

1 **Landscape heterogeneity strengthens the relationship between β -diversity and ecosystem**
2 **function**

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21

22 **Abstract**

23 Consensus has emerged in the literature that increased biodiversity enhances the capacity of
24 ecosystems to perform multiple functions. However, most biodiversity/ecosystem function
25 studies focus on a single ecosystem, or on landscapes of homogenous ecosystems. Here we
26 investigate how increased landscape-level environmental dissimilarity may affect the
27 relationship between different metrics of diversity (α , β , or γ) and ecosystem function. We
28 produced a suite of simulated landscapes, each of which contained four experimental outdoor
29 aquatic mesocosms. Differences in temperature and nutrient conditions of the mesocosms
30 allowed us to simulate landscapes containing a range of within-landscape environmental
31 heterogeneities. We found that the variation in ecosystem functions was primarily controlled by
32 environmental conditions, with diversity metrics accounting for a smaller (but significant)
33 amount of variation in function. When landscapes were more homogeneous, α , β , and γ diversity
34 was not associated with differences in primary production, and only γ was associated with
35 changes in decomposition. In these homogeneous landscapes, differences in these two ecosystem
36 functions were most strongly related to nutrient and temperature conditions in the ecosystems.
37 However, as landscape-level environmental dissimilarity increased, the relationship between α ,
38 β , or γ and ecosystem functions strengthened, with β being a greater predictor of variation in
39 decomposition at the highest levels of environmental dissimilarity than α or γ . We propose that
40 when all ecosystems in a landscape have similar environmental conditions, species sorting is
41 likely to generate a single community composition that is well suited to those environmental
42 conditions, β is low, and the efficiency of diversity-ecosystem function couplings is similar
43 across communities. Under this low β , the effect of abiotic conditions on ecosystem function will
44 be most apparent. However, when environmental conditions vary among ecosystems, species

45 sorting pressures is different among ecosystems, producing different communities among
46 locations in a landscape. These conditions lead to stronger relationships between β and the
47 magnitude of ecosystem functions. Our results illustrate that abiotic conditions and the
48 homogeneity of communities influence ecosystem function expressed at the landscape-scale.

49

50 **Introduction**

51 Human activities have dramatic impacts on the abiotic conditions and biota of natural
52 ecosystems (Vitousek et al. 1997, Cardinale et al. 2012a). Atmospheric pollutants have affected
53 global temperatures (Forster et al. 2007), while a shift towards industrial-scale agriculture has
54 accelerated levels of nutrient release (Tilman 1999, Bouwman et al. 2009), leading to increased
55 rates of eutrophication (Dupas et al. 2015). The realized impacts of changes in temperature and
56 nutrient levels are not uniformly distributed across time and space, increasing heterogeneity in
57 abiotic conditions among ecosystems within a landscape and producing novel environmental
58 conditions (Ashcroft et al. 2009, Hobbs et al. 2009). Moreover, the dispersal of nutrient
59 pollutants within a landscape varies considerably depending on soil type, hydrology, land use
60 and topography (Heathwaite et al. 2005, Okubo and Levin 2013). Human activities may
61 therefore increase heterogeneity in temperature and nutrient conditions (hereon termed
62 “environmental dissimilarity”) above levels generated by natural processes. These changes to
63 environmental conditions may directly alter rates of ecosystem functions (Gruber and Galloway
64 2008, Shurin et al. 2012), but also present critical challenges for understanding
65 biodiversity/ecosystem function relationships at the landscape scale.

66 Biodiversity varies among and within ecosystems on every spatial and temporal scale
67 (Barbour et al. 1999, Bailey et al. 2004, Resh 2007, Lefcheck et al. 2015), and its measure is

68 both scale- and question-dependent. Local diversity, the number of species occurring within a
69 local ecosystem is usually referred to as α -diversity (hereon “ α ”). Landscape-level or regional
70 diversity (i.e., the number of species observed across individual ecosystems) is termed γ -
71 diversity (hereon γ). Turnover among communities within a region (differences in community
72 composition or α among local ecosystems) has been broadly referred to as β -diversity (hereon
73 “ β ”, Whittaker 1972).

