

1 **Title:** Assessing the suitability of diversity metrics to detect biodiversity change

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38 **Abstract**

39 A large number of diversity metrics are available to study and monitor biodiversity, and their
40 responses to biodiversity changes are not necessarily coherent with each other. The choice of
41 biodiversity metrics may thus strongly affect our interpretation of biodiversity change and, hence,
42 prioritization of resources for conservation. Therefore it is crucial to understand which metrics
43 respond to certain changes, are the most sensitive to change, show consistent responses across
44 different communities, detect early signals of species decline, and are insensitive to demographic
45 stochasticity. Here we generated synthetic communities and simulated changes in their composition
46 according to 9 scenarios of biodiversity change to investigate the behaviour of 14 biodiversity
47 metrics. Metrics showed diverse abilities to detect changes under different scenarios. Sørensen
48 similarity index, arithmetic and geometric mean abundance, species and functional richness were
49 the most sensitive to community changes. Sørensen similarity index, species richness and geometric
50 abundance showed consistent responses across all simulated communities and scenarios. Sørensen
51 similarity index and geometric mean abundance were able to detect early signals of species decline.
52 Geometric mean abundance, and functional evenness under certain scenarios, had the greatest
53 ability to distinguish directional trends from stochastic changes, but Sørensen similarity index and
54 geometric mean abundance were the only indices to show consistent signals under all replicates and
55 scenarios. Classic abundance-weighted heterogeneity indices (e.g. Shannon index) were insensitive
56 to certain changes or showed misleading responses, and are therefore unsuitable for comparison of
57 biological communities. We therefore suggest that separate metrics of species composition,
58 richness, and abundance should be reported instead of (or in addition to) composite metrics like
59 Shannon index.

60

61 **Keywords:** Abundance, Biodiversity indicators, Biodiversity monitoring, Similarity Index,
62 Functional Diversity, Phylogenetic Diversity, Shannon Index, Simpson Index, Synthetic community.

63

64 **1. Introduction**

65 In a period of rapid global change, monitoring biodiversity changes is key to detect early
66 warning signals of decline, infer the causes of such decline, and develop effective conservation
67 strategies to mitigate it (Ash et al., 2009; Balmford et al., 2005, 2003; Buckland et al., 2005;
68 Butchart et al., 2010; Gregory et al., 2005; Nichols and Williams, 2006; Tittensor et al., 2014). The
69 multifaceted nature of biodiversity (Gaston, 1996; Purvis and Hector, 2000) is studied through a
70 large number of metrics. Different metrics measure different components of biodiversity such as
71 species richness, abundance, evolutionary history (i.e. phylogenetic diversity; Faith, 1992), and
72 functional traits (Mason et al., 2005). However, as no single metric captures all relevant aspects of
73 biodiversity, none of them taken individually can provide a full picture of the patterns of change.
74 Further, metrics can even be misleading if considered individually. For instance, the geometric
75 mean abundance can increase if rare species increase in abundance, while total abundance is
76 decreasing (Schipper et al., 2016). Similarly, invasive species can increase species richness or
77 functional and phylogenetic diversity, while having negative impacts on the abundances of native
78 species (Thomas, 2013; Winter et al., 2009). The rate and direction of change in a metric may also
79 depend on idiosyncrasies in the state of the initial community, and/or natural ecological succession.
80 Moreover, in addition to directional changes in biodiversity, species relative abundances may
81 fluctuate over shorter time frames due to demographic stochasticity or competitive and predator-
82 prey dynamics. This “noise” can confound the signal of interest (i.e. directional change in response
83 to a specific driver).

84 The choice and response of biodiversity metrics may strongly affect our interpretation of
85 biodiversity change and, hence, prioritization of resources for conservation (Gaston and Spicer,
86 2004; Purvis and Hector, 2000). Thus, it is crucial to understand how alternative metrics respond to
87 specific changes, which metrics are the most sensitive in order to detect early signals of biodiversity
88 decline, and which ones respond consistently to changes. Empirical datasets allow investigating
89 how metrics change in space and time, but have several limitations. These include the limited

90 number of possible scenarios and communities represented, and the lack of control on the
91 underlying cause of change, the likely co-existence of several mechanisms of decline (e.g., decline
92 of habitat specialists due to the loss of their habitat type and decline of large species due to
93 overexploitation). This complicates the attempts to link the behaviour of a diversity metric to a
94 definite mechanism of biodiversity change. Virtual datasets allow full control of both the
95 community composition and the mechanism of decline, and thus allow the comparison of the
96 relative responses of the diversity metrics (Zurell et al., 2010) by simulating ecological processes
97 under alternative scenarios (Dornelas, 2010; Lamb et al., 2009; Münkemüller and Gallien, 2015;
98 Olden and Poff, 2003; Supp and Ernest, 2014).

99 In this study, we explored the behaviour of a set of diversity metrics under different
100 scenarios of biodiversity change. To this end, we generated synthetic communities and simulated
101 changes in their composition to investigate the responses of the metrics. We recorded how metrics
102 changed over time under each scenario, and identified those that were most sensitive to these
103 community changes and showed a consistent response irrespective of the state of the original
104 community. We also assessed non-linearity in metrics responses, and their effect on our ability to
105 detect early warning signals of biodiversity change. Finally, we measured the signal-to-noise ratio
106 (SNR) of the metrics under each scenario to compare the metrics' ability to detect directional
107 changes in biological communities.

108

109 **2. Methods**

110

111 2.1 Virtual dataset

112 We assumed a landscape area of 10,000 km² consisting of two habitats, one dominant and one
113 secondary. For convenience we will refer to these habitats as forest and grassland, respectively. The
114 size of the landscape was chosen such that it was large enough to allow each species to form a
115 population from ~15 to >50,000 individuals. Forest covered a random proportion between 0.7 and

116 0.9 of the entire landscape.

117 We generated 150 species, and randomly assigned to each a diet, body mass, population
118 density, and affinity level for each of the two habitats. The number of species was chosen as a
119 compromise between representativeness of a biological community and computation time for the
120 simulations. For simplicity, we simulated static assemblages with no interactions among species,
121 and restricted the species pool to the consumers in the community.

122 To simulate realistic communities, we followed established macroecological rules.
123 Specifically, our synthetic communities had the following properties: 1) species in higher trophic
124 levels tended to be larger than species in lower trophic levels; and 2) smaller species tended to be
125 more common than large species (Fig. 1). This was implemented as follows. We sampled a diet
126 category for each species, where herbivores (H), omnivores (O) and carnivores (C) had relative
127 probabilities of 0.5, 0.3 and 0.2 respectively. The body masses (kg) were then sampled from log-
128 normal distributions (Loder et al., 1997) reflecting the negative relationship between trophic level
129 and body mass (H: log-mean = 0.5, log-sd = 1.5; C: log-mean = 0.5 multiplied by a random value
130 between 0.5 and 4, log-sd = 1.5; O: log-mean = mean between the log-mean for H and C, log-sd =
131 1.5; see predator-prey body mass ratio reported by Brose et al., 2006). Based on the species' body
132 mass and diet category, we estimated population density (ind/km²) for each species using allometric
133 relationships (log population density vs. log body mass), where the slope of the relationship was
134 sampled from a normal distribution (mean = -0.75, sd = 0.1; Blackburn and Gaston, 1997).

135 We assumed forest habitat to be richer in species than grassland habitat: within the
136 community, 40% of the species were exclusively forest specialists (affinity of 1 to forest and 0 to
137 grassland), 20% were exclusively grassland specialists (affinity of 1 to grassland and 0 to forest),
138 and 40% were ubiquitous. The affinity value of ubiquitous species to forest habitat was sampled
139 from a symmetric beta distribution (shape parameters = 2; so that central values were more frequent
140 than extreme values), and the habitat affinity to grassland was equal to 1-affinity to forest (i.e. the
141 two affinity values summed to 1). The affinity values were multiplied by the estimated species

142 population abundance (in turn obtained by multiplying density by habitat area) in each of the two
143 habitats to produce a realized abundance for each species.

144 Finally, we simulated two phylogenetic trees that described the relatedness among the
145 species in the dataset. The first phylogenetic tree assumed that species with similar traits are more
146 phylogenetically similar. For this, for each community we randomly sampled one or more
147 biological traits (body mass, diet, affinity for the two habitats), and used them to generate a distance
148 matrix based on Gower's distance, as it allows using both continuous and categorical data types
149 (Gower, 1971). The phylogenetic tree was obtained by applying a neighbour joining approach on
150 the distance matrix. The second phylogenetic tree assumed no dependency on biological traits. For
151 this, we followed the same procedure of as described above, yet with biological traits randomly
152 shuffled across species before calculating the distance matrix.

153

154 2.2 Biodiversity change scenarios

155 To explore how metrics behave under diverse conditions, we prepared nine scenarios of biodiversity
156 change. Scenarios (Table 1) ranged from the uniform or proportional decline of all species in the
157 community, to the decline of a subset of species sharing certain characteristics (e.g. traits, relative
158 abundance), to the change in the area available for different species (i.e. extent of habitat). These
159 scenarios span the range of disturbances considered by Dornelas (2010), and expand it to
160 accommodate different susceptibilities to change among different types of species. To measure
161 metrics' sensitivity to noise, we considered an additional scenario of stochastic demographic
162 fluctuations (see section 2.4; Table 1). The simulations consisted of 10 time steps, whereby the first
163 step represented the initial community and the nine subsequent time steps were used to simulate
164 change until reaching an equilibrium (e.g. extinction of a given group of species). Each scenario
165 was deterministic, but was replicated 1,000 times over independently sampled initial communities
166 to account for stochasticity in the simulation parameters (% of forest, body-mass distribution,
167 density distribution, diet categories distribution, habitat preferences).

168

169 2.3 Diversity metrics

170 We recorded a set of metrics (Table 2) encompassing change in community composition from an
171 initial community (temporal turnover), species abundance, taxonomic diversity, functional diversity
172 and phylogenetic diversity. The set included 12 metrics: Sørensen similarity to the species
173 composition of the original community (i.e. time step 1), arithmetic mean abundance, geometric
174 mean abundance, species richness, Simpson diversity index, Shannon index, Faith's phylogenetic
175 diversity, weighted Faith's phylogenetic diversity, functional evenness, functional divergence,
176 functional dispersion and functional richness. Functional diversity metrics covered four traits: body
177 mass, diet category, and the affinity levels for the two habitats.

178 Sørensen similarity index measures the change composition between two or more
179 communities. It is commonly used to compare the composition of different communities in space (β
180 diversity), but can also be used to compare the same community between consecutive time steps, or
181 to a single baseline time period (temporal turnover; Dornelas et al., 2014; Shimadzu et al., 2015).
182 The geometric mean abundance tends to be more sensitive to changes in abundances of rare species
183 than the arithmetic mean, and acts as a composite measure of evenness and abundance (Buckland et
184 al., 2011; Gregory and van Strien, 2010; Gregory et al., 2005; Schipper et al., 2016; van Strien et
185 al., 2012). Because the geometric mean cannot handle zero values, it is common to add a small
186 constant to all values prior the calculation, and to remove the constant from the result (Buckland et
187 al., 2011, 2005). Here, we added 1 to all abundances prior the calculation, and removed 1 from the
188 geometric mean. The Simpson and Shannon indices measure species diversity on the basis of
189 species richness and evenness in abundance. Simpson diversity index tends to be more sensitive
190 than Shannon index to the dominant species in the community (Nagendra, 2002). Faith's
191 phylogenetic diversity is calculated as the total length of all branches of the phylogenetic tree
192 linking species in the community (Faith, 1992). The weighted Faith's phylogenetic diversity is
193 weighted by species' relative abundance (Swenson, 2014). Functional richness represents the

194 amount of functional trait space filled by the community and is calculated as the volume of the
195 convex hull of the trait space (Villéger et al., 2008). Functional dispersion also measures the trait
196 diversity in the community, but differs from functional richness in being less sensitive to outliers.
197 Functional dispersion is calculated as the weighted mean distance in multidimensional trait space of
198 individual species to the weighted centroid of all species, where weights correspond to the relative
199 abundances of the species (Laliberté and Legendre, 2010). Functional evenness describes the
200 evenness of abundance distribution in the functional trait space (Mason et al., 2005). Functional
201 divergence represents how abundance is spread along a functional trait axis, within the range
202 occupied by the community (Mason et al., 2005); it takes lower values when the most abundant
203 species have functional traits that are close to the community centre of functional trait space, and
204 higher when at the extremes.

