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Predicting ecosystem vulnerability to biodiversity loss from community composition

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31

32 **ABSTRACT:**

33 Ecosystems vary widely in their responses to biodiversity change, with some losing function
34 dramatically while others are highly resilient. However, generalizations about how species- and
35 community-level properties determine these divergent ecosystem responses have been elusive
36 because potential sources of variation (e.g., trophic structure, compensation, functional trait
37 diversity) are rarely evaluated in conjunction. Ecosystem vulnerability, or the likely change in
38 ecosystem function following biodiversity change, is influenced by two types of species traits:
39 *response traits* that determine species' individual sensitivities to environmental change, and
40 *effect traits* that determine a species' contribution to ecosystem function. Here we extend the
41 response-effect trait framework to quantify ecosystem vulnerability and show how trophic
42 structure, within-trait variance, and among-trait covariance affect ecosystem vulnerability by
43 linking extinction order and functional compensation. Using *in silico* trait-based simulations we
44 found that ecosystem vulnerability increased when response and effect traits positively covaried,
45 but this increase was attenuated by decreasing trait variance. Contrary to expectations, in these
46 communities, both functional diversity and trophic structure increased ecosystem vulnerability.
47 In contrast, ecosystem functions were resilient when response and effect traits covaried
48 negatively, and variance had a positive effect on resiliency. Our results suggest that although
49 biodiversity loss is often associated with decreases in ecosystem functions, such effects are
50 conditional on trophic structure, and the variation within and covariation among response and
51 effect traits. Taken together, these three factors can predict when ecosystems are poised to lose
52 or gain function with ongoing biodiversity change.

53 *Keywords:* biodiversity loss; compensation; disassembly; ecosystem function and services;
54 functional traits; functional diversity; vulnerability; resilience; resistance

55 **INTRODUCTION**

56 Biodiversity change is a central feature of the Anthropocene and is compromising the
57 magnitude and stability of many ecosystem functions, threatening both the systems themselves
58 and the essential services they provide (Naeem et al. 2012). Species responses to external drivers
59 (e.g., climate change, over-exploitation, habitat fragmentation) are mediated by specific traits

60 such as body size, dispersal ability, and thermal tolerances, and thus, to a degree, are predictable
61 (Payne et al. 2016). In contrast, ecosystem responses to biodiversity loss can vary widely, with
62 some functions changing dramatically, while others remain unaffected or even increase (Bunker
63 et al. 2005, Oliver et al. 2015). Potential sources of this variation include how individual species
64 contribute to function, the identity of extinct species, community trophic structure, and how
65 populations fluctuate with external drivers; however, these factors are rarely explored in
66 traditional biodiversity-ecosystem function experiments. Despite the emerging scientific
67 consensus on the mechanisms underpinning the impacts of biodiversity on ecosystem properties,
68 linking species processes to the ecosystem scale to forecast how functions respond to altered
69 biodiversity remains a challenge (Cardinale et al. 2012, Tilman et al. 2014).

70 Estimating the degree to which ecosystem function is likely to change due to biodiversity
71 loss, an ecosystem property which we term *ecosystem vulnerability*, is critical for understanding
72 why ecosystems vary in their response to ongoing environmental change. Ecosystem
73 vulnerability depends on the order in which species are lost from a community (i.e.,
74 disassembly; Ives and Cardinale 2004, Zavaleta et al. 2009), the functional contribution of
75 individual species (Suding et al. 2008, Díaz et al. 2013), intraspecific variation, and how
76 remaining species in a community may compensate for biodiversity change (Naeem 1998,
77 Thomsen et al. 2017). The response-effect trait framework has been frequently used to link traits
78 that increase an individual species' sensitivity to external drivers (response traits) to how they
79 contribute to function (effect traits; Lavorel and Garnier 2002). While response traits can be used
80 to predict the order of community disassembly, effect traits can be used to predict the change of
81 function associated with species loss or gain (Lavorel and Garnier 2002, Suding et al. 2008, Díaz
82 et al. 2013). As such, when response and effect traits covary positively, large decreases in
83 ecosystem function can be expected with ongoing biodiversity loss. However, a central feature of
84 multitrophic communities is their ability to compensate for changing composition, and extending
85 trait-based frameworks to quantify ecosystem vulnerability also requires predicting how species
86 functional contributions change in response to alterations in community composition (Connell
87 and Ghedini 2015, Thomsen et al. 2017).

88 The ability of communities to functionally compensate in response to biodiversity change
89 is associated with community level compensatory dynamics, which can cause aggregate
90 community biomass or density to remain stable despite changes in community composition

91 (Peres and Dolman 2000, Gonzalez and Loreau 2009). As a process, compensation is associated
92 with a number of community properties, including how niche differences and competitive
93 interactions are distributed across a community (Ives and Cardinale 2004). Trophic structure can
94 thus determine biomass compensation by limiting competitive release associated with changing
95 community composition to specific trophic levels (Gonzalez and Loreau 2009). Similarly,
96 functional compensation might be restricted in multitrophic communities if response and effect
97 traits are clustered based on trophic level. For example, high-level consumers can be
98 characterized by shared response traits (e.g., large body size) that are correlated with shared
99 effect traits (e.g., long distance seed dispersal; Peres et al. 2016). As a result, functions
100 associated with specific trophic guilds might be irreplaceable by species in other trophic levels.
101 In contrast, if trophic level is unrelated to how species contribute to function, trophic structure
102 could have little impact on ecosystem vulnerability by not restricting functional compensation to
103 specific guilds. While the effect of compensatory dynamics on community properties has
104 received considerable attention (Gonzalez and Loreau 2009, Connell and Ghedini 2015,
105 Thomsen et al. 2017), trait-based approaches rarely consider their role in maintaining ecosystem
106 function with ongoing biodiversity change.

