751 their magnitudes. Numbers equivalents let us move beyond mere statistical conclusions.

752

753 Numbers equivalents correct the anomalous behavior of the "similarity" measure H_α/H_γ
754 described above; converting the raw alpha and gamma indices in this ratio to their
755 numbers equivalents produces a similarity or homogeneity measure, ${}^qD_\alpha/{}^qD_\gamma$, that
756 accurately reflects the proportion of regional diversity contained in the average sample.
757 This measure equals $1/N$ when applied to N equally-weighted, completely distinct
758 samples, no matter which diversity index is used and no matter what the species
759 frequencies, so it provides an absolute benchmark from which to judge the distinctness of
760 a set of samples. Equation 20 transforms this onto the interval $[0,1]$.

761

762 All standard diversity indices of a given order group communities into the same "level
763 surfaces" and differ only in the way they label these level surfaces. It is therefore
764 reasonable to standardize on the labelling system that gives the most intuitive results, the
765 numbers equivalents; in doing so we are not ignoring the many other aspects of
766 compositional complexity but rather converting them all to common and intuitive units.

767

768 Numbers equivalents also provide a powerful mathematical tool for proving index-
769 independent theorems of great generality. The most interesting of these theorems is the
770 main result of this paper, a generalization of Whittaker's law: if alpha and beta
771 components of a diversity index are independent, their numbers equivalents must be
772 multiplicative. That is, the product of their numbers equivalents must give the numbers
773 equivalent of the gamma diversity index.

774

775 Numbers equivalents reveal a deep unity between all standard diversity indices. The
776 numbers equivalents of all of them are given by a single equation (Eq. 2). The numbers
777 equivalents of standard diversity indices also generate and unify the standard similarity
778 and overlap indices of ecology (Section 7).

779

780 *New alpha and beta versus old*

781

782 For most non-Shannon indices, the traditional additive beta component was not
783 independent of the alpha component, and had no special value when all communities
784 were distinct. The "numbers equivalent" of the beta component of an index bore no
785 relation to the "numbers equivalents" of the alpha and gamma components of that index.
786 The beta component often did not use the same metric as the alpha component, in the

787 sense that a given number denoted different amounts of diversity or uncertainty
788 depending on which component it came from.

789

790 These anomalies are corrected by the new alpha and beta components of diversity
791 indices. For N equally-weighted communities (the only case for which non-Shannon
792 indices are valid), the new alpha components of all non-Shannon standard diversity
793 indices are given by Eq. 12 (the alpha Shannon entropy is the same as the traditional
794 one); the new beta components of the most common diversity indices are given by Eq.
795 15a-g. These alpha and beta now use exactly the same metric as gamma, and beta
796 provides complete information about the relative degree of community complementarity,
797 without confounding this with alpha.

798

799 Converting these new alpha and beta components of a diversity index to their numbers
800 equivalents makes them easily interpretable. For N equally-weighted communities (the
801 only case for which non-Shannon indices are valid), the numbers equivalent of H_β for any
802 standard diversity index has a uniform interpretation, indicating the effective number of
803 distinct communities in the region, which ranges from 1 to N . When there are N distinct
804 equally-weighted communities, this true beta diversity is always N , regardless of the
805 index used and regardless of the species frequencies.

806

807 Diversity is most easily analyzed by bypassing traditional diversity indices and
808 calculating the alpha, beta, and gamma numbers equivalents directly, using Eqs. 16 and
809 17. The numbers equivalents deserve to be considered the true alpha, beta, and gamma
810 diversities (of order q) of the system under study. The order q determines the emphasis on
811 the dominant species (with q greater than 1 emphasizing dominant species).

812

813 *Importance of Shannon measures*

814

815 Shannon measures are the only standard diversity indices that can be decomposed into
816 meaningful independent alpha and beta components when community weights are
817 unequal. Shannon measures do not need to be borrowed from information theory; the
818 exponential of Shannon entropy and related functions are derived here from the natural
819 conditions on beta discussed in Section 2.

820

821 An often-repeated criticism of Shannon measures is that they have no clear biological
822 interpretation. Shannon entropy does in fact have an interpretation in terms of
823 interspecific encounters (Patil and Taillie 1982), and both H_{Shannon} and $\exp(H_{\text{Shannon}})$ can
824 be related to characteristics of maximally-efficient species keys (Jost 2006) and to
825 biologically reasonable notions of uncertainty (Shannon 1948) and average rarity (Patil
826 and Taillie 1982).

827

828 Some authors (e.g. Lande 1996, Magurran 2004) recommend the Gini-Simpson index
829 over Shannon entropy on the grounds that the former converges more rapidly to its final
830 value and has an unbiased estimator. However, the Gini-Simpson index and all other
831 order 2 indices emphasize dominant species (which is why it converges more rapidly to
832 its final value), and this may not always be desirable. Furthermore, since the Gini-

833 Simpson index cannot generally be decomposed into independent alpha and beta
834 components which satisfy Lande's condition that alpha never exceed gamma, it cannot be
835 used for studies that involve landscape alpha or beta. (It --or rather its numbers
836 equivalent-- is fine for studies comparing communities directly, using equal statistical
837 weights, when it is desired to emphasize the dominant species.) The recent development
838 of a nearly unbiased nonparametric estimator for Shannon entropy (Chao and Shen 2003)
839 makes sampling criticisms less relevant. This nonparametric estimator for Shannon
840 entropy converges rapidly with little bias even when applied to small samples.