205

206 2.4 Analyses

207 To quantify the sensitivity of biodiversity metrics under different scenarios, for each of the
208 1,000 replicates, we fitted a linear regression model between the biodiversity metric values and time
209 (10 time steps). Biodiversity metrics were first standardized to a mean of zero and a SD of one
210 across all replicates and scenarios, to obtain comparable slopes among the metrics under alternative
211 scenarios. Trends are thus represented as standardized slopes, which indicate the rate of change in
212 the metrics. The higher the slope values, the higher the sensitivity of the metrics to a given scenario
213 of biodiversity change. We evaluated the consistency of the slope sign over all replicates, and
214 considered metric responses significantly consistent if the slope sign was the same in >95% of the
215 replicates. Thus, the response of metrics showing significant slopes can be considered more
216 consistent across diverse communities. In order to detect differential abilities of the metrics to catch
217 early (EWS) vs. late warning signals (LWS) of biodiversity change (non-linear responses), we also
218 calculated the standardized slopes for the first two and the following eight time steps separately.

219 Finally, to compare the metrics' abilities to detect directional changes rather than stochastic

220 fluctuations in species abundances, we computed the signal-to-noise ratio (SNR) by dividing the
221 slope of each replicate under each scenario by the standard deviation of the slopes of all replicates
222 in the scenario of “Neutral community with stochastic fluctuations”. SNR was computed only for
223 those metrics that are weighted by species abundance, and not for other metrics such as species
224 richness that are by definition insensitive to stochastic demographic fluctuations unless these lead
225 species to extinction. However, under the “Neutral community with stochastic fluctuations” we
226 assumed that extinctions were compensated by colonizations of species with similar characteristics
227 (see Table 1). We considered the SNR sign significantly consistent if it was the same in >95% of the
228 replicates.

229 The simulation was entirely done in R v. 3.0.3 (R Core Team, 2016). We calculated the
230 Simpson, Shannon and Sørensen indices using the ‘vegan’ package v. 2.2. (Oksanen et al., 2012),
231 Faith’s phylogenetic diversity using ‘picante’ package v. 1.6 (Kembel et al., 2010) and functional
232 diversity metrics using ‘FD’ package v. 1.0. (Laliberté et al., 2014).

233

234 **3. Results**

235 3.1 Metric behaviour under alternative scenarios

236 The diversity metrics exhibited different temporal trends under the nine scenarios of biodiversity
237 change (Fig. 2, 3, Fig. A1-8). Under the “Uniform decline” scenario, where all species decreased by
238 the same number of individuals and rare species went extinct first, all metrics showed a decrease,
239 especially species richness, functional richness and functional dispersion (Fig. 2). The “Proportional
240 decline” scenario, where all species declined but their relative abundance remained unchanged until
241 extinction, was characterized by a decrease in all metrics, especially the Sørensen similarity index,
242 Simpson index and functional divergence (Fig. A1). When common species declined, the Sørensen
243 similarity index and arithmetic mean abundance decreased most, followed by geometric mean
244 abundance and species and functional richness. Conversely, the Simpson and Shannon indices

245 increased, as did functional dispersion, evenness and divergence, and weighted phylogenetic
246 diversity (Fig. A2). In the “Toward evenness” scenario, where the community gradually converged
247 to an even abundance distribution, geometric abundance, richness and functional metrics weighted
248 by abundance increased; arithmetic abundance and species richness remained stable; and Sørensen
249 similarity index decreased (Fig. A4). Both the “Rare species decline” and “Large species decline”
250 scenarios were characterized by a slight decrease in geometric mean abundance, species richness
251 and functional richness (Fig. A3, A5). Under the “Invasive species” scenario, metric responses were
252 weak, with some negative and some positive changes but all close to zero (Fig. A6). In the “Habitat
253 loss” scenario, where forest extent was gradually decreased, the Sørensen similarity and the
254 arithmetic mean abundance decreased, followed by the geometric mean abundance, species richness
255 and functional richness, while functional dispersion, evenness and divergence, and the weighted
256 phylogenetic diversity (using the trait-based tree) increased (Fig. A7). When the forest habitat loss
257 was replaced by grassland, the metrics behaved similarly to the “Habitat loss” scenario, with the
258 exception of the arithmetic mean abundance, which, despite decreasing, was partly balanced by the
259 increase in abundance of grassland species (Fig. A8).

260

261 3.2 Metric sensitivity

262 In general, the responsiveness of the metrics was mostly determined by the specific change in the
263 community: richness-based metrics (species richness, functional richness, phylogenetic diversity)
264 showed stronger responses when the change led to a higher number of extinctions, abundance
265 metrics (arithmetic and geometric mean) responded strongest when abundance declined in many
266 species, and abundance-weighted metrics (Simpson, Shannon, weighted phylogenetic diversity, and
267 functional dispersion, evenness and divergence) mainly responded to changes in species abundance
268 distributions. The metrics most sensitive to biodiversity change (i.e., those with steeper slopes) were
269 the Sørensen similarity index, arithmetic and geometric mean abundance, species richness and

270 functional richness. The weighted phylogenetic diversity metrics and functional divergence were
271 less sensitive in most scenarios (Fig. 3).

272

273 3.3 Metrics' consistency across iterations

274 Sørensen similarity index, species richness and geometric mean abundance were the only metrics
275 that exhibited consistent responses in more than 95% of the replicates under all scenarios.

276 Arithmetic mean abundance, Simpson and Shannon indices, and functional richness were consistent
277 in most of the scenarios, whereas phylogenetic diversity, weighted phylogenetic diversity,
278 functional dispersion, evenness and divergence often showed inconsistent responses across
279 replicates (Fig. 3).

280

281 3.4 Early versus Late warning signals of biodiversity change

282 Many metrics showed non-linear responses (Fig. 4): some showed convex (accelerating) or concave
283 (deaccelerating) responses, or inverted their trend. Species richness and functional richness
284 generally showed a convex response, remaining stable until species went extinct. Under the
285 “Proportional decline” scenario all abundance-weighted metrics behaved similarly, with a stable
286 initial pattern followed by a steep decline when species went extinct. Similarly, geometric mean
287 abundance response was stronger at later stages under the “Habitat replacement” scenario. Concave
288 responses were rare, and only occurred in particular instances, such as geometric mean abundance
289 and species richness and functional richness under the “Uniform decline” scenario (Fig. 2). In other
290 instances, the trend reversed during the simulation, for example functional evenness under “Rare
291 species decline” and “Large species decline”, which decreased at first, but increased when species
292 went extinct (Fig. A3, A5). Similarly, under the “Habitat replacement” scenario the geometric mean

293 abundance, Simpson and Shannon indices, and functional evenness and dispersion first increased
294 influenced by grassland species growth, but later decreased as a consequence of forest species
295 decline and extinction (Fig. 4, A8). Among the metrics considered, Sørensen similarity index and
296 geometric mean abundance showed more consistent responses in the first two and last eight time
297 steps.

298

299 3.5 Sensitivity to demographic fluctuations

300 The metrics which were least confounded by demographic stochasticity (highest SNR) were
301 the geometric mean abundance (to a lesser extent under the “Invasive species” scenario), the
302 functional evenness under the “Proportional decline” and “Toward evenness” scenarios, and the
303 functional divergence under the “Proportional decline” (Fig. 5). The other metrics did not show
304 evident differences in SNR. The SNRs of the Sørensen similarity index and the geometric mean
305 abundance exhibited consistent responses under all scenarios. Arithmetic mean abundance was also
306 fairly consistent in most scenarios, whereas Shannon and Simpson indices, weighted phylogenetic
307 diversity and functional dispersion, divergence and evenness were often inconsistent.

308

309 **4. Discussion**

310 Simulating biodiversity change through time allowed us to explore the behaviour of a set of
311 biodiversity metrics and assess their suitability for monitoring biodiversity change, including
312 declines in species’ abundances that can be of conservation concern. Richness-based metrics require
313 presence data, which is less time-consuming and costly to collect than abundance data (Costello et
314 al., 2016). Knowing which species are present, particularly those that are ecologically important, or
315 may be of conservation concern, is fundamental to biodiversity data analysis (Asaad et al., 2016;
316 Latombe et al., 2016). Functional richness can also provide important complementary information

317 that can be more directly related to ecosystem function and stability. However, richness-based
318 metrics are not sufficient on their own for biodiversity monitoring, because they only respond to
319 species extirpations or colonizations. Hence, they are inadequate for detecting early warning signals
320 of biodiversity change.

321 The Sørensen similarity index was used as a temporal beta-diversity index, and showed high
322 sensitivity to changes, as it detects any change in composition and abundance of the species relative
323 to the initial community. The extent of its change is proportional to the magnitude of the change,
324 which, although desirable in some instances, it may under-estimate small but significant change.
325 For example, the decline of elephants in Savanna would have little impact on the Sørensen
326 similarity index, but potentially large indirect impacts on the habitat structure and the community.
327 Interpretation of why this, and other beta-diversity indices, are changing requires knowing which
328 species occurrences and abundances are changing.

329 Abundance metrics are appealing for biodiversity monitoring, because a change in
330 abundance of one or more species may lead to a change from one community to another, may
331 reflect the decline or recovery of a threatened species, or an alien species becoming invasive.
332 However, trends in population abundance can be easily confounded by two factors: demographic
333 and environmental stochasticity, and abundance compensations. Populations of some species, such
334 as microbes, invertebrates and plants, may live at high population densities and fluctuate by orders
335 of magnitude due to natural reproductive cycles and weather events (Damuth, 1987; Sinclair, 2003).
336 As a consequence, such species may dominate the arithmetic mean abundance of a given
337 community, either being common or during outbreaks, and can easily confound temporal trends by
338 natural demographic fluctuations. In this respect, the geometric mean abundance appears to be more
339 useful by being more sensitive to the rare species of the community (van Strien et al., 2012),
340 whether this is because they live at low densities or are close to extinction. Less abundant species,
341 such as top predators or large herbivores, may be keystone species (Estes et al., 2011; Leleu et al.,

342 2012; Ripple et al., 2015, 2014) that tend to be more vulnerable to extinctions (Cardillo et al., 2005;
343 Purvis et al., 2000) and hence deserve particular conservation attention. On the other hand, small
344 common species may be fundamental for ecosystem functioning and services (Gaston and Fuller,
345 2008).