107 In addition to trophic structure, the community-level frequency distribution of species
108 traits has received little attention although it could strongly affect functional compensation and
109 by extension, ecosystem vulnerability. Changes in species composition can alter ecosystem
110 function even if compensatory dynamics cause total biomass to remain stable, because of
111 functional trait differences between species. When the contributions of species to ecosystem
112 function are driven by dominance rather than because of their unique effect traits, biomass
113 compensation should mitigate the impact of changing species composition on ecosystem
114 function (Davies et al. 2011, Pan et al. 2016). However, biomass compensation will not ensure
115 resilient ecosystem functions when effect traits between the extinct and extant species are
116 different (i.e., trait redundancy; Naeem 1998, Oliver et al. 2015). While traits are often assumed
117 to be normally or uniformly distributed within communities (Díaz et al. 2016), alternative
118 distributions are also common (e.g., lognormal; Savage et al. 2007). Thus, a community's trait
119 frequency distribution can have strong implications for functional compensation and
120 consequently, ecosystem vulnerability.

121 Beyond linking a species' sensitivity to change to their contribution to function, the
122 covariation between response and effect traits also links extinction order and compensation. In
123 both plants and animals, trait tradeoffs are ubiquitous, with community-scale trait covariation
124 affecting a number of community processes (e.g., assembly, succession; Winemiller et al. 2015,
125 Díaz et al. 2016). However, how community-scale trait covariation affects the response of
126 function to biodiversity loss, by linking community processes (i.e., extinction and compensation)
127 to ecosystem properties (i.e., ecosystem vulnerability), is underexplored. Empirical evidence
128 suggests that traits that make a species more sensitive to external drivers (e.g., body size) often
129 covary with traits that increase their contribution to function (e.g., pollination rates, nutrient
130 excretion rates; Larsen et al. 2005, McIntyre et al. 2007), but this covariation can also be
131 negative or non-existent, resulting in alternate relationships between species change and
132 ecosystem responses, which are rarely considered in conjunction with compensation. Exploring
133 the consequences of these different trait relationships in conjunction with the distribution of traits
134 across multiple trophic levels is critical for gaining insight into why some ecosystem functions
135 change so drastically with biodiversity loss, while others remain resilient, and may facilitate
136 prediction of ecosystem responses to environmental change.

137 We develop a framework for estimating ecosystem vulnerability based on linking
138 processes across species- (contribution to function and species vulnerabilities), community-
139 (compensatory dynamics and disassembly) and ecosystem-scales (ecosystem vulnerability).
140 Based on this framework, we evaluate the relationship between biodiversity and ecosystem
141 vulnerability by developing an "ecosystem stress test," *in silico* trait-based simulations for
142 evaluating the outcomes of different extinction scenarios on ecosystem function. Each scenario
143 quantifies ecosystem vulnerability by identifying the number of species needed to maintain
144 ecosystem function above a set threshold. We then test the framework through simulations that
145 employ a range of common community-scale trait frequency distributions (normal, uniform, and
146 lognormal) as well as different degrees of covariation between response and effect traits
147 (positive, negative, and non-existent). Through these simulations, we bridge across species,
148 community and ecosystem scales, linking common species-level metrics to ecosystem
149 vulnerability, and begin to decipher the implications of changes in biodiversity for maintaining
150 ecosystem function. Specifically, through our simulations we asked:
151 1) To what extent can compensation reduce ecosystem vulnerability?

- 152 2) How does trophic structure influence compensation outcomes, and consequently, ecosystem
 153 vulnerability?
- 154 3) What role does community-level covariance between response and effect traits play in
 155 influencing ecosystem vulnerability?
- 156 4) How does the distribution of trait values within a community affect ecosystem vulnerability?
- 157 5) How well do community-scale vulnerability properties (*sensu* Weeks et al. 2016) predict
 158 ecosystem vulnerability?

159 Biodiversity is often assumed to increase the resistance and resilience of ecosystem
 160 function to biodiversity loss (Oliver et al. 2015). However, increasing biodiversity can increase
 161 community vulnerability since more speciose communities are likely to include functionally
 162 distinct and sensitive species (Mouillot et al. 2013, Weeks et al. 2016). By examining how traits
 163 mediate the interaction between extinction order and functional compensation, our framework
 164 integrates the effect of resistance and resilience on ecosystem function in natural systems.
 165 Additionally, numerical models that input trait data to predict ecosystem vulnerability are often
 166 difficult to apply across ecosystems. In contrast, we provide an unbiased method to predict the
 167 ability of ecosystems to provide services despite ongoing biodiversity loss, which can be
 168 achieved empirically by collecting relevant information on response and effect traits together
 169 with community trophic structure. Ultimately, scaling existing species-based approaches to the
 170 ecosystem level using the ecosystem stress test developed can enable rapid assessments of the
 171 impact of biodiversity change on the ability of ecosystems to maintain function and provide
 172 services that are central to human wellbeing.

173

174 **METHODS**

175 *Contribution to function*

176 We assume that species i contributes to a function a ($F_{a,i}$) via an effect trait ($E_{a,i}$) and the
 177 species' biomass in the system (m_i) (following Lavorel and Garnier 2002, Solan et al. 2004,
 178 Bunker et al. 2005), such that the total function, T_a , in a community with S species, is

$$179 \quad T_a = \sum_i^S F_{a,i} \quad (1)$$

180 where

$$181 \quad F_{a,i} = m_i E_{a,i} \quad (2)$$

182 This approach assumes that for all species, $F_{a,i}$ is linearly related to m_i and $E_{a,i}$, and yields units
 183 related to the particular function (e.g., grams of carbon per unit mass). While this approach only
 184 considers mass ratio effects (*sensu* Grime 1998), and thus does not explicitly account for the
 185 impacts of species interactions on their contributions to function, it is flexible, with the potential
 186 to be expanded to include multiple functions.

187 *Species-level vulnerability index*

188 Individual species vulnerabilities were calculated as a function of each species' exposure
 189 to a threat, and the species-specific sensitivity:

$$190 \quad V_{i,k} = \varepsilon_k R_{i,k} \quad (3)$$

191 where $V_{i,k}$ is the vulnerability of species i to external driver k , ε_k is the exposure of species i to
 192 driver k , and $R_{i,k}$ is the response trait of species i associated with the driver k . Exposure varies
 193 across landscapes, and thus vulnerabilities are expected to vary across a species' range. This
 194 equation assumes that all species are spatially bound in one community, and thus all species face
 195 the same exposure to a threat. However, species differ in their sensitivities, and $V_{i,k}$ provides a
 196 relative extinction probability for all species within a community based on exposure and
 197 sensitivity. When evaluated at a community scale, these vulnerability indices provide a means
 198 for developing probabilistic scenarios of species loss from a community.