841
842 Some authors who are critical of Shannon measures because of their sampling properties
843 (e.g. Magurran 2004) recommend species richness and its associated similarity and
844 overlap measures, the Jaccard and Sorensen indices. These measures have worse
845 sampling properties than Shannon measures (Lande 1996, Magurran 2004). Since they
846 are completely insensitive to differences in species frequencies, they are poor choices for
847 distinguishing communities or comparing pre- and post-treatment diversities, and they
848 converge more slowly than any other measure as sample size increases. They are also not
849 ecologically realistic; ecologically meaningful differences between communities are
850 matters of differences in species frequencies, not in their mere presence or absence.
851 Communities almost always have rare vagrants, but presence-absence measures give
852 them the same weight as shared dominant species in calculating the similarity or overlap
853 of two communities. Frequency data provide important information that should be used
854 when available. The new expressions for alpha and beta remove the anomalies of the
855 traditional definitions, and the conversion of properly-defined frequency-based measures
856 to their numbers equivalents makes them linear with respect to our intuitive ideas of
857 diversity. They are now almost as easy to interpret as species richness, and much more
858 reliable and informative. The same is true for similarity and overlap measures; the Horn
859 index of overlap (Eq. 24) is more informative, discriminating, and reliable than either the
860 Jaccard or Sorensen indices.

861

862 *Species richness beta*

863

864 Much landscape data consists only of presence/absence records, which force us to use
865 species richness as our diversity measure. The proofs of Section 5 show that species
866 richness can only be partitioned into independent alpha and beta components if we treat
867 each sample with equal statistical weight, and use Whittaker's multiplicative formula.
868 Only then will alpha, beta, and gamma satisfy the essential properties 1-5 described in
869 Section 2. This beta diversity is not really a characteristic of the landscape but rather a
870 direct measure of compositional similarity between N samples (without regard to their
871 relative sizes). As such it is equivalent to the N-community generalization of the
872 Sorensen or Jaccard indices, which are independent of alpha. The turnover rate $({}^0D_{\beta}-$
873 $1)/(N-1)$ (Harrison et al. 1992) is also independent of alpha and is a useful measure of
874 regional heterogeneity.

875

876 *Scope of these results*

877

878 The proof that Shannon measures are the only ones that can always be decomposed into
879 meaningful independent alpha and beta components applies only to the class of standard
880 diversity indices, as defined in Section 3. A few nonparametric diversity measures used
881 in biology are excluded from this proof because they do not belong to this class. The
882 Hurlbert-Smith-Grassle index for $m > 2$ is such a measure, since it cannot generally be
883 written in terms of $^q\lambda$. Although nothing in the present paper excludes the possibility that
884 this index may be decomposable into meaningful independent alpha and beta components
885 when m is greater than 2, the index does fail to decompose when $m = 2$, and it seems
886 unlikely that higher values of m would change this property.

887
888 While Fisher's alpha is not strictly a nonparametric index, it is sometimes used as if it
889 were (Magurran 2004). The results presented here do not exclude the possibility that it
890 could be decomposed into meaningful independent alpha and beta components for data
891 from a log series distribution. However there are strong reasons to avoid this index for
892 general use. When the data are not log-series distributed this index is difficult to interpret,
893 and as it is usually calculated (Magurran 2004) it throws away almost all the information
894 in the sample (since it depends only on the sample size and the number of species in the
895 sample, not the actual species frequencies). For example, a sample containing ten species
896 with abundances
897 [91, 1, 1, 1, 1, 1, 1, 1, 1, 1]
898 has the same diversity, according to this method of calculating Fisher's alpha, as a
899 sample containing ten species with abundances
900 [10, 10, 10, 10, 10, 10, 10, 10, 10, 10], whereas ecologically and functionally the second
901 community is much more diverse than the first.

902
903 ***Relation of the new alpha and beta to results in other sciences***

904
905 Since 1988 physicists have begun to use new measures of entropy such as the HCDT or
906 Tsallis entropy, which includes as special cases the standard diversity indices of biology:
907 Shannon entropy, the Gini-Simpson index, and species richness minus one (Keylock
908 2005). Physicists have recently proposed a new definition of alpha or conditional HCDT
909 entropy (Tsallis et al. 1998, Abe and Rajagopal 2001; in physics and information theory,
910 the ecologists' alpha is called the "conditional entropy") which is identical to the
911 expression that I have derived here (Eq. 10) from very different premises. They were led
912 to this new definition of conditional or alpha entropy by thinking about theoretical issues
913 in nonextensive thermodynamics, such as the thermodynamics of black holes and
914 quantum-mechanical systems. Jizba and Arimitsu (2004) have proposed a definition of
915 Renyi conditional entropy for thermodynamics, and this also turns out to be the same
916 definition of alpha entropy that I have derived here. It is remarkable that studies of stars,
917 electrons, and butterflies converge on these same expressions.

918
919
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921
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927
928

929 **11. References**

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