74 There is growing consensus among ecologists that higher biodiversity often begets increased
75 levels of ecosystem functioning across many types of ecosystems (Cardinale et al. 2012a). In
76 addition, the specific species present, particularly the functionally dominant species, can have
77 major impacts on ecosystem function (Grime 1998, Naeem et al. 2012, Atwood et al. 2014a).
78 However, with a few notable exceptions (Pasari et al. 2013, Barnes et al. 2016, Burley et al.
79 2016, Hautier et al. 2018, Winfree et al. 2018), the majority of empirical investigations of
80 biodiversity-ecosystem function relationships have focused on local species richness (α). This
81 focus on local species richness overlooks the scale dependence of the biodiversity-ecosystem
82 function relationship (Isbell et al. 2017), and assumes that the processes driving the relationship
83 are equal at the ecosystem and landscape level.

84 Within a single ecosystem, or a homogeneous landscape of abiotically similar ecosystems,
85 species sorting may lead to a single, “functionally optimal” community, composed of taxa with a
86 series of traits and population densities that are well suited to exploit available resources.
87 Furthermore, theory suggests that community composition should be similar across such
88 landscapes because the available niches ought to be filled by the same species in each ecosystem
89 (Kraft et al. 2008). In this case, we would therefore expect that α would be similar among
90 ecosystems, and both β and γ should be relatively low. In contrast, as environmental conditions

91 across landscapes differ, species sorting should result in local communities that differ in species
92 composition (Barnes et al. 2016). Each of these different communities then consists of species
93 best adapted to each local habitat (Winder et al. 2009), and potentially meaning that species
94 turnover (β) is more important to maintain ecosystem function than α at larger spatial scales
95 (Winfree et al. 2018). We therefore expect that as we move from the ecosystem scale to the
96 landscape scale, environmental heterogeneity within a landscape may mean there is no single,
97 functionally optimal community that is able to best perform ecosystem functions (Isbell et al.
98 2017, Winfree et al. 2018). In landscapes with a high degree of environmental heterogeneity, we
99 might observe similar levels of α if each ecosystem provides a similar amount of niche space, but
100 higher β and γ than in homogeneous landscapes. Moreover, higher levels of β may be associated
101 within increased ecosystem functioning in heterogeneous landscapes, as different communities
102 may perform different functions, and perform some functions to a greater degree, under different
103 environmental conditions (Thompson and Gonzalez 2016, Isbell et al. 2017). In addition,
104 changes to abiotic conditions may increase the importance of stochastic determinants of
105 community composition (Chase 2010), leading to changes in α , β , and γ and ecosystem functions
106 either directly (Burley et al. 2016) or indirectly (Barnes et al. 2016).

107 To understand how differences in landscape-level environmental dissimilarity can alter the
108 relationships among ecosystem functions and α β γ , we used data from an outdoor freshwater
109 mesocosm experiment in which invertebrate community composition and core ecosystem
110 functions were measured. Temperature and nutrient conditions were manipulated, and the
111 subsequent variation in conditions among mesocosms was used to create simulated landscapes
112 with differing levels of environmental dissimilarity. This approach allowed us to examine how
113 the relationships between ecosystem functions and α β γ varied with environmental dissimilarity.

114 For each mesocosm we measured two ecosystem functions that represent basal trophic resources
115 in aquatic food webs: primary production and leaf litter decomposition. We predicted that much
116 of the variation in these ecosystem functions would be controlled by nutrient and temperature
117 levels in the landscape due to the importance of bottom-up control, especially the role of
118 nutrients in controlling primary production (Harpole et al. 2011). With respect to the role of
119 diversity, we hypothesized that at low levels of environmental dissimilarity, α and γ would be
120 more strongly associated with landscape-level ecosystem functions than β . In this case, the
121 absolute diversity within both individual ecosystems and the landscape as whole would influence
122 landscape-level ecosystem function, and a single functionally optimal community would occupy
123 all habitats within the landscape. However, at higher levels of environmental dissimilarity, we
124 hypothesized that β would be more strongly associated with landscape-level ecosystem functions
125 than either α or γ . When environmental conditions among ecosystems in a landscape differ, each
126 ecosystem within the landscape has the potential to have a different community that is well
127 adapted to the particular abiotic conditions of that ecosystem.