199 *Ecosystem Stress Test*

200 We simulated communities in which we varied the community scale trait frequency
 201 distributions together with the strength of covariation between response and effect traits. We
 202 assumed that there was only one stress and set the exposure at 1, such that all species experience
 203 the same level of the threat. These simplifying assumptions allowed us to specifically analyze the
 204 role of trophic structure, trait distribution and covariance on compensation outcomes, while
 205 holding all other factors constant. Thus, relating vulnerability and contribution to function relied
 206 on fitting the following relationship:

$$207 \quad R_{i,k} = \alpha m_i E_{a,i} \quad (4)$$

208 where α describes the correlation between $V_{i,k}$ and $F_{a,i}$, which in this case is directly determined
 209 by the covariation between response and effect traits ($R_{i,k}$ and $E_{a,i}$ respectively). We factorially
 210 manipulated trait distributions (uniform, normal, and lognormal) and covariation between traits
 211 (i.e., $\alpha = 1, 0, -1$) so that 500 simulated communities were created for each of the nine different
 212 trait scenarios. Subsequently, F_i and V_i were scaled so that all species had values between 0 and

213 1 by dividing every species by the maximum value in each community. Additionally, in each of
214 the communities, all species were assigned as primary producer, herbivore or predator based on
215 the ratio of 7:2:1. This ratio was chosen to maintain sufficient variability in trophic structure
216 while approximating an ecosystem dominated by lower trophic levels. To explore how trophic
217 structure influences compensation outcomes, we assigned trophic identity both randomly and
218 such that it was positively related to V_i . The values used in all simulations are detailed in Table
219 1.

220 We applied an ecosystem stress test to each of the communities to determine the
221 ecosystem's vulnerability, which was quantitatively evaluated as the number of species needed
222 to maintain functioning above a defined threshold (Fig. 1). This trait-based simulation approach
223 relies on modeling species extinction scenarios such that the probability of a species being lost
224 from a community is directly proportional to the vulnerability of that species ($V_{i,k}$; equation 3).
225 At each time step, a species is first lost and the remaining total function (T_a ; equation 1) is
226 measured, without compensation. Subsequently, the remaining species compensate for the lost
227 biomass associated with the extinct species based on two replacement scenarios: random
228 replacement (i.e., all remaining species have same probability of replacing extinct species) and
229 trophic guild replacement (i.e., only remaining species within the same trophic guild are able to
230 replace extinct species). These replacement rules assume that the biomass of an extinct species is
231 allocated to the compensating species, and in the scenario including trophic guild replacement
232 rules, once the last member of a trophic guild is extinct, the biomass in the system is lost (Solan
233 et al. 2004, Bunker et al. 2005, McIntyre et al. 2007). Finally, the number of species, as a
234 proportion of the total initial species richness, needed to maintain function above a set threshold
235 of initial function is evaluated. The choice of threshold can be manipulated, and this provides a
236 comparable measurement of vulnerability between different communities such that the higher the
237 number of species needed to maintain function above a threshold, the higher the ecosystem
238 vulnerability. To analyze and compare ecosystem vulnerability across a range of communities
239 (see below), we set the function threshold at 75%, 50% and 25% ($S_{T=75}$, $S_{T=50}$ and $S_{T=25}$
240 respectively).

241 *Analysis of relationship between community level properties and ecosystem vulnerability*

242 We calculated the total community vulnerability (V_{TOT}) by summing the vulnerabilities
243 of all species within each of the initial simulated communities (Weeks et al. 2016). Given that

244 these community vulnerabilities are not independent from functional diversity, to characterize
245 the variation in community vulnerability of the simulated communities, we used the standard
246 deviation of the whole community vulnerability (V_{SD}) as well as the mean vulnerability in the
247 community (V_{Mean}). We fit linear models with the different thresholds (e.g., $S_{T=50}$) as the
248 response variable and either V_{TOT} , V_{SD} or V_{Mean} as the predictor variable for each replacement
249 scenario. These relationships were analyzed for communities with positive trait covariation (i.e.,
250 $\alpha = 1$) to explore the relationships between vulnerability and function in communities that
251 always lost function with decreasing biodiversity. All analyses and simulations were conducted
252 in R (R Core Team 2016; see Data S1 for simulation code).

253

254 RESULTS

255 Across all simulated communities, compensation reduced ecosystem vulnerability by
256 decreasing the proportion of species needed to retain the 50% ecosystem function by an average
257 of 31.69 species (± 19.54 SD). Similar results hold for the other thresholds (Appendix S1), but for
258 simplicity we hereafter only present only results for $S_{T=50}$.

259 Covariance between response and effect traits had a strong effect on ecosystem
260 vulnerability (Fig. 2). Communities with positive correlations between response and effect traits
261 ($\alpha = 1$) needed an average of 58.14 species (± 18.70 SD) to maintain function above the 50%
262 threshold, whereas communities with $\alpha = 0$ needed 14.31 species (± 21.13 SD), and those with α
263 $= -1$ needed 7.85 species (± 12.24 SD) at the same threshold (Fig. 3, Appendix S1 Fig S6-8).
264 Covariation also had a strong impact on compensation outcomes (Fig. 2). While communities
265 with $\alpha = 1$ never recovered function to the initial level, communities with $\alpha = -1$ always
266 overcompensated, with function commonly surpassing 100% in all replacement scenarios (Fig.
267 2). In communities with $\alpha = -1$, only 1.14 species (± 0.51 SD) were needed to maintain function
268 above the 50% threshold with compensation. Similarly, in communities with $\alpha = 0$,
269 compensation typically caused function to return to initial levels in all compensation scenarios
270 (mean $S_{T=50} = 2.22 \pm 1.98$ SD), but this pattern became increasingly stochastic as more species
271 were lost (Fig. 2, Appendix S1).