346 Abundance compensation may occur, for example when the increase of one species leads to
347 the decline of another (e.g. invasive species), or conversely when the decline of one species prompts
348 the increase of another one (e.g. competitive release), or just by the occurrence of two simultaneous
349 but unrelated events. In any of these cases, arithmetic mean abundance may be easily confounded,
350 while geometric mean abundance would respond by being sensitive to the change in the rarer of the
351 two species. An example is given by the “Toward evenness” scenario where the arithmetic mean
352 was unresponsive, but the geometric mean abundance increased in response to the growth of
353 populations of rare species. For these reasons abundance metrics on their own may not provide
354 sufficient information for biodiversity monitoring. It is therefore essential that the identities of the
355 species whose abundance is changing are also recorded.

356 Abundance-weighted heterogeneity indices carry more information than richness alone and
357 are sensitive to population changes. However, their weighting of richness and relative abundance
358 varies (Magurran, 2004) and these components can vary independently (e.g. Costello and Myers,
359 1987). Thus they may exhibit counter-intuitive trends and non-linear responses. An illustrative
360 example is presented by the Shannon and Simpson indices, which increase if common species
361 decline but abruptly change when these species go extinct (Fig. S2). This questions the reliability of
362 such metrics for biodiversity monitoring (van Strien et al., 2012). In addition, our results question
363 the validity of such metrics for the comparison of the biodiversity state between biological
364 communities. Evenness is certainly an aspect of diversity, but we should also recognize that
365 abundance distributions are naturally skewed (Magurran and Henderson, 2003) and an increase of
366 evenness does not necessarily indicate greater ‘biodiversity’ (Schipper et al., 2016; van Strien et al.,

367 2012). This problem is further exacerbated in metrics that cannot account for extinct species, such
368 as functional diversity metrics (i.e. that do not allow for zero abundance values). Functional
369 diversity metrics weighted by abundance might increase after the loss of rare and particular species
370 (in terms of traits), thus leading to the conclusion that an impoverished community is actually more
371 diverse than an intact community. All in all, we consider that phylogenetic and functional diversity
372 metrics can only be informative when considered in relation to the more fundamental variables of
373 species composition, richness and abundance and where they have been studied for long enough to
374 relate their dynamics to actual changes in community structure.

375 In this study, we employed a simplified model of biological communities where the decline
376 or loss of a certain biodiversity component does not prompt an increase or decrease in another. Such
377 interactions can be highly complex and unpredictable (Rossberg, 2013; Yodzis, 1988), and are
378 likely to complicate interpretation. The trends that we have depicted are thus useful to investigate
379 metrics' behaviour under controlled conditions, but may not be considered realistic representations
380 of community change under specific pressures. We considered one form of noise deriving from
381 population demographic stochasticity, but in practice, another form of noise is errors in abundance
382 estimates due to e.g. detection bias. The influence of error in abundance estimates on diversity
383 metrics is treated in Lamb *et al.* (2009). In our simulations, we simulated communities
384 characterized by certain macroecological patterns in order to simulate realistic species assemblages
385 (e.g. body mass distribution, trophic levels, body mass-density relationship). However in practice,
386 another source of uncertainty is the choice of the empirical sample of species monitored (Maurer
387 and McGill, 2011). These samples often focus on a given taxon or are collected on an opportunistic
388 basis. Further research is needed to investigate the extent to which incomplete samples can inform
389 about overall changes in a biological community.

390 The Convention on Biological Diversity (CBD) has renewed the commitment to halt or at
391 least reduce the rate of biodiversity loss (CBD, 2010). To this end, it is necessary to collect

392 biodiversity data in a systematic way, capturing those key biodiversity dimensions that allow us to
393 monitor biodiversity change through time (Pereira et al., 2013), and prevent further biodiversity loss
394 by prioritizing conservation funding and actions. Our results clearly indicate that no single metric
395 should be employed for biodiversity monitoring. However, Sørensen similarity index and geometric
396 mean abundance share several ideal properties for biodiversity monitoring such as the sensitivity to
397 most scenarios of change, consistency in their responses irrespective of the original community
398 composition, the ability to capture early signals of biodiversity change, and robustness to
399 demographic stochasticity. Species richness and functional richness also share several of these
400 properties. Therefore we recommend that biodiversity monitoring include the following primary
401 data: (1) presence of species in the community (i.e. species composition), and (2) species
402 abundance. From these at least the geometric mean abundance, Sørensen's similarity index (or
403 similar turnover measures) and species richness should be calculated. While metrics such as
404 phylogenetic and functional diversity may also be useful, scientists should consider whether they
405 provide added value in terms of conveying useful information to end-users such as conservation
406 managers. For example, phylogenetic diversity and functional richness are often correlated with
407 species richness (Schipper et al., 2016). Generally, a small set of complementary and conceptually
408 simple metrics is more transparent, intuitive and informative for policy makers on the underlying
409 causes of changes in biodiversity (e.g. Latombe et al. 2016 for invasive species).

410

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415 Cooperation in Science and Technology).

416 **Table 1.** Description of the scenarios of biodiversity change. Each of the scenario is simulated for 9
 417 consecutive steps (from the 2nd to the 10th).
 418

| Scenario | Description | Rationale |
|-----------------------|---|--|
| Uniform decline | At each time step all species are reduced by 1/9 of the mean abundance of all species (i.e. species decline at different rates). By the end of the simulation half of the species have gone extinct. | Extreme scenario to investigate metric behaviour where all species are losing the same number of individuals. |
| Proportional decline | At each time step all species are reduced by 1/9 of their original population size (i.e. species decline at the same rate). By the end of the simulation all species have gone extinct. | General decline of all species, e.g. in response to the loss of natural areas. |
| Large species decline | At each time step all large species are reduced by 1/9 of their original population size. By the end of the simulation all large species have gone extinct. Large species are defined as those having a body mass larger than the 75 th percentile of the body mass of all species in the initial community. | Large species are generally more vulnerable to extinction (Cardillo et al., 2005; Purvis et al., 2000), and are often targeted for subsistence or trophy hunting. |
| Rare species decline | At each time step all rare species are reduced by 1/9 of their original population size. By the end of the simulation all rare species have gone extinct. Rare species are defined as those having a population size lower than the 25 th percentile of the population size of all species in the initial community. | Trophy hunting/Collection of rare animals (e.g. seashells, corals, butterflies..), together with higher genetic/demographic or environmental stochasticity, can easily |

| | | |
|------------------------|--|---|
| | | trigger extinction vortex (Courchamp et al., 2006; Gilpin and Soulé, 1986). |
| Common species decline | At each time step all common species are reduced by 1/9 of their original population size. By the end of the simulation all common species have gone extinct. Common species are defined as those having a population size higher than the 75 th percentile of the population size of all species in the initial community. | Common species may be those more commonly hunted/fished. Common grassland species are also impacted by agricultural intensification (Gaston and Fuller, 2008). |
| Toward evenness | At each time step abundance is added to the rarer and or removed from the more common species. The increase/decrease in abundance was set to 1/9 of the species difference to the mean abundance of the community. By the end of the simulation all species have the same abundance. | The decline of common species may be partly compensated by an increase in rare species (Schipper et al., 2016). We consider an extreme case to assess how metrics respond to an increase in evenness. |
| Habitat loss | At each time step forest habitat is reduced by 1/9 of its original extent. At each time step species abundance in forest is recalculated according to the new extent. The habitat is not replaced, it is just lost (i.e. converted to unsuitable habitat for all species). By the end of the simulation forest habitat is entirely lost. | Habitat loss is one of the first cause of biodiversity loss (Hoffmann et al., 2010). |
| Habitat replacement | At each time step, 1/9 of the original forest habitat extent is replaced by grassland. At each time step species abundance is recalculated according to the new extent of the two habitats. By the end of the simulation forest habitat is entirely lost and grassland habitat covers the entire landscape. | Often habitat is replaced by habitat suitable to different species. Land cover change can be induced by climate change or human disturbance (e.g. fire). |

| | | |
|--|--|---|
| Invasive species | <p>In the second step a new species (invasive species) is added to the community. The species originally has $1/9^{\text{th}}$ of its potential population size, and at each step it is increased by an additional $1/9^{\text{th}}$. Meanwhile, a sample of five species in the community (sensitive species), decline by $1/9^{\text{th}}$ of their population size. By the end of the simulation, the invasive species has reached its carrying capacity, while the sensitive species have gone extinct. The invasive species is sampled randomly from ubiquitous species living at high population density ($>75^{\text{th}}$ percentile of the population density of all species in the community). Sensitive species are sampled randomly from the community.</p> | <p>Invasive species are one of the main cause of biodiversity loss and homogenization (Hoffmann et al., 2010). We consider the scenario as one case of confounding effect on the metrics due to the population growth of alien species.</p> |
| Neutral community with stochastic fluctuations | <p>Species abundances fluctuate randomly while the total biomass remains constant, where the extent of the fluctuation depends on species body mass (Brown et al., 2004; Korhonen et al., 2010; $\text{Abundance } t = 1 = \text{Abundance } t \times \exp[N(\mu = 0, \sigma = 0.1 \times (\text{body_mass})^{-1/4})]$; Peters, 1983). When a species is lost from the community, an individual of a species with the exact same characteristics colonizes the community (i.e. trait distribution remains stable).</p> | <p>Demographic stochasticity where species are characterized by demographic rates (Hubbell, 2001; Rossberg, 2013).</p> |

420 **Table 2.** Description of the diversity metrics employed in the simulation. Ab = Population
421 abundance; N_{sp} = Number of species; BL = Branch length of the phylogenetic tree. In the Sørensen
422 similarity formula: $_1$ = original community and $_2$ = community at time step x.
423

| Diversity metric | Formula/Definition | Reference |
|---|---|----------------------------|
| Sørensen similarity | $x = 1 - \frac{\sum_{i=1}^{n_{sp}} Ab_{i1} - Ab_{i2} }{\sum_{i=1}^{n_{sp}} Ab_{i1} + Ab_{i2} }$ | (Sorensen, 1948) |
| Arithmetic mean abundance | $x = \frac{\sum_{i=1}^{n_{sp}} Ab_i}{n_{sp}}$ | |
| Geometric mean abundance | $x = \exp\left(\frac{\sum_{i=1}^{n_{sp}} \ln Ab_i}{n_{sp}}\right)$ | |
| Species richness | $x = n_{sp}[Ab > 0]$ | |
| Gini-Simpson Index | $x = 1 - \sum_{i=1}^{n_{sp}} Ab_i^2$ | (Simpson, 1949) |
| Shannon Index | $x = - \sum_{i=1}^{n_{sp}} Ab_i * \ln Ab_i$ | (Shannon and Weaver, 1949) |
| Faith's phylogenetic diversity | $x = \sum_{i=1}^{NB} BL_i$ | (Faith, 1992) |
| Weighted Faith's phylogenetic diversity | $x = NB * \frac{\sum_{i=1}^{NB} BL_i * Ab_i}{\sum_{i=1}^{NB} BL_i}$ | (Swenson, 2014) |
| Functional Richness | The convex hull volume of the individual species in | (Villéger et al., 2008) |

multidimensional trait space

(Villéger et al. 2008).

| | | |
|---------------------|---|-------------------------|
| Functional evenness | The regularity with which species abundances are distributed along the minimum spanning tree which links all the species in the multidimensional functional space | (Villéger et al., 2008) |
|---------------------|---|-------------------------|

(Villéger et al. 2008).

| | | |
|-----------------------|---|------------------------|
| Functional divergence | Species deviance from the mean distance to the centre of gravity weighted by relative abundance within multidimensional trait space | (Villéger et al. 2008) |
|-----------------------|---|------------------------|

(Villéger et al. 2008).

| | | |
|-----------------------|--|-------------------------------|
| Functional dispersion | The weighted mean distance in multidimensional trait space of individual species to the centroid of all species. Weights are species relative abundances | (Laliberté and Legendre 2010) |
|-----------------------|--|-------------------------------|

(Laliberté and Legendre 2010)

424

425

426 **Fig. 1.** (a) Distribution of body mass (\log_{10} kg) in the virtual community. (b) Relationship between
427 body mass (\log_{10} kg) and population density (\log_{10} ind/km²). Green = Herbivores; Orange =
428 Omnivores; Red = Carnivores.