128

129 **Methods**

130 *Experimental set-up and data collection*

131 Experimental ponds consisted of twenty, 1136 L Rubbermaid[®] cattle water tanks housed at the
132 University of British Columbia's pond facility (Vancouver, Canada) and represented a subset of
133 treatments from a broader experiment (Greig et al. 2012, Kratina et al. 2012). This broader
134 experiment contained mesocosms where a top predator had been added, and we elected to
135 exclude these treatments from the current analysis to focus on the effects of nutrients and

136 temperature. Nutrient and temperature conditions among the ponds were directly manipulated in a
137 2 x 2 fully factorial design. Nutrient levels within each pond were designated as either ambient
138 or elevated, with elevated conditions being achieved through monthly additions of 264 μg of
139 nitrogen L^{-1} (as NaNO_3) and 27 μg of phosphorus L^{-1} (as KH_2PO_4). Temperature treatments were
140 designated as either ambient or elevated. Heating tanks with 300W Hagen[®] aquarium heaters
141 produced temperatures 3°C above ambient tank temperatures. Nutrient and warming treatments
142 were randomly assigned to the 20 ponds, to generate four experimental treatment combinations
143 of five replicates each.

144 At the start of the experiment, mesocosms were inoculated with phytoplankton,
145 zooplankton, macroinvertebrates and sediments from local sources. The experimental conditions
146 were maintained for 16 months, during which time the tanks were open to allow natural
147 colonization of macroinvertebrates and plankton from local sources. We assume that due to the
148 close spatial proximity of the mesocosms (1m between mesocosms) there were minimal
149 differences in dispersal rates. This lack of differential dispersal rates, together with the fact that
150 identical communities were initially inoculated, would mean that differences in diversity were
151 generated predominantly through species sorting under the different treatment conditions within
152 the mesocosm, and stochastic processes. After 12 months, abundance data on 25 benthic macro-
153 invertebrates and 16 zooplankton taxa were used to calculate α , β , and γ diversity of consumers.
154 Benthic macroinvertebrates were sampled with two 0.02m² cylinder pipe samples per tank along
155 with quantitative wall and water column sweeps, whereas zooplankton were collected in a 10L
156 depth-integrated water column samples (details in Shurin et al. 2012; Kratina et al. 2012). We
157 also collected data on two ecosystem functions: leaf litter decomposition and net ecosystem
158 productivity (NEP). Decomposition rates were calculated by fitting negative exponential decay

159 models to the mass of leaf matter (bigleaf maple, *Acer macrophyllum*) present in 10 mm mesh
160 Nitex[®] bags at 0 and 8 weeks (Benfield 2007, Greig et al. 2012). Net ecosystem productivity was
161 calculated as the difference in O₂ concentrations between dawn and dusk for each mesocosm
162 (Shurin et al. 2012). This metric of NEP therefore measures the difference between
163 photosynthesis and respiration of the whole community over the course of the daylight hours.

164

165 *Simulated landscapes*

166 The 20 experimental ponds were arranged in all possible combinations to construct 4845 unique
167 simulated landscapes. These simulated landscapes were generated by randomly selecting a
168 unique, random sample without replication of 4 of the 20 ponds (Pasari et al. 2013). As there was
169 no spatial component to the experiment, the ecosystems placed into each experimental landscape
170 were selected independently of their spatial location. Environmental heterogeneity within the
171 landscape was indexed using a 2 x 2 matrix of environmental conditions. Each experimental
172 pond within the landscape was classified according to its environmental conditions, i.e. whether
173 its nutrient levels were ambient [1] or elevated [2], and whether temperature was ambient [1] or
174 elevated [2]. The environmental dissimilarity index was then calculated as the Manhattan
175 distance between the ecosystems.