272 The distribution of response and effect traits in the community had a strong effect on
273 ecosystem vulnerability (Fig. 2 and Fig. 3). Trait distribution interacted with covariance and
274 compensation to affect the shape of the relationship between the proportion of function

275 remaining and the proportion of species lost (Fig. 2). Qualitatively, in communities with $\alpha = 1$,
 276 compensation caused the relationship between the proportion of species lost and the proportion
 277 of function remaining to be concave up when traits were lognormally distributed, and concave
 278 down in communities with normally and uniformly distributed traits (Fig. 2). To maintain
 279 function above the 50% threshold $\alpha = 1$ communities in which traits were lognormally
 280 distributed required 73.35 species (± 9.69 SD), whereas communities in which traits were
 281 normally distributed required 43.06 species (± 18.93 SD), and communities in which traits were
 282 uniformly distributed required 58.01 species (± 11.74 SD). In contrast, in communities with $\alpha = -$
 283 1, lognormal trait distributions caused higher gains in function than communities with traits
 284 normally or uniformly distributed.

285 Replacement scenarios also had a strong effect on ecosystem vulnerability (Fig. 2).
 286 Comparing communities with the same distribution and the same trait covariance structure (i.e.,
 287 $\alpha = 1$, $\alpha = 0$, $\alpha = -1$) revealed that when trophic position was not correlated with extinction risk,
 288 the mitigating effects of compensation were similar to random compensation (Fig. 2). In contrast,
 289 when trophic position was correlated with extinction risk, compensation resulted in more species
 290 needed to maintain function in all covariance and distribution scenarios (Fig. 2. and Fig. 3).

291 V_{TOT} and V_{Mean} were both associated with fewer species needed to maintain function
 292 across all distributions in communities with positive trait covariation (Fig. 3). In contrast, the
 293 higher V_{SD} , the more species were needed to maintain function across all distributions in
 294 communities with positive trait variation (Fig. 3). These relationships did not hold for ecosystem
 295 functions in communities where $\alpha = 0$ and $\alpha = -1$, since for most of these communities, function
 296 usually recovered above all thresholds (Appendix S1).

297

298 DISCUSSION

299 Our study links species traits, community processes and ecosystem properties to identify
 300 key factors that determine the vulnerability of ecosystem functions to biodiversity loss. Further,
 301 our framework provides a means for assessing when disassembly and compensation will affect
 302 the ability of ecosystems to maintain function. We report four major findings. First, despite the
 303 role of compensation, the covariance between response and effect traits, which affects the
 304 relationship between individual species' probabilities of extinction and their contributions to
 305 ecosystem functioning (i.e., V_i and F_i), predicts whether an ecosystem loses or gains function as

306 species are lost. Given the ubiquity of trait trade-offs in animals and plants (Winemiller et al.
307 2015, Díaz et al. 2016), we expect covariance between response and effect traits to be common
308 features of natural communities. Secondly, trophic structure restricts the degree to which
309 remaining species can compensate for lost species. Consequently, trophic structure increases
310 ecosystem vulnerability when response and effect traits covary positively, and decreases
311 resilience when response and effect traits covary negatively. Thirdly, while some species within
312 communities may compensate for the loss of function associated with community disassembly,
313 the community-scale trait frequency distribution affects the degree to which functional
314 compensation mitigates the impacts of changing composition. Finally, while the positive
315 relationship between functional diversity and ecosystem function is well established, we show
316 that increasing trait variance also increases ecosystem vulnerability when response and effect
317 traits covary positively, a counterintuitive pattern with some empirical support (Weeks et al.
318 2016). Given current rates of biodiversity change, the need to quantify ecosystem vulnerability
319 has received considerable attention. Our findings suggest identifying relevant response and effect
320 traits, and analyzing their covariation and frequency distribution in multitrophic communities
321 may be key to predicting the ability of ecosystems to maintain function and associated services
322 despite biodiversity loss.

323 Covariance between response and effect traits was the primary factor affecting whether
324 ecosystems lost or gained function with ongoing disassembly and compensation (Fig. 2). In
325 communities where response and effect traits positively covaried, ecosystems invariably lost
326 function despite the mitigating impacts of compensation. This is because the high effect trait
327 values of the most sensitive species could not be replaced by other species. In ecosystems in
328 which functions are driven by vulnerable species with unique effect traits, changing composition
329 affects ecosystem function, despite the maintenance of biomass through compensation (Solan et
330 al. 2004, McIntyre et al. 2007). In contrast, communities with no covariance between response
331 and effect traits resembled unordered extinctions (Ives and Cardinale 2004). In such cases,
332 function remained relatively unchanged at low levels of extinction. However, as the number of
333 remaining species decreased, the proportion of function remaining tended to become increasingly
334 stochastic since the remaining pool of effect traits was a random sample from the community.
335 Finally, communities with negatively covarying traits tended to experience increases in function
336 with disassembly because the biomass of species with high response trait values (i.e. the most

337 vulnerable) was allocated to species with higher effect trait values, thus increasing total function.
338 While examples of extinction increasing function are less common, the importance of rare
339 species is often attributed to their ability to increase resiliency through compensation (Jain et al.
340 2014, Leitao et al. 2016). Similarly, invulnerable species can play an insuring role in
341 compensating loss function (Yachi and Loreau 1999). Ultimately, if these rare or invulnerable
342 species have higher effect trait values and can compensate for extinct species, their inclusion in
343 communities should decrease ecosystem vulnerability.