429

430 **Fig. 2.** Temporal trends in biodiversity metrics under the “Uniform decline” scenario. Each line
431 represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
432 comparability (mean = 0; sd = 1).

433

434 **Fig. 3.** Heatmap representing the mean trend (standardized mean slopes over time; Color bar) of
435 biodiversity metrics for the alternative scenarios of biodiversity change. Standardized slopes
436 represent the rate of change in the metrics. * indicate metrics that show consistent trends (same
437 sign) in >95% of the replicates. The heatmap can be read by row or by column, depending on
438 whether one wants to compare metric behaviour in a given scenario or a given metric’s behaviour
439 across scenarios. Ar = arithmetic; Gm = geometric; Phil = phylogenetic; Div = diversity; wPhil =
440 phylogenetic weighted by abundance; F = Functional; T indicates phylogenetic trees based on
441 Traits; R indicates Random trees.

442

443 **Fig. 4.** Heatmap representing the early (EWS) vs. late warning (LWS) signals of biodiversity
444 change for the alternative scenarios of biodiversity change. Both are represented as standardized
445 mean slopes over time, where EWS is calculated in the first 2 steps, and LWS in the second 8 steps.
446 The heatmap can be read by comparing the color (standardized slopes) of EWS and LWS within the
447 a given metric for a given scenario: the colors differ if the metric response is non-linear. Ar =
448 arithmetic; Gm = geometric; Phil = phylogenetic; Div = diversity; wPhil = phylogenetic weighted
449 by abundance; F = Functional; T indicates phylogenetic trees based on Traits; R indicates Random
450 trees.

451

452 **Fig. 5.** Heatmap representing signal to noise ratio (SNR) (Color bar) of biodiversity metrics
453 weighted by abundance for alternative scenarios of biodiversity change. SNR is the strength of the
454 signal (biodiversity change measured as standardized slopes) relative to the noise in the metric
455 resulting from demographic fluctuations (SD in metric values under the “Neutral community with
456 stochastic fluctuations” scenario). * indicate SNR that show consistent trends (same sign) in >95%
457 of the replicates. The heatmap can be read by row or by column, depending on whether one wants
458 to compare metric behaviour in a given scenario or a given metric’s behaviour across scenarios. Ar
459 = arithmetic; Gm = geometric; Phil = phylogenetic; Div = diversity; wPhil = phylogenetic weighted
460 by abundance; F = Functional; T indicates phylogenetic trees based on Traits; R indicates Random
461 trees.
462

463 **Supplementary material:**

464 **Appendix A**

465

466 **Fig. A1.** Temporal trends in biodiversity metrics under the “Proportional decline” scenario. Each
467 line represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
468 comparability (mean = 0; sd = 1).

469 **Fig. A2.** Temporal trends in biodiversity metrics under the “Common species decline” scenario.
470 Each line represents one of the 1,000 replicates. Metrics values are standardized on the same scale
471 for comparability (mean = 0; sd = 1).

472 **Fig. A3.** Temporal trends in biodiversity metrics under the “Rare species decline” scenario. Each
473 line represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
474 comparability (mean = 0; sd = 1).

475 **Fig. A4.** Temporal trends in biodiversity metrics under the “Toward evenness” scenario. Each line
476 represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
477 comparability (mean = 0; sd = 1).

478 **Fig. A5.** Temporal trends in biodiversity metrics under the “Large species decline” scenario. Each
479 line represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
480 comparability (mean = 0; sd = 1).

481 **Fig. A6.** Temporal trends in biodiversity metrics under the “Invasive species” scenario. Each line
482 represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
483 comparability (mean = 0; sd = 1).

484 **Fig. A7.** Temporal trends in biodiversity metrics under the “Habitat loss” scenario. Each line
485 represents one of the 1,000 replicates. Metrics values are standardized on the same scale for
486 comparability (mean = 0; sd = 1).

487 **Fig. A8.** Temporal trends in biodiversity metrics under the “Habitat replacement” scenario. Each
488 line represents one of the 1,000 replicates. Metrics values are standardized on the same scale for

489 comparability (mean = 0; sd = 1).

490 **References**

- 491 Asaad, I., Lundquist, C.J., Erdmann, M.V., Costello, M.J., 2016. Biodiversity variables for
492 prioritization and monitoring of conservation areas. *Biol. Conserv.* Submitted.
- 493 Ash, N., Jürgens, N., Leadley, P., Alkemade, R., Araújo, M.B., Asner, G.P., Bachelet, D., Costello,
494 M.J., Finlayson, M., Lavorel, S., Mace, G., Mooney, H., Parr, T., Scholes, R., Soberon, J.,
495 Turner, W., Prieur- Richard, A.H., Larigauderie, A., Walther, B.A., 2009. bioDISCOVERY:
496 Assessing, monitoring and predicting biodiversity. DIVERSITAS Report No. 7.
- 497 Balmford, A., Bennun, L., Brink, B. Ten, Cooper, D., Côte, I.M., Crane, P., Dobson, A., Dudley, N.,
498 Dutton, I., Green, R.E., Gregory, R.D., Harrison, J., Kennedy, E.T., Kremen, C., Leader-
499 Williams, N., Lovejoy, T.E., Mace, G., May, R., Mayaux, P., Morling, P., Phillips, J., Redford,
500 K., Ricketts, T.H., Rodríguez, J.P., Sanjayan, M., Schei, P.J., van Jaarsveld, A.S., Walther, B. a,
501 2005. The Convention on Biological Diversity's 2010 target. *Science* 307, 212–213.
502 doi:10.1126/science.1106281
- 503 Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. *Trends Ecol.*
504 *Evol.* 18, 326–330. doi:10.1016/S0169-5347(03)00067-3
- 505 Blackburn, T.M., Gaston, K.J., 1997. A critical assessment of the form of the interspecific
506 relationship between abundance and body size in animals. *J. Anim. Ecol.* 66, 233–249.
507 doi:10.2307/6025
- 508 Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L.,
509 Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H. a., Dell, T., Edwards, F.,
510 Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K.,
511 Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J.,
512 Woodward, G., Cohen, J.E., 2006. Consumer-resource body-size relationships in natural food
513 webs. *Ecology* 87, 2411–2417. doi:10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2
- 514 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory

515 of ecology. *Ecology* 85, 1771–1789. doi:10.1890/03-9000

516 Buckland, S.T., Magurran, A.E., Green, R.E., Fewster, R.M., 2005. Monitoring change in
517 biodiversity through composite indices. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 360, 243–
518 254. doi:10.1098/rstb.2004.1589

519 Buckland, S.T., Studeny, A.C., Magurran, A.E., Illian, J.B., Newson, S.E., 2011. The geometric
520 mean of relative abundance indices: a biodiversity measure with a difference. *Ecosphere* 2,
521 art100. doi:10.1890/ES11-00186.1

522 Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A.,
523 Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., et al., 2010. Global biodiversity: indicators
524 of recent declines. *Science* (80-.). 328, 1164–1168.

525 Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme,
526 C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species.
527 *Science* (80-.). 309, 1239–1241.

528 CBD, 2010. Strategic plan for Biodiversity 2011-2020. Montreal.

529 Costello, M.J., Ariño, A.H., J., D., Hobern, D., Krishtalka, L., Peterson, A.T., Soberón, J., 2016.
530 Distinguishing essential and fundamental biodiversity variables. *Biol. Conserv.* Submitted.

531 Costello, M.J., Myers, A.A., 1987. Amphipod fauna of the sponges *Halichondria panicea* and
532 *Hymeniacidon perleve* in Lough Hyne, Ireland. *Mar. Ecol. Prog. Ser.* 41, 115–121.
533 doi:10.3354/meps041115

534 Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L., Meinard, Y., 2006. Rarity
535 value and species extinction: The anthropogenic allee effect. *PLoS Biol.* 4, 2405–2410.
536 doi:10.1371/journal.pbio.0040415

537 Damuth, J., 1987. Interspecific allometry of population density in mammals and other animals: the
538 independence of body mass and population energy-use. *Biol. J. Linn. Soc.* 31, 193–246.

539 Dornelas, M., 2010. Disturbance and change in biodiversity. *Philos. Trans. R. Soc. Lond. B. Biol.*
540 *Sci.* 365, 3719–3727. doi:10.1098/rstb.2010.0295

541 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E.,
542 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*
543 (80-.). 344, 296–299. doi:10.1126/science.1248484

544 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R.,
545 Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine,
546 R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B.,
547 Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet
548 Earth. *Science* (80-.). 333, 301–306.

549 Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.

550 Gaston, K.J., 1996. *Biodiversity: A biology of numbers and difference*. Blackwell Science, Oxford.

551 Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology.
552 *Trends Ecol. Evol.* 23, 14–19. doi:10.1016/j.tree.2007.11.001

553 Gaston, K.J., Spicer, J.I., 2004. *Biodiversity: an introduction*, 2th ed. Blackwell Publishing, Oxford,
554 UK.

555 Gilpin, M., Soulé, M., 1986. Minimum viable populations: processes of species extinction, in:
556 *Conservation Biology: The Science of Scarcity and Diversity*. pp. 19–34.

557 Gower, J.C., 1971. A General Coefficient of Similarity and Some of Its Properties. *Biometrics* 27,
558 857–871. doi:10.2307/2528823

559 Gregory, R.D., van Strien, A., 2010. Wild Bird Indicators: Using Composite Population Trends of
560 Birds as Measures of Environmental Health. *Ornithol. Sci.* 9, 3–22. doi:10.2326/osj.9.3

561 Gregory, R.D., van Strien, A., Vorisek, P., Gmelig-Meyling, A.W., Noble, D.G., Foppen, R.P.B.,
562 Gibbons, D.W., 2005. Developing indicators for European birds. *Philos. Trans. R. Soc. Lond.*

563 B. Biol. Sci. 360, 269–288. doi:10.1098/rstb.2004.1602

564 Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M.,
565 Carpenter, K.E., Chanson, J., Collen, B., Cox, N. a, Darwall, W.R.T., Dulvy, N.K., Harrison,
566 L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F.,
567 Vié, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F.,
568 Andrew, P., Aquino Ortiz, A.L., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P.,
569 Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G, W., Burfield, I.J., Burton, J. a, Capper,
570 D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M.,
571 Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Cortez Fernandez, C.F.,
572 Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C.,
573 Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler,
574 S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G. a, Harris,
575 R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Icochea M, J., Inger,
576 R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M.,
577 Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison,
578 R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K.,
579 McIvor, A., Moehlman, P.D., Molur, S., Muñoz Alonso, A., Musick, J. a, Nowell, K.,
580 Nussbaum, R. a, Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro,
581 B. a, Pourkazemi, M., Racey, P. a, Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin,
582 A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de
583 Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan,
584 C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith,
585 A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J.,
586 Timmins, R., Tobias, J. a, Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S. V, van Dijk, P.P.,
587 Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E. a, Xie, F., Young, B.E.,
588 Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G. a B.,