176 The number of potential ecosystem combinations that can produce landscapes with
177 different environmental dissimilarities is substantially different (e.g. there are 20 different
178 mesocosm combinations that produce landscapes with a dissimilarity of 0, but 2000
179 combinations produce a dissimilarity of 7). We thus resampled simulated landscapes within each
180 level of environmental dissimilarity 2000 times to balance the number of landscapes across
181 dissimilarity levels. The experimental design includes two levels of temperature and two levels

182 of nutrients. Although changes in the two factors are unlikely to be exactly biologically
183 equivalent, both increased nutrients and increased temperature represent ecosystem-level
184 stressors that may generate pools of tolerant species that differ from communities under ambient
185 conditions. Note that environmental dissimilarity index values of 1, 2 and 5 are mathematically
186 impossible with this design.

187 For each simulated landscape, we calculated landscape-level values of α , β , and γ . The
188 total diversity (γ) was partitioned into α and β components by decomposing the Shannon entropy
189 (Jost 2007, 2010). This method of partitioning means that α and β components are independent
190 of each other and can then be converted into their numbers equivalents (or true diversity) by
191 taking the exponential value of each metric (Jost 2007). As this method generates α and β
192 diversities that are independent of each other (Jost 2007), they can be included as uncorrelated
193 variables within the statistical analyses. In addition, the partitioning of Shannon entropy into α
194 and β components means that the resulting values depend both on the number of species and the
195 number of individuals of each species (i.e. both species richness and species evenness), making
196 them less sensitive to the detection of rare species and under-sampling (Beck et al. 2013). All
197 these processes were performed using the “entropart” package in R programming language
198 (Marcon and Hérault 2015).

199

200 *The relationships between environmental dissimilarity, diversity, and ecosystem functions*

201 To quantify how environmental dissimilarity affected each of α , β , and γ , we regressed each
202 diversity type against the environmental dissimilarity index. As previous experiments have
203 demonstrated relationships between biodiversity and both temperature and nutrient levels (Worm
204 et al. 2002, Wang et al. 2009), the number of mesocosms that had elevated nutrients or elevated

205 temperature were included as covariates. The environmental dissimilarity index is independent of
206 the number of elevated nutrient or temperature mesocosms as there are multiple ways to produce
207 different values of the index. However, landscapes with an environmental dissimilarity of 8
208 always contained two mesocosms with elevated nutrients and two with elevated temperature
209 crossed in a 2x2 manner, hence nutrient and temperature levels were completely redundant in
210 landscapes with environmental dissimilarities of 8. We therefore excluded temperature and
211 nutrient covariates from these regressions.

212 We further determined how two ecosystem functions (NEP and leaf litter decomposition)
213 were associated with α , β , and γ . As NEP was estimated as the difference between
214 photosynthesis (of both phytoplankton and periphyton) and respiration (of both the planktonic
215 and benthic communities), we used measures of α , β , and γ based on the benthic
216 macroinvertebrates and zooplankton taxa within each mesocosm. However, in the case of leaf
217 litter decomposition, we used measures of α , β , and γ based only on non-predatory benthic
218 macroinvertebrates because zooplankton do not consume benthic leaf litter (Shurin et al. 2012).
219 First, we analyzed a single “global” model for each ecosystem function, and tested for an
220 interaction between each metric of diversity and environmental dissimilarity. A significant
221 interaction would indicate the relationship between landscape level and ecosystem function
222 differs with the level of environmental dissimilarity. After we found a significant
223 β :environmental dissimilarity interaction, we separately analyzed the relationship between each
224 ecosystem function and α , β , and γ with data from each of the six landscapes with environmental
225 dissimilarities of 0, 3, 4, 6, 7, and 8. These six separate analyses each produced a slope of the
226 relationship between each ecosystem function and α , β , or γ . As we were running six different
227 regressions, we applied a Bonferroni correction (Weisstein 2004) to avoid inflating the chances

228 of type 1 errors. This Bonferroni correction meant that we used an alpha level of 0.008 to
229 determine significant differences. In order to understand the relative importance of α , β , γ and
230 elevate temperature and nutrients, the R^2 value for the linear models was decomposed among
231 factors using “lmg” metric from the “calc.relimp” function within the relaimpo package
232 (Grömping 2006) in R. This metric decomposes the total R^2 value into non-negative portions for
233 each variable, that sum up to the total R^2 (Lindeman et al. 1980). As the order in which variables
234 are added to a model can influence their relative importance, this metric takes the relative
235 importance of each variable averaged over every order in which the variables can be added into
236 the linear model (Lindeman et al. 1980, Johnson and LeBreton 2004, Grömping 2006).