344 Examining the effects of trait distributions on ecosystem vulnerability leads to two
345 related insights into the role of functionally distinct species and community-level trait variance.
346 First, as the distance in trait space between the most vulnerable and functionally unique species
347 and the rest of the community increases (i.e., where a species falls on the trait frequency
348 distribution), the ability of the remaining community to compensate for the lost species
349 decreases. While this low potential for functional compensation is often attributed to a lack of
350 community redundancy, and is consistent with studies that suggest a positive relationship
351 between ecosystem vulnerability and the presence of unique species (Mouillot et al. 2013,
352 Ricotta et al. 2016), our results suggest that unique species should mainly affect ecosystem
353 vulnerability when that species is also among the most vulnerable. Further, while redundancy is
354 often used as an estimate of ecosystem vulnerability (Ricotta et al. 2016), our results indicate that
355 ecosystem function is particularly sensitive to which traits are considered (response or effect),
356 how they covary with other traits, and the inclusion of outlier species, factors which can be
357 obfuscated by common redundancy metrics. Thus, collecting information on trait distributions
358 and covariance, and evaluating communities using an ecosystem stress test could improve
359 estimates of ecosystem vulnerability.

360 Second, increased community-level trait variance increases both functional diversity and
361 the vulnerability of ecosystem function. V_{SD} is directly proportional to community functional
362 diversity, and across distributions, the larger V_{SD} , the more species were needed to meet a set
363 threshold of function (Fig. 3, Appendix S1). In contrast, changing composition in communities
364 with low V_{SD} had a smaller influence on ecosystem vulnerability because biomass effects
365 underlay the relationship between biodiversity and ecosystem function. Thus, as trait variance
366 increases in a community, the mitigating effects of compensation decreases. However, when
367 traits covary negatively, variance increases the resiliency of functions in accordance with

368 expected relationships between functional diversity and resiliency (Fig. 2; Oliver et al. 2015). In
369 addition to examining the influence of V_{SD} , we expected to find a positive relationship between
370 V_{TOT} , V_{Mean} and ecosystem vulnerability, but communities with overall higher trait values also
371 had higher trait variance. Although studies quantifying vulnerability properties beyond the
372 species scale are rare, some evidence suggests a positive relationship between biodiversity and
373 total community vulnerability, which could be mediated by increasing trait variance (Mouillot et
374 al. 2013, Weeks et al. 2016). While we did not explicitly examine the role of species richness in
375 affecting ecosystem vulnerability, increasing functional diversity and trait variance is often
376 associated with increasing ecosystem function and resistance to change due to increasing the
377 diversity of species responses to external drivers (Elmqvist et al. 2003, Laliberté et al. 2010).
378 However, our results suggest that increasing trait variance is also expected to increase the
379 vulnerability of ecosystem functions if response and effect traits covary positively because this
380 reduces the compensatory abilities of species by decreasing redundancy. While this provides a
381 mechanistic explanation, disentangling whether biodiversity jointly increases ecosystem function
382 and ecosystem vulnerability is a paradox that requires further empirical evaluation.

383 While a large body of work examines the effect of plant biodiversity on ecosystems
384 (Cardinale et al. 2012, Tilman et al. 2014), our multitrophic models suggest that single trophic
385 studies may overestimate ecosystem resiliency and underestimate the vulnerability of ecosystems
386 to biodiversity change in comparison to communities with one trophic level (Fig. 2). In
387 communities where species trophic position was related to response traits, and trait covariation
388 was positive, trophic structure increased ecosystem vulnerability, resulting in abrupt declines in
389 function once the least sensitive species in trophic level went extinct. This suggests that
390 communities in which high effect trait values are unique to a particular trophic level, functional
391 compensation by other trophic levels will be restricted (e.g. long-distance seed dispersal; Peres et
392 al. 2016). Similarly, when response-effect trait covariation was negative, trophic structure
393 decreased the resiliency of functions associated with compensation. In these communities,
394 biomass of the extinct trophic level was not allocated to other trophic levels, restricting the
395 increase in function associated with compensation. In contrast to communities where trophic
396 position was related to extinction probability, communities where trophic position was
397 randomized exhibited a lower ecosystem vulnerability when response and effect traits covaried
398 positively, and higher levels of function achieved when traits covaried negatively. The effects of

399 compensation in these communities were indistinguishable from random compensation, and thus
400 akin to communities with one trophic level. Extensions of work on biodiversity and ecosystem
401 function beyond single trophic levels are rare, but given that trophic position is associated with
402 increased extinction risk (Payne et al. 2016) our results suggest that trophic structure may be an
403 important, but underestimated, contributor to ecosystem vulnerability.

404 Quantifying ecosystem vulnerability relies on predicting how communities compensate
405 as constituent taxa are lost. The different compensation scenarios we modeled were meant to
406 represent the various replacement rules commonly employed (e.g., Solan et al. 2004, Bunker et
407 al. 2005). However, a few potentially insightful replacement rules were not explored. First,
408 compensation was treated as a zero sum process, so that total community biomass remained
409 constant; however, biomass under- and over-compensation are common, and parameterizing
410 these processes will be important for empirically estimating ecosystem vulnerability in nature
411 (Gonzalez and Loreau 2009). Additionally, species populations can change in biomass, but not
412 go extinct, which could be accommodated in our framework by changing biomass parameters for
413 individual species. Second, our approach considers only mass ratio type effects (*sensu* Grime
414 1998), which excludes more complex abundance-function relationships, such as discontinuous
415 traits or traits that do not directly contribute to function. Third, our modeling of trophic structure
416 scenarios represented boundary conditions where either a whole trophic level went extinct, or
417 disassembly was completely unrelated to trophic position. While this left out a number of
418 possibilities (e.g., trophic cascades, keystone species, omnivory), the framework is flexible and
419 can be expanded to accommodate more complex compensation scenarios with adequate natural
420 history knowledge of a specific system. Finally, the degree to which biodiversity is decreasing or
421 increasing, is inconclusive (Vellend et al. 2013, Dornelas et al. 2014). While community trait
422 structure varies across spatial and temporal scales, and response traits may also cause some
423 species to increase in abundance, our framework can also accommodate alternative biodiversity
424 change scenarios. Despite these nuances, ecosystem stress tests provide a flexible framework for
425 estimating ecosystem vulnerability that can be easily employed and modified to guide future
426 theoretical, empirical and applied ecological investigations.