589 Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S. a, McNeely, J. a, Mittermeier, R. a, Reid,
590 G.M., Rodriguez, J.P., Rosenberg, A. a, Samways, M.J., Smart, J., Stein, B. a, Stuart, S.N.,
591 2010. The impact of conservation on the status of the world's vertebrates. *Science* (80-.). 330,
592 1503–9. doi:10.1126/science.1194442

593 Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princet. Univ.
594 Press. Princeton, NJ 32, 375. doi:10.1111/j.1939-7445.2005.tb00163.x

595 Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg,
596 S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology.
597 *Bioinformatics* 26, 1463–4. doi:10.1093/bioinformatics/btq166

598 Korhonen, J.J., Soininen, J., Hillebrand, H., 2010. A quantitative analysis of temporal turnover in
599 aquatic species assemblages across ecosystems. *Ecology* 91, 508–517. doi:10.1890/09-0392.1

600 Laliberté, A.E., Legendre, P., Shipley, B., Laliberté, M.E., 2014. FD: measuring functional diversity
601 from multiple traits, and other tools for functional ecology. *R Packag.* 0–12. doi:http://cran.r-
602 project.org/web/packages/FD/FD.pdf

603 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity
604 from multiple traits. *Ecology* 91, 299–305. doi:10.1890/08-2244.1

605 Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J., Haughland, D.L., 2009.
606 Indices for monitoring biodiversity change: Are some more effective than others? *Ecol. Indic.*
607 9, 432–444. doi:10.1016/j.ecolind.2008.06.001

608 Latombe, G., Pyše, P., Jeschke, J.M., Blackburn, T.M., Bacher, S., Capinha, C., Costello, M.J.,
609 Fernández, M., Gregory, R.D., Hobern, D., Hui, C., Jetz, W., Kumschick, S., Pergl, J., Roy,
610 H.E., Scalera, R., Squires, Z.E., Wilson, D.R.U., Winter, M., Genovesi, P., McGeoch, M.A.,
611 2016. A vision for global monitoring of biological invasions. *Biol. Conserv.* Submitted.

612 Leleu, K., Remy-Zephir, B., Grace, R., Costello, M.J., 2012. Mapping habitats in a marine reserve
613 showed how a 30-year trophic cascade altered ecosystem structure. *Biol. Conserv.* 155, 193–

- 614 201. doi:10.1016/j.biocon.2012.05.009
- 615 Loder, N., Blackburn, T.M., Gaston, K.J., 1997. The slippery slope: towards an understanding of the
616 body size frequency distribution. *Oikos* 78, 195–201.
- 617 Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford.
- 618 Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species
619 abundance distributions. *Nature* 422, 714–716. doi:10.1038/nature01547
- 620 Mason, N.W.H.H., de Bello, F., Mouillot, D., Pavoine, S., Dray, S., Lee, W.G., Wilson, J.B., 2005.
621 Functional richness, functional evenness and functional divergence: The primary components
622 of functional diversity. *Oikos* 111, n/a–n/a. doi:10.1111/jvs.12013
- 623 Maurer, B.A., McGill, B.J., 2011. Measurement of species diversity, in: Magurran, A.E., McGill,
624 B.J. (Eds.), *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford
625 University Press, USA.
- 626 Münkemüller, T., Gallien, L., 2015. VirtualCom: a simulation model for eco-
627 evolutionarycommunity assembly and invasion. *Methods Ecol. Evol.* 6, 735–743.
- 628 Nagendra, H., 2002. Opposite trends in response for the Shannon and Simpson indices of landscape
629 diversity. *Appl. Geogr.* 22, 175–186. doi:10.1016/S0143-6228(02)00002-4
- 630 Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. *Trends Ecol. Evol.* 21, 668–673.
631 doi:10.1016/j.tree.2006.08.007
- 632 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O’Hara, R.B., Simpson, G.L., Solymos, P.,
633 Stevens, M.H.H., Wagner, H., 2012. *vegan: Community Ecology Package*. R Packag. version.
634 doi:10.4135/9781412971874.n145
- 635 Olden, J.D., Poff, N.L., 2003. Toward a mechanistic understanding and prediction of biotic
636 homogenization. *Am. Nat.* 162, 442–460. doi:10.1086/378212
- 637 Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford,

638 M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P.,
639 Freyhof, J., Gregory, R.D., Heip, C., Höft, R., Hurr, G., Jetz, W., Karp, D.S., McGeoch, M.A.,
640 Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N.,
641 Turak, E., Walpole, M., Wegmann, M., 2013. Essential Biodiversity Variables. *Science* (80-).
642 339, 277–278. doi:10.1126/science.1229931

643 Peters, R.H., 1983. *The ecological implications of body size*, Cambridge studies in ecology.

644 Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom Extinction and the Loss
645 of Evolutionary History. *Science* (80-). 288, 328–330.

646 Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212–219.
647 doi:10.1038/35012221

648 R Core Team, 2016. *R: A language and environment for statistical computing*. R Found. Stat.
649 Comput. Vienna, Austria. <http://www.R-project.org/>.

650 Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J.,
651 Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing,
652 A.J., 2014. Status and Ecological Effects of the World’s Largest Carnivores. *Science* (80-).
653 343, 1241484.

654 Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W.,
655 Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom,
656 C.J., Terborgh, J., Van Valkenburgh, B., 2015. Collapse of the world’s largest herbivores. *Sci.*
657 *Adv.* 1, e1400103.

658 Rossberg, A.G., 2013. *Food Webs and Biodiversity: Foundations, Models, Data*. John Wiley &
659 Sons, Chichester.

660 Schipper, A.M., Belmaker, J., Miranda, M., Navarro, L.M., Böhmig-Gaese, K., Costello, M.J.,
661 Dornelas, M., Foppen, R.P.B., Hortal, J., Huijbregts, M.A.J., Martín-López, B., Pettorelli, N.,
662 Queiroz, C., Rossberg, A.G., Santini, L., Schiffrers, K., Steinmann, Z.J.N., Visconti, P.,

663 Rondinini, C., Pereira, H.M., 2016. Contrasting changes in the abundance and diversity of
664 North American bird assemblages from 1971 to 2010. *Glob. Chang. Biol.*
665 doi:10.1111/gcb.13292

666 Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. *Math. theory*
667 *Commun.* 27, 117. doi:10.2307/3611062

668 Shimadzu, H., Dornelas, M., Magurran, A.E., 2015. Measuring temporal turnover in ecological
669 communities. *Methods Ecol. Evol.* 6, 1384–1394. doi:10.1111/2041-210X.12438

670 Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.

671 Sinclair, A.R.E., 2003. Mammal population regulation, keystone processes and ecosystem
672 dynamics. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 358, 1729–1740.
673 doi:10.1098/rstb.2003.1359

674 Sorensen, T., 1948. A method of establishing groups of equal amplitude in plant socio-logy based on
675 similarity of species content and its application to analyses of the vege-tation on Danish
676 commons. *Biol. Skr.* 5, 1–34.

677 Supp, S.R., Ernest, S.K.M., 2014. Species-level and community-level responses to disturbance: A
678 cross-community analysis. *Ecology* 95, 1717–1723. doi:10.1890/13-2250.1

679 Swenson, N.G., 2014. Functional and Phylogenetic Ecology in R. *Funct. Phylogenetic Ecol.* R 9–
680 26. doi:10.1007/978-1-4614-9542-0

681 Thomas, C.D., 2013. The Anthropocene could raise biological diversity. *Nature* 502, 7.
682 doi:10.1038/502007a

683 Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart,
684 S.H.M., Leadley, P.W., Regan, E.C., Alkamade, R., Baumung, R., Bellard, C., Bouwman, L.,
685 Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D.,
686 Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch,

687 T., Hoft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., J., L.,
688 Lojenga, R.K., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, T., Noonan-
689 Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L.,
690 Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., van Kolck, J., Visconti, P., Ye,
691 Y., 2014. A mid-term analysis of progress towards international biodiversity targets. *Science*
692 (80-.). 346, 241–244.

693 van Strien, A.J., Soldaat, L.L., Gregory, R.D., 2012. Desirable mathematical properties of indicators
694 for biodiversity change. *Ecol. Indic.* 14, 202–208. doi:10.1016/j.ecolind.2011.07.007

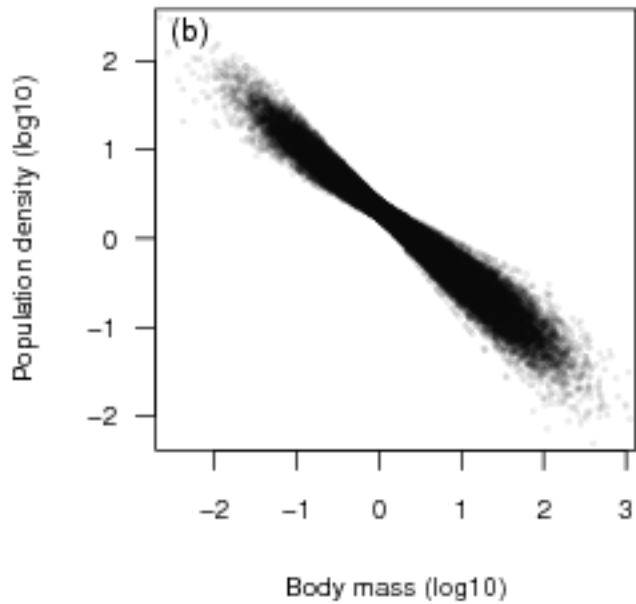
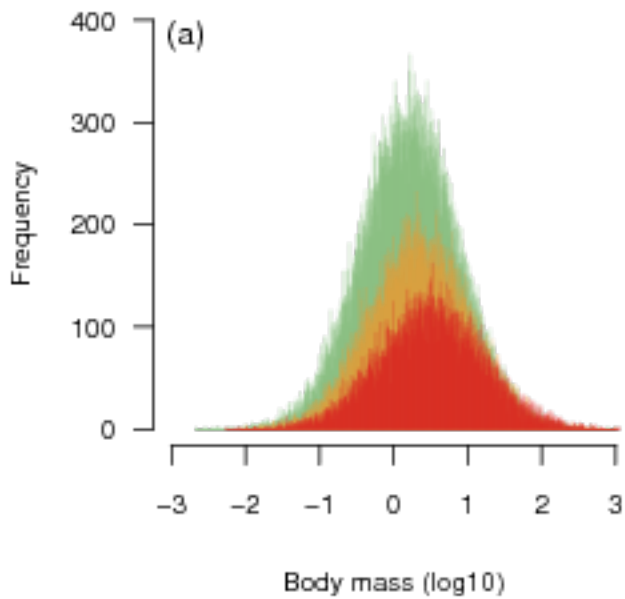
695 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices
696 for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.