237 Many previous analyses of the relationships between biodiversity and ecosystem
238 functions have utilized biodiversity metrics based on species richness, rather than abundance-
239 weight metrics (Loreau et al. 2001, Cardinale et al. 2006, Lefcheck et al. 2015). In order to make
240 our results more comparable to previous studies, we repeated the whole analysis using species
241 richness instead of abundance weighed metrics and present the results as a supplementary
242 sections (*Supplementary materials*). However, as the use of abundance weighted metrics has the
243 potential to increase the amount of information contained in diversity measures (Barwell et al.
244 2015), and may have a greater impact on ecosystem functions than richness (Winfree et al.
245 2015), we focus on the abundance-weighted measures in the main text.

246

247 **Results**

248 When α , β , and γ were measured in terms of their numbers equivalents (true diversity),
249 landscape-level mean α did not have a significant relationship with either the environmental

250 dissimilarity index, but was reduced by 1.06 ± 1.04 (mean \pm S.E., $n=4845$) for every elevated
251 temperature mesocosm. Mean α also decreased by 1.01 ± 1.002 for every elevated nutrient
252 mesocosm within the landscape ($F_{(1,4841)} = 71.43$, $P < 0.001$). Landscape level β increased with
253 increasing environmental heterogeneity, being 1.04 ± 1.006 (mean \pm s.e.) higher when the
254 environmental dissimilarity index was 8 compared with 0 (linear regression, $F_{(1,4841)} = 161.22$, P
255 < 0.001 , Fig. 2). However, we observed a wide range of β across all levels of environmental
256 dissimilarity, and there was substantial overlap of the ranges (Fig. 2). This high level of overlap
257 in β is critical to the following analyses, as it allows us to compare the relationship between β
258 and ecosystem functions across the different levels of environmental dissimilarity. In addition, β
259 increased by 1.03 ± 1.0035 for each mesocosm containing elevated nutrients ($F_{(1,4841)} = 1108.43$,
260 $P < 0.001$), and increased by 1.03 ± 1.003 for each mesocosm with elevated temperature ($F_{(1,4841)}$
261 $= 8.42$, $P < 0.001$). Landscape-level γ increased with environmental dissimilarity ($F_{(1,4841)} =$
262 99.21 , $P < 0.001$), increased by 1.015 ± 1.0025 for every elevated nutrient mesocosm ($F_{(1,4841)} =$
263 248.38 , $P < 0.001$) and decreased by 1.011 ± 1.0023 for each elevated temperature mesocosm
264 ($F_{(1,4841)} = 144.51$, $P < 0.001$).

265 To understand the relationships between ecosystem processes, diversity metrics and
266 environmental conditions, we regressed both NEP and decomposition against α , β , γ , and the
267 number of mesocosms containing elevated temperature and nutrient treatments. Our global
268 analysis of landscape-level NEP revealed a significant interaction between environmental
269 dissimilarity and β (multiple linear regression, $F_{(1,4835)} = 8.69$, $P = 0.003$). Specifically, the
270 positive effect of β on NEP and the amount of variation explained by β increased as
271 environmental dissimilarity increased (Fig. 2). NEP was associated with significant changes in α
272 and γ ($P < 0.001$), although neither diversity metric significantly interacted with environmental