427

428 **CONCLUSION**

429 While biodiversity may increase the resistance and resilience of ecosystem function
 430 (Oliver et al. 2015), our results suggest that this positive effect is conditional on the relationship
 431 between trait covariance and distribution. Critically, the vulnerability of an ecosystem's
 432 functions, and the services derived from them, is directly related to the community's species
 433 composition and functional diversity. At a minimum, how a biota will respond to environmental
 434 change and how the altered community may maintain ecosystem function can be predicted with
 435 knowledge of (1) the degree to which species can compensate for one another, (2) the degree to
 436 which trophic position, response, and effect traits covary, and (3) the frequency distributions of
 437 traits in a community. Together, these three factors explain the variety of ecosystem responses to
 438 biodiversity change observed in nature. Additionally, by providing an unbiased estimate of
 439 ecosystem vulnerability, our methodology can aid conservation and policy in identifying those
 440 ecosystem functions and services that might be most vulnerable to novel drivers of change.
 441 Ultimately, given that ecosystem vulnerability is directly related to the species found in an
 442 ecosystem, changes in biodiversity affect not only the magnitude and variability of ecosystem
 443 function but also the sensitivity of ecosystem function to environmental change.

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447 **LITERATURE CITED**

- 448 Bunker, D. E., F. DeClerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M.
 449 Sankaran, and S. Naeem. 2005. Species Loss and Aboveground Carbon Storage in a
 450 Tropical Forest. *Science* 310:1029–1031.
- 451 Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G.
 452 M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A.
 453 Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on
 454 humanity. *Nature* 486:59–67.
- 455 Connell, S. D., and G. Ghedini. 2015. Resisting regime-shifts: the stabilising effect of
 456 compensatory processes. *Trends in Ecology & Evolution* 30:513–515.
- 457 Davies, T. W., S. R. Jenkins, R. Kingham, J. Kenworthy, S. J. Hawkins, and J. G. Hiddink. 2011.
 458 Dominance, Biomass and Extinction Resistance Determine the Consequences of
 459 Biodiversity Loss for Multiple Coastal Ecosystem Processes. *PLOS ONE* 6:e28362.

- 460 Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C.
461 Wirth, I. C. Prentice, E. Garnier, G. Bönsch, M. Westoby, H. Poorter, P. B. Reich, A. T.
462 Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. J. Wright, S. N. Sheremet'ev,
463 H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S.
464 Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The
465 global spectrum of plant form and function. *Nature* 529:167.
- 466 Díaz, S., A. Purvis, J. H. C. Cornelissen, G. M. Mace, M. J. Donoghue, R. M. Ewers, P. Jordano,
467 and W. D. Pearse. 2013. Functional traits, the phylogeny of function, and ecosystem
468 service vulnerability. *Ecology and Evolution* 3:2958–2975.
- 469 Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran.
470 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss.
471 *Science* 344:296–299.
- 472 Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003.
473 Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the*
474 *Environment* 1:488–494.
- 475 Gonzalez, A., and M. Loreau. 2009. The Causes and Consequences of Compensatory Dynamics
476 in Ecological Communities. *Annual Review of Ecology, Evolution, and Systematics*
477 40:393–414.
- 478 Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder
479 effects. *Journal of Ecology* 86:902–910.
- 480 Ives, A. R., and B. J. Cardinale. 2004. Food-web interactions govern the resistance of
481 communities after non-random extinctions. *Nature* 429:174–177.
- 482 Laliberté, E., J. A. Wells, F. DeClerck, D. J. Metcalfe, C. P. Catterall, C. Queiroz, I. Aubin, S. P.
483 Bonser, Y. Ding, J. M. Fraterrigo, S. McNamara, J. W. Morgan, D. S. Merlos, P. A.
484 Vesk, and M. M. Mayfield. 2010. Land-use intensification reduces functional redundancy
485 and response diversity in plant communities. *Ecology Letters* 13:76–86.
- 486 Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem
487 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- 488 McIntyre, P. B., L. E. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient
489 recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences*
490 104:4461–4466.

- 491 Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M.
492 Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud, and W.
493 Thuiller. 2013. Rare Species Support Vulnerable Functions in High-Diversity
494 Ecosystems. *PLOS Biology* 11:e1001569.
- 495 Naeem, S. 1998. Species Redundancy and Ecosystem Reliability. *Conservation Biology* 12:39–
496 45.
- 497 Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age
498 of Extinction. *Science* 336:1401–1406.
- 499 Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A.
500 Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace,
501 B. Martín-López, B. A. Woodcock, and J. M. Bullock. 2015. Biodiversity and Resilience
502 of Ecosystem Functions. *Trends in Ecology & Evolution* 30:673–684.
- 503 Pan, Q., D. Tian, S. Naeem, K. Auerswald, J. J. Elser, Y. Bai, J. Huang, Q. Wang, H. Wang, J.
504 Wu, and X. Han. 2016. Effects of functional diversity loss on ecosystem functions are
505 influenced by compensation. *Ecology* 97:2293–2302.
- 506 Payne, J. L., A. M. Bush, N. A. Heim, M. L. Knope, and D. J. McCauley. 2016. Ecological
507 selectivity of the emerging mass extinction in the oceans. *Science*:aaf2416.
- 508 Peres, C. A., and P. M. Dolman. 2000. Density compensation in neotropical primate
509 communities: evidence from 56 hunted and nonhunted Amazonian forests of varying
510 productivity. *Oecologia* 122:175–189.
- 511 Peres, C. A., T. Emilio, J. Schiatti, S. J. M. Desmoulière, and T. Levi. 2016. Dispersal limitation
512 induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the*
513 *National Academy of Sciences* 113:892–897.
- 514 Ricotta, C., F. de Bello, M. Moretti, M. Caccianiga, B. E. L. Cerabolini, and S. Pavoine. 2016.
515 Measuring the functional redundancy of biological communities: a quantitative guide.
516 *Methods in Ecology and Evolution* 7:1386–1395.
- 517 Savage, V. M., C. T. Webb, and J. Norberg. 2007. A general multi-trait-based framework for
518 studying the effects of biodiversity on ecosystem functioning. *Journal of Theoretical*
519 *Biology* 247:213–229.