697 Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C.,
698 Delipetrou, P., Didziulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pysek, P., Roy,
699 D.B., Kühn, I., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic
700 homogenization of the European flora. *Proc. Natl. Acad. Sci. U. S. A.* 106, 21721–21725.
701 doi:10.1073/pnas.0907088106

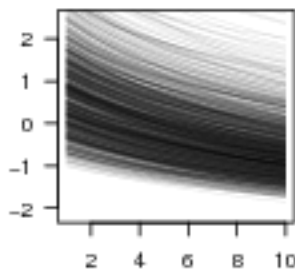
702 Yodzis, P., 1988. The indeterminacy of ecological interactions as perceived through perturbation
703 experiments. *Ecology*. doi:10.2307/1940449

704 Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N.,
705 Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach:
706 Simulating data and observers. *Oikos* 119, 622–635. doi:10.1111/j.1600-0706.2009.18284.x

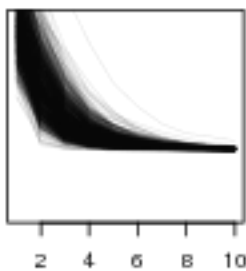
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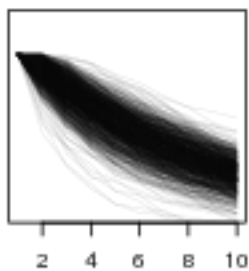
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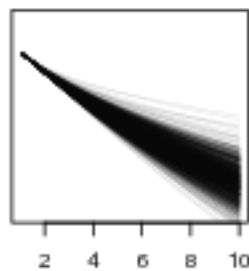
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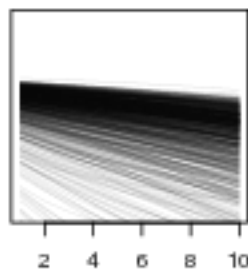
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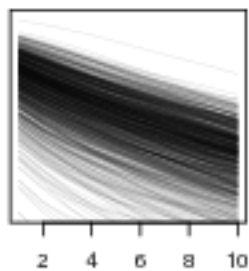
Sorensen



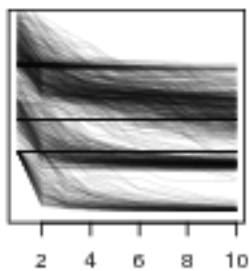
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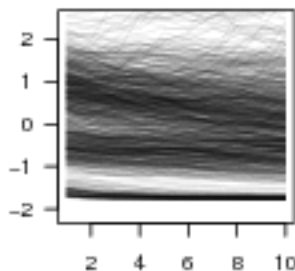
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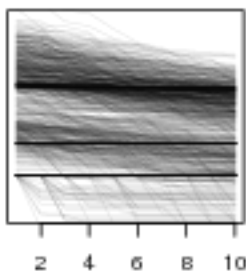
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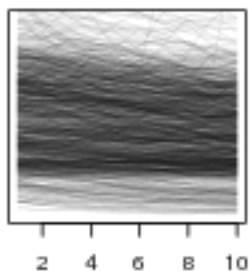
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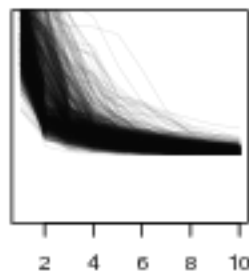
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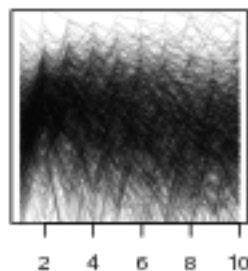
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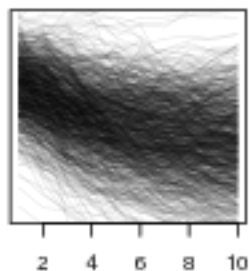
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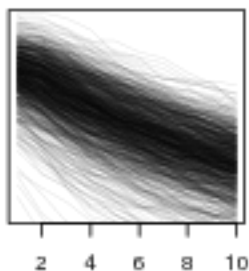
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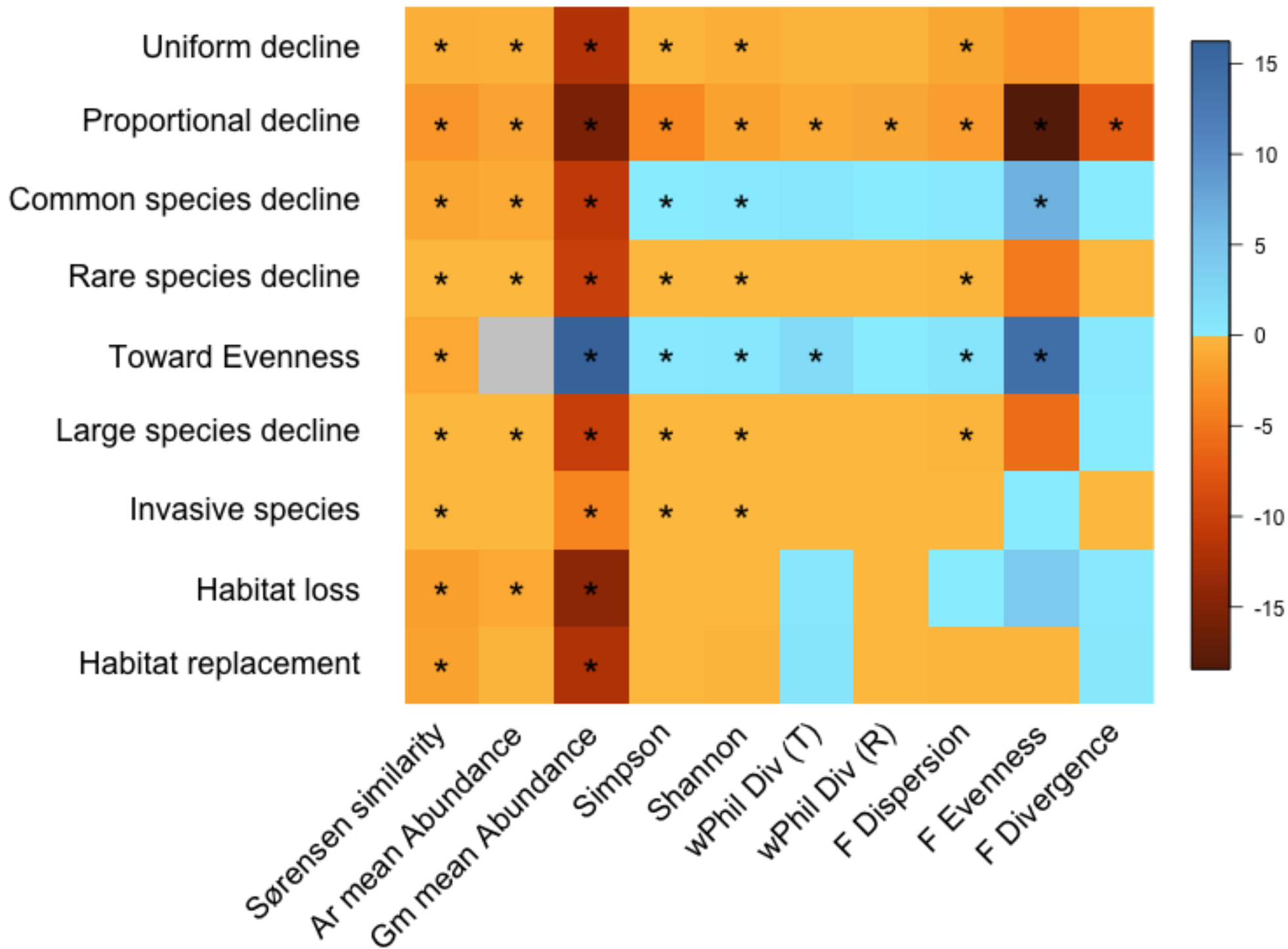
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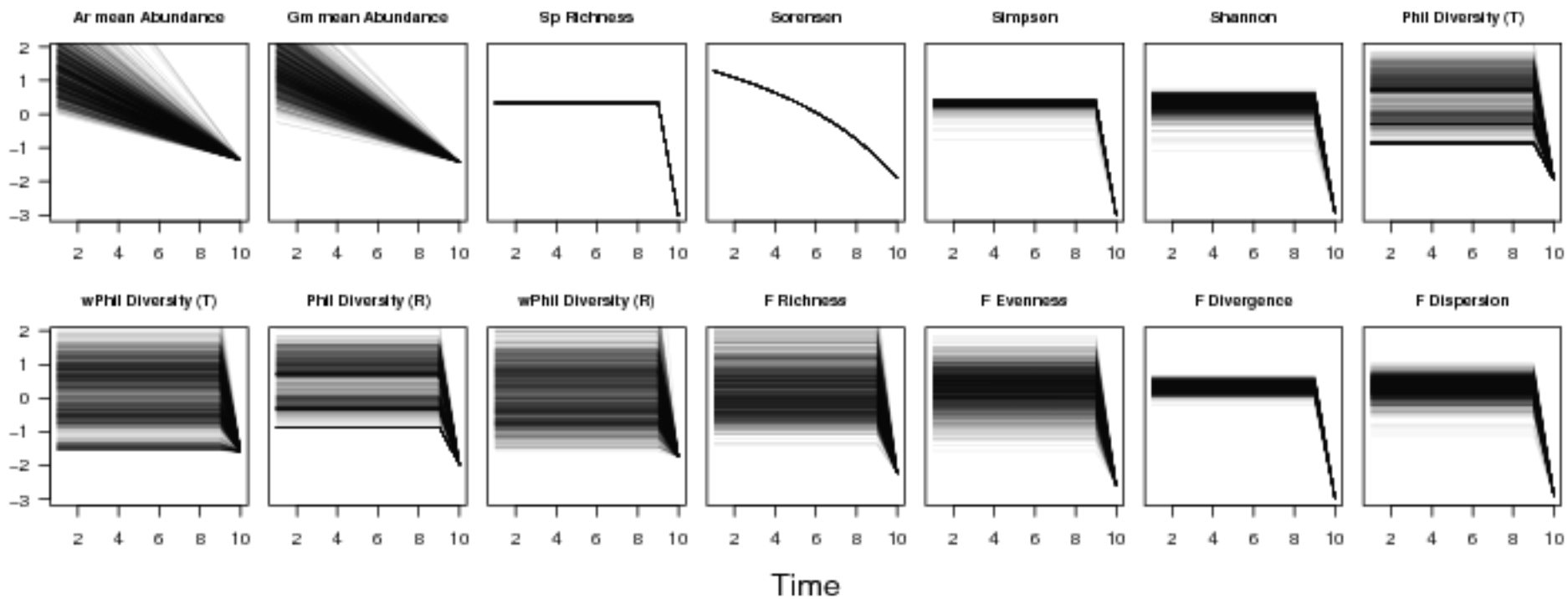


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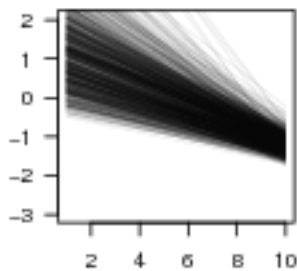


Time

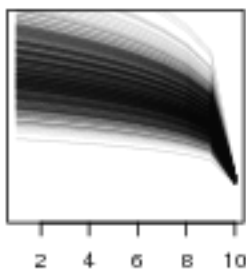




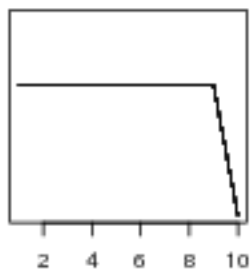
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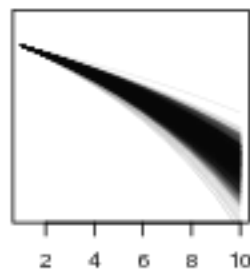
Gm mean Abundance



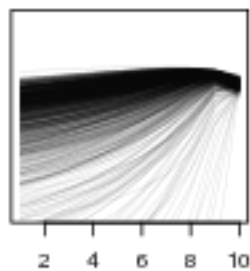
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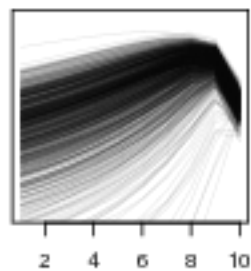
Sorensen