273 dissimilarity. NEP increased by $13.65\% \pm 1.88\%$ for each mesocosm containing elevated
274 nutrients ($F_{(1,4835)} = 74.91$, $P < 0.001$), and increased by $2.75\% \pm 0.63\%$ for each elevated
275 temperature mesocosm ($F_{(1,4835)} = 17.67$, $P < 0.001$). NEP significantly increased as mean α
276 increased at all levels of environmental dissimilarity ≥ 3 (Fig. 2a). Across all levels of
277 environmental dissimilarity, the proportional change in NEP associated with α varied from 0.030
278 when environmental dissimilarity was 3, to 0.044 when environmental dissimilarity was 8 (Fig.
279 2b). NEP was involved in a significant positive relationship with β at environmental dissimilarity
280 levels ≥ 3 (Fig. 2a), and accounted for between 0.034 and 0.080 of the variation in NEP (Fig.
281 2b). The relationships between NEP and γ were positive when environmental dissimilarity was \geq
282 3 (Fig. 2a). The proportion of variation in NEP associated with γ ranged between 0.037 and
283 0.060 (Fig. 2b). The relationship between NEP and nutrients was positive across all
284 environmental dissimilarities where it could be assessed (level 8 could not be assessed) (Fig. 2a),
285 and changes in the number of elevated nutrient mesocosms were associated with most of the
286 proportional variation (0.41-0.53, Fig. 2b). The relationship between NEP and temperature was
287 positive across all levels of environmental dissimilarity where it could be assessed (Fig. 2a), and
288 temperature accounted for between 0.010 and 0.017 of the proportional variation (Fig. 2b).

289 The global analysis revealed that landscape-level leaf litter decomposition was
290 significantly associated with an interaction between β and environmental dissimilarity ($F_{(1,4835)} =$
291 32.12 , $P < 0.001$). The direction of this interaction indicated that the slope of the relationships
292 between β and decomposition increased with increasing environmental dissimilarity.
293 Decomposition rates varied with both α and γ (both $P < 0.001$), although neither one significantly
294 interacted with environmental dissimilarity ($P = 0.79$ and $P = 0.23$ respectively). Decomposition
295 rates also increased by $9.46\% \pm 0.43\%$ for each elevated nutrient mesocosm ($F_{(1,4835)} = 21.95$, P

296 < 0.001), and increased by $13.02\% \pm 0.50\%$ for each elevated temperature mesocosm in the
297 landscape ($F_{(1,4835)} = 26.20$, $P < 0.001$).

298 When landscapes with different environmental dissimilarity values were assessed
299 separately, there was a positive relationship between decomposition and landscape α when
300 environmental dissimilarity was 3, a positive relationship when environmental dissimilarity was
301 8, but no significant relationship when environmental dissimilarity was 0, or 4 - 7 (Fig. 3a). The
302 proportion of variation in decomposition explained by α was generally low (0.007 – 0.01 of the
303 total variation, Fig. 3b). Our data showed a positive relationship between decomposition and β at
304 all levels of environmental dissimilarity other than 0, and the slope coefficient of the relationship
305 between decomposition and β increased as the environmental dissimilarity index increased (Fig.
306 3a). The proportion of variation in decomposition explained by β ranged between 0.01 and 0.14
307 (Fig. 3b). Decomposition was positively associated with γ at all levels of environmental
308 dissimilarity (Fig. 3a), although the amount of variation accounted for by γ decreased with
309 increasing environmental dissimilarity from 0.27 to 0.06 (Fig. 3b). At levels of environmental
310 dissimilarity where they could be assessed (< 8), decomposition rates were higher in landscapes
311 with elevated nutrient and elevated temperature mesocosms (Fig. 3a). These environmental
312 conditions accounted for the majority of the variation in decomposition (up to 0.35 for
313 temperature at environmental dissimilarity =0), although the proportion they accounted for
314 decreased (Fig. 3b).

315 Quantitatively similar relationships between environmental dissimilarity, diversity, and
316 ecosystem functions were found for the analysis based on species richness rather than
317 abundance-weighted metrics (*Supplementary materials*). However, when diversity measures
318 were calculated using abundance-weighted metrics, they tended to account for slightly more of

319 the variation in ecosystem function than when based on species richness. This increase in
320 variation is likely linked to the extra information included in abundance weighted metrics, and
321 may also be related to a pattern of