- 520 Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S.
 521 Srivastava. 2004. Extinction and Ecosystem Function in the Marine Benthos. *Science*
 522 306:1177–1180.
- 523 Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg,
 524 D. U. Hooper, S. T. Jackson, and M.-L. Navas. 2008. Scaling environmental change
 525 through the community-level: a trait-based response-and-effect framework for plants.
 526 *Global Change Biology* 14:1125–1140.
- 527 Thomsen, M. S., C. Garcia, S. G. Bolam, R. Parker, J. A. Godbold, and M. Solan. 2017.
 528 Consequences of biodiversity loss diverge from expectation due to post-extinction
 529 compensatory responses. *Scientific Reports* 7:43695.
- 530 Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. *Annual*
 531 *Review of Ecology, Evolution, and Systematics* 45:471–493.
- 532 Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P. D.
 533 Frenne, K. Verheyen, and S. Wipf. 2013. Global meta-analysis reveals no net change in
 534 local-scale plant biodiversity over time. *Proceedings of the National Academy of*
 535 *Sciences* 110:19456–19459.
- 536 Weeks, B. C., N. Gregory, and S. Naeem. 2016. Bird assemblage vulnerability depends on the
 537 diversity and biogeographic histories of islands. *Proceedings of the National Academy of*
 538 *Sciences* 113:10109–10114.
- 539 Winemiller, K. O., D. B. Fitzgerald, L. M. Bower, and E. R. Pianka. 2015. Functional traits,
 540 convergent evolution, and periodic tables of niches. *Ecology Letters* 18:737–751.
- 541 Zavaleta, E., J. Pasari, J. Moore, D. Hernández, K. B. Suttle, and C. C. Wilmers. 2009.
 542 Ecosystem Responses to Community Disassembly. *Annals of the New York Academy of*
 543 *Sciences* 1162:311–333.

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546 **TABLES**

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549 **Table 1.** Symbols and parameter values used in the simulation.

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Symbol	Explanation	Value in the Simulation
T_a	Total ecosystem function a	specified by equation 1
$F_{a,i}$	Contribution to function a by species i	$F_{a,i} = m_i E_{i,a}$
S	Number of species	$S = 100$
m_i	Mass of species i	$m_i = F_{a,i} / E_{i,a}$
$E_{a,i}$	Effect trait linked to function a of species i	$E_{a,i} \sim \text{rnorm}[0,1], \text{runif}[0,1], \text{rlnorm}[0,1]$ Allocated either randomly to all species in a community in the ratio of 7:2:1, or correlated with $V_{i,k}$
TG	Trophic guild	of 7:2:1, or correlated with $V_{i,k}$
$V_{i,k}$	Vulnerability of species i to driver k	$V_{i,k} = \varepsilon_{i,k} R_{i,k}$
$\varepsilon_{i,k}$	Exposure of species i to driver k	$\varepsilon_{i,k} = 1$
$R_{i,k}$	Response trait of species i linked to driver k	$R_{i,k} = E_{i,k}, -E_{i,k}, \text{runif}[0,1]$

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553 **FIGURE LEGENDS**

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555 **Figure 1.** The ecosystem stress test to quantify ecosystem vulnerability. In the first step (A), we
556 obtain the total current ecosystem function, and use the species vulnerabilities to seed the
557 probabilistic trait-based extinction scenarios. In the second step (B), a stress is applied whereby a
558 species is lost and the post-extinction ecosystem function is measured without compensation. In
559 the third step (C), biomass compensation is modeled by allocating the lost biomass associated
560 with the extinct species to a remaining species based on replacement scenarios (see *Methods*).
561 Finally, after all species are extinct (D), the number of species needed to maintain ecosystem
562 function above a set threshold is examined, and used as a metric of ecosystem vulnerability.
563 Figure adapted from Bunker et al. (2005) and Peres et al. (2016).

564 **Figure 2.** Effects of response and effect trait covariation and distribution on the relationship
565 between the proportion of species lost and the proportion of initial ecosystem function
566 remaining. Columns are different trait covariation scenarios while rows depict different trait
567 distributions. Each point is a result of one simulation, with colors representing the effects of
568 different compensation scenarios (black: no replacement; red: random replacement; green:
569 uncorrelated trophic-guild replacement; blue: correlated trophic-guild replacement). The lines are
570 the median value of each replacement simulation.

571 **Figure 3.** The effect of trait distribution and compensation on the relationship between initial
572 community vulnerability properties (V_{TOT} : total initial community vulnerability: A, D, G; V_{SD} :
573 initial community trait standard deviation: B, E, H; V_{Mean} : initial mean community vulnerability:
574 C, F, I) and ecosystem vulnerability, measured as the number of species needed to maintain
575 function above 50% of initial ecosystem function. Colors represent different replacement
576 scenarios (as in Figure 2; see *Methods*).