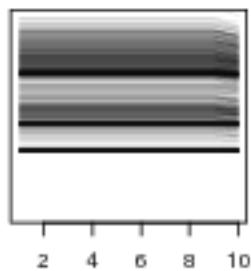
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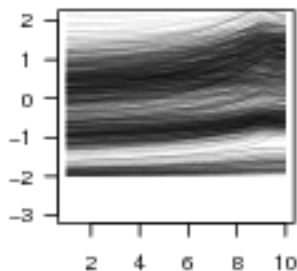
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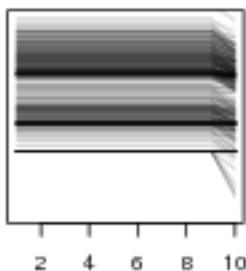
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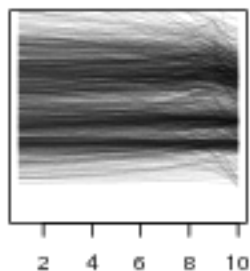
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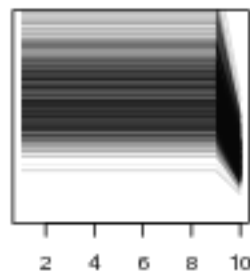
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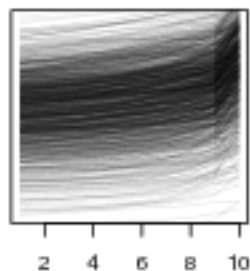
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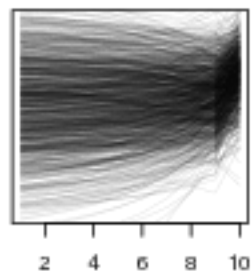
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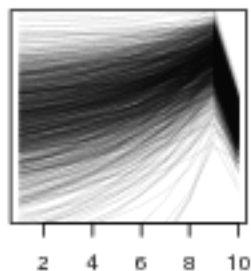
F Evenness



F Divergence

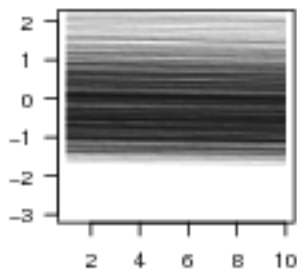


F Dispersion

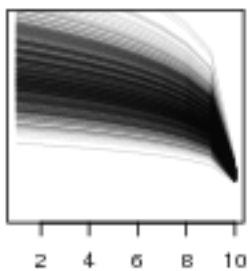


Time

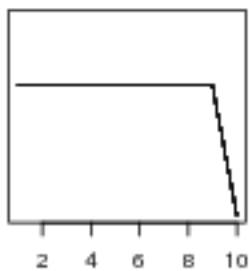
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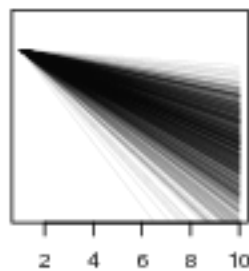
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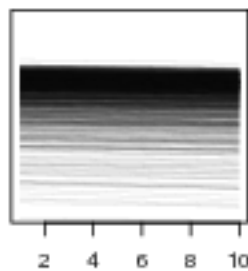
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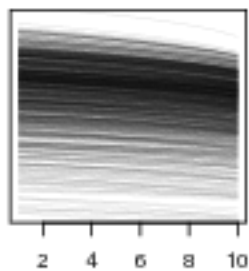
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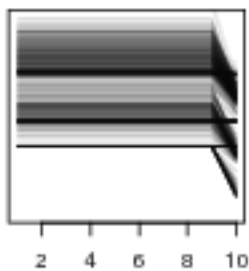
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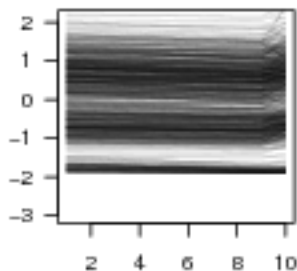
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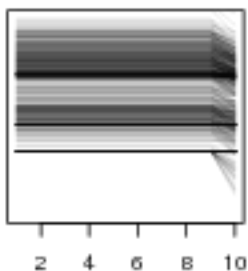
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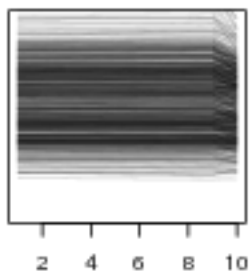
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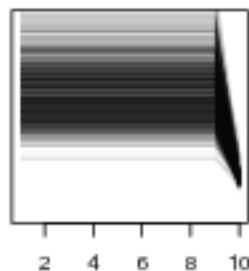
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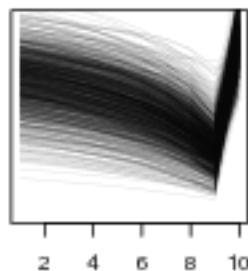
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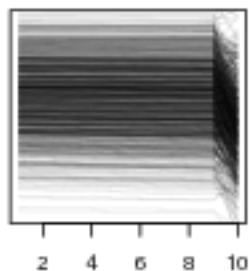
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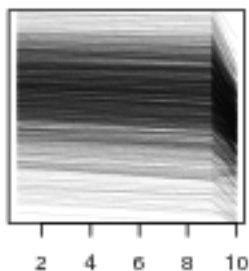
F Evenness



F Divergence

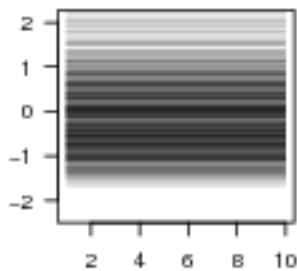


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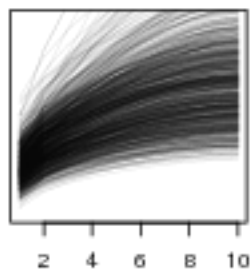


Time

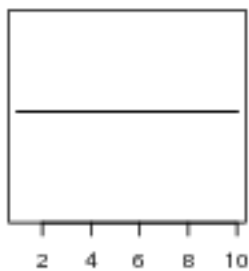
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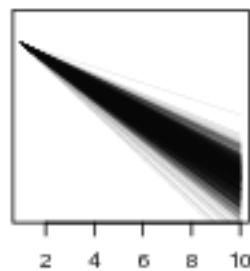
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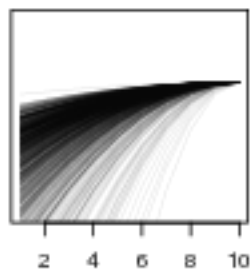
Sp Richness



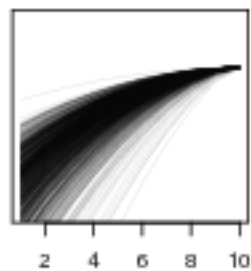
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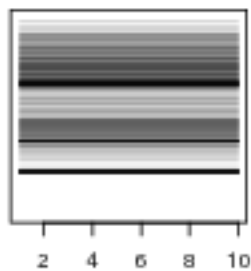
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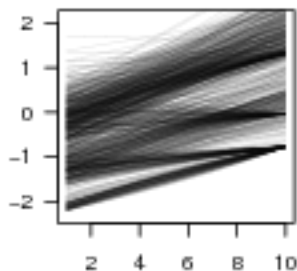
Shannon



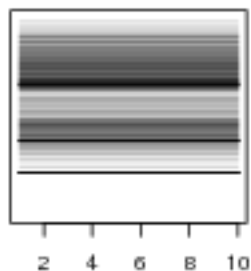
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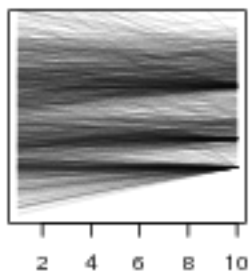
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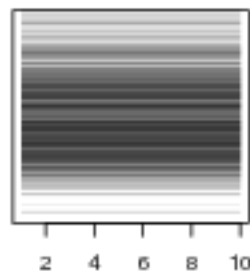
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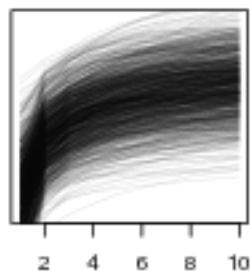
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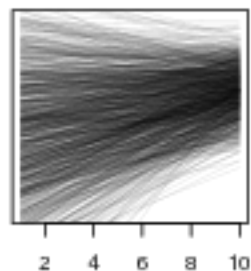
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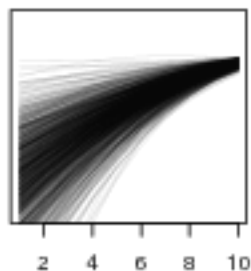
F Evenness



F Divergence

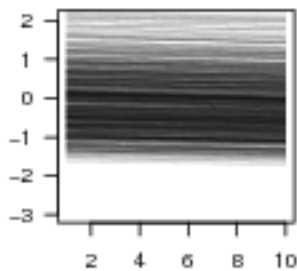


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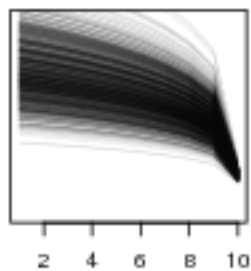


Time

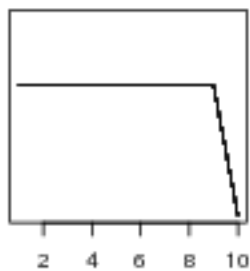
Ar mean Abundance



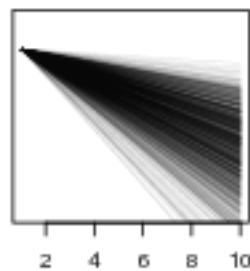
Gm mean Abundance



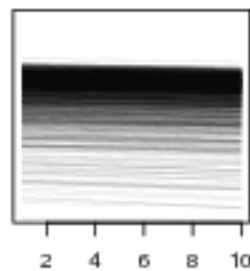
Sp Richness



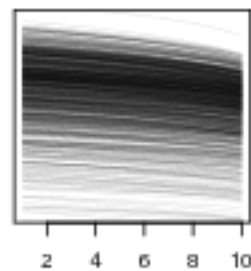
Sorensen



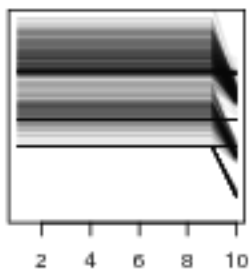
Simpson



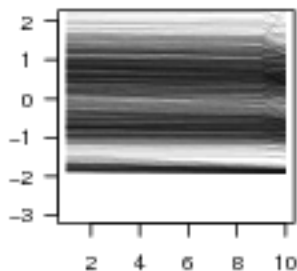
Shannon



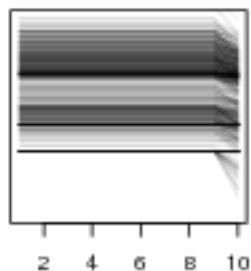
Phi Diversity (T)



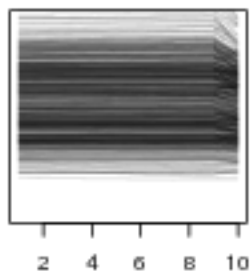
wPhi Diversity (T)



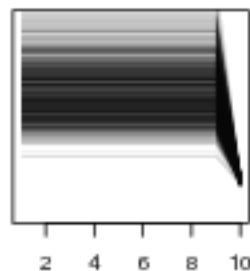
Phi Diversity (R)