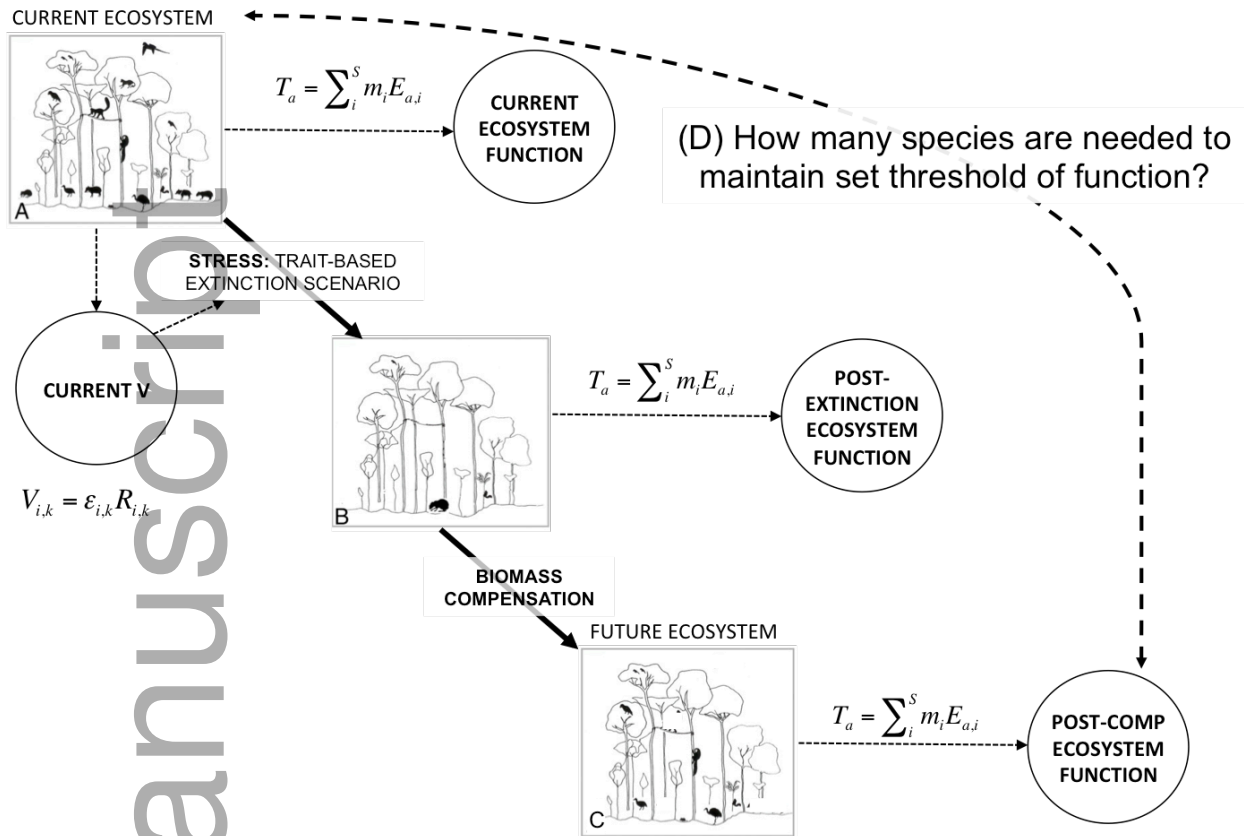
577 FIGURES

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579 Figure 1

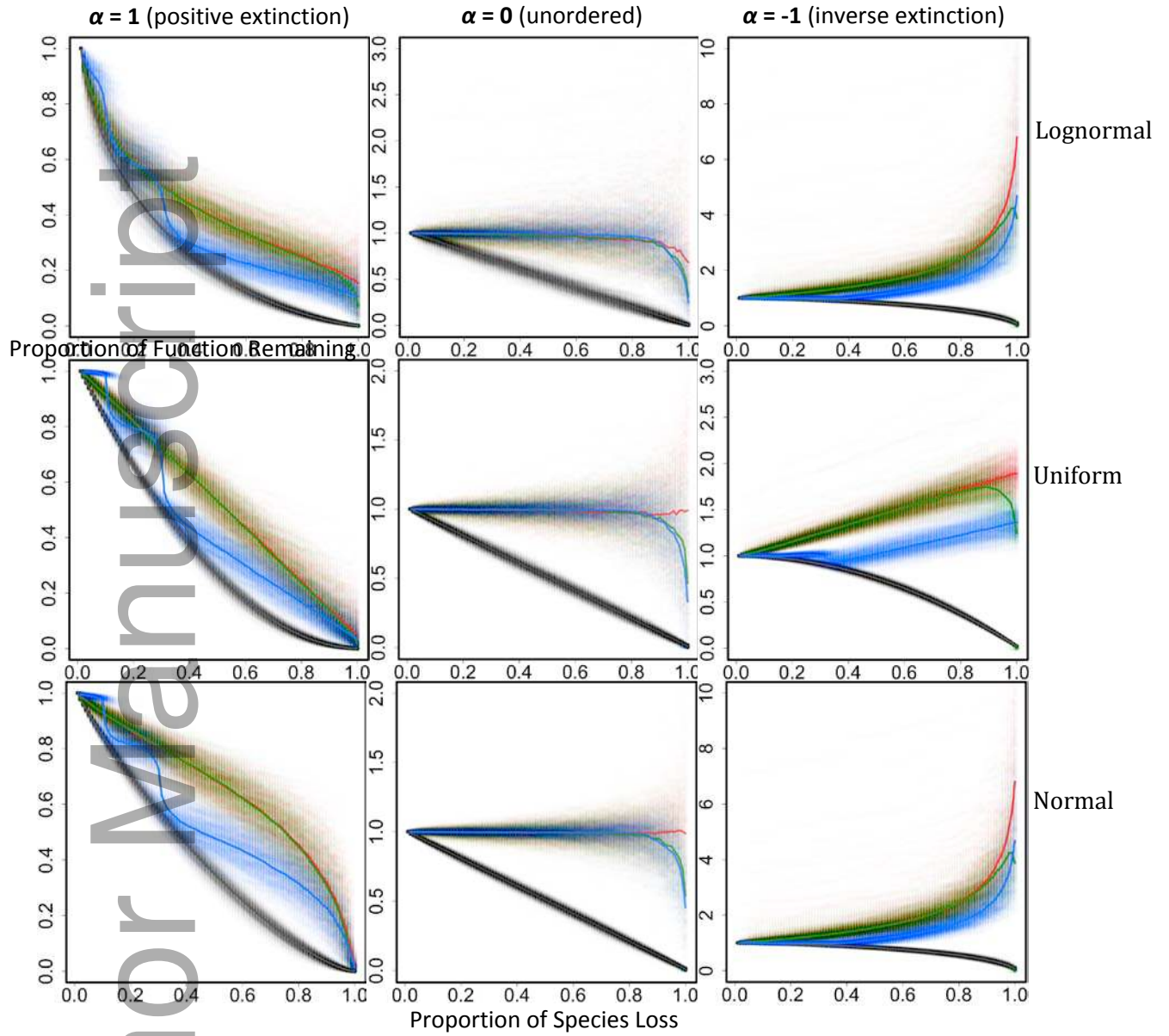
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583 **Figure 2**



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Figure 3