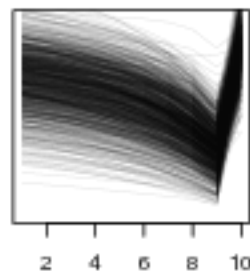
wPhi Diversity (R)



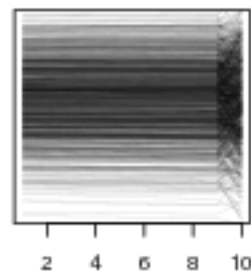
F Richness



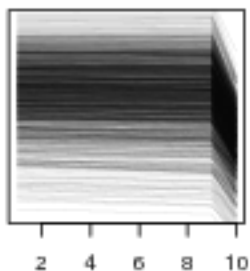
F Evenness



F Divergence

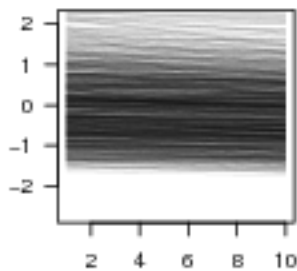


F Dispersion

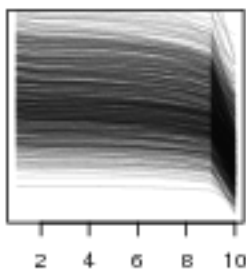


Time

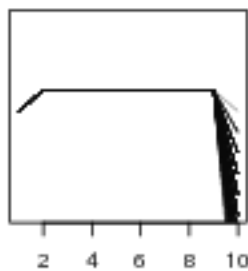
Ar mean Abundance



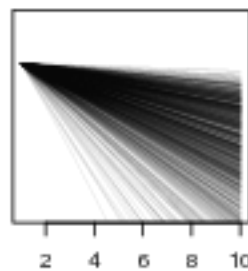
Gm mean Abundance



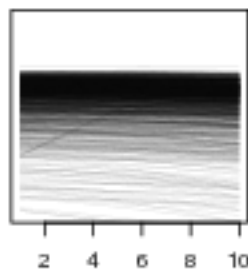
Sp Richness



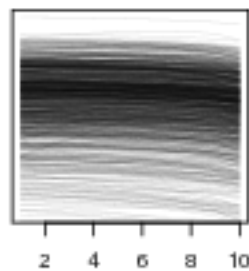
Sorensen



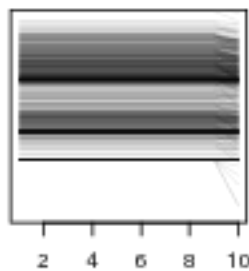
Simpson



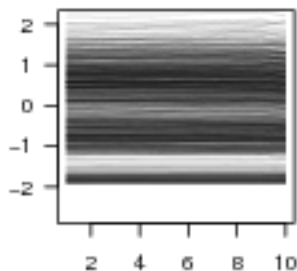
Shannon



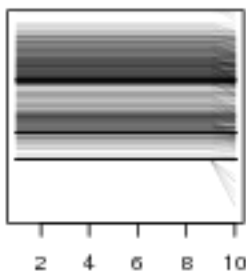
Phi Diversity (T)



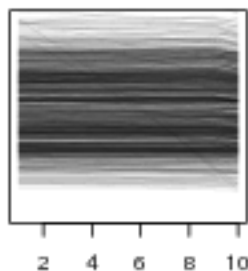
wPhi Diversity (T)



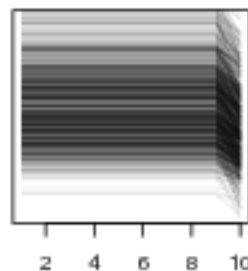
Phi Diversity (R)



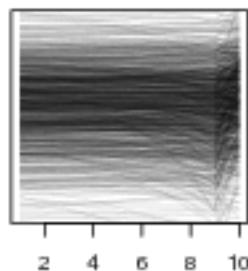
wPhi Diversity (R)



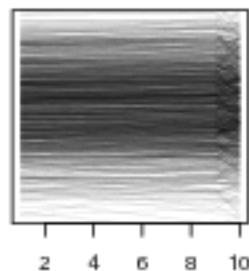
F Richness



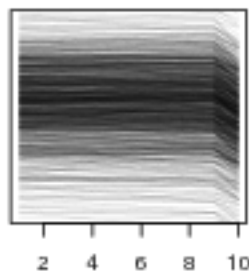
F Evenness



F Divergence

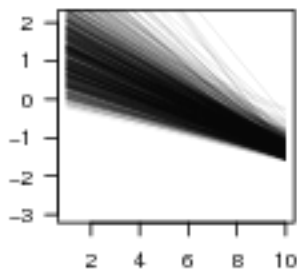


F Dispersion

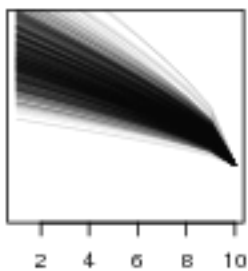


Time

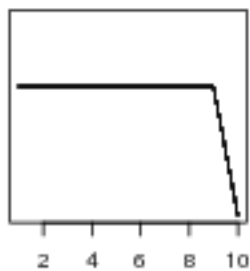
Ar mean Abundance



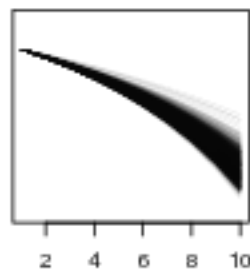
Gm mean Abundance



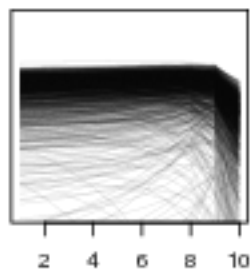
Sp Richness



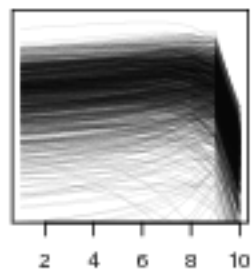
Sorensen



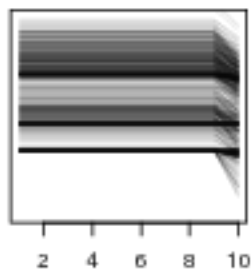
Simpson



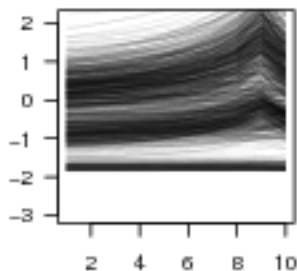
Shannon



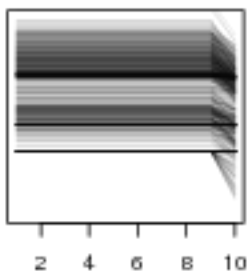
Phi Diversity (T)



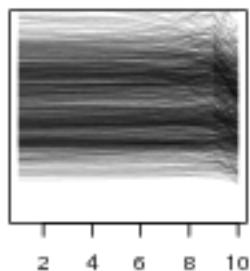
wPhi Diversity (T)



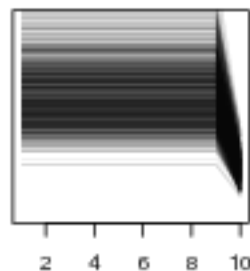
Phi Diversity (R)



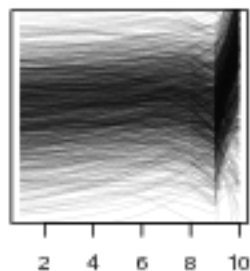
wPhi Diversity (R)



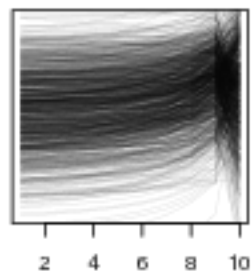
F Richness



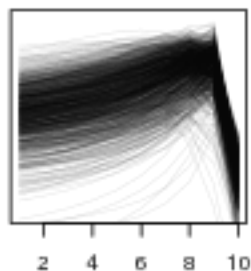
F Evenness



F Divergence

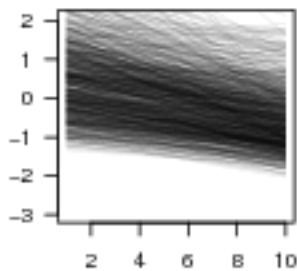


F Dispersion

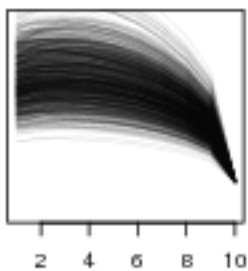


Time

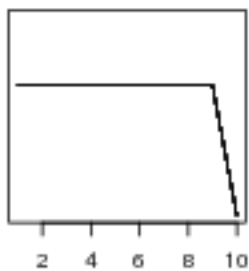
Ar mean Abundance



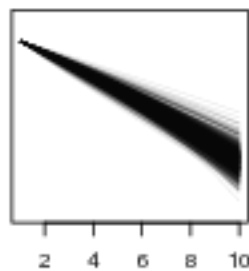
Gm mean Abundance



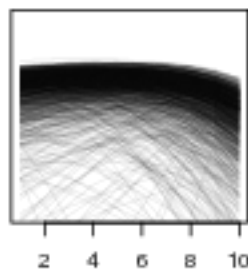
Sp Richness



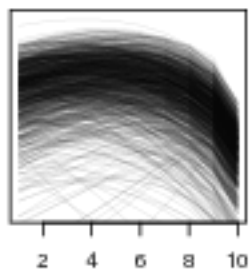
Sorensen



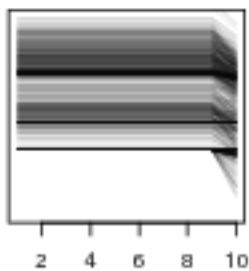
Simpson



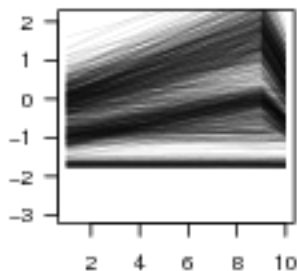
Shannon



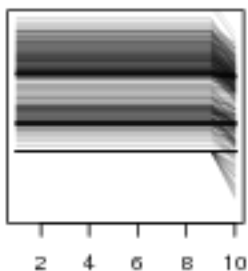
Phi Diversity (T)



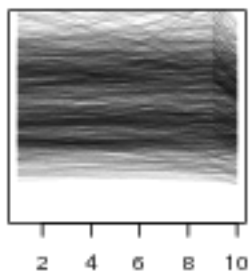
wPhi Diversity (T)



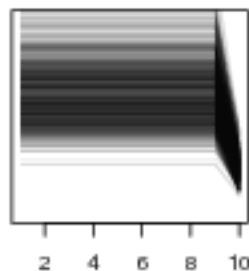
Phi Diversity (R)



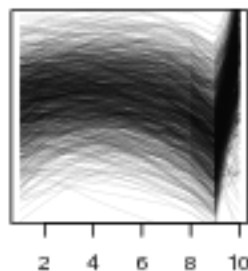
wPhi Diversity (R)



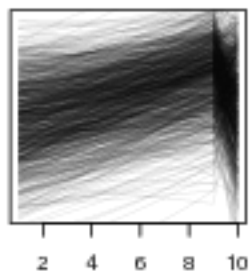
F Richness



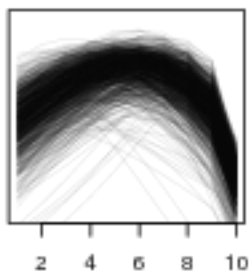
F Evenness



F Divergence



F Dispersion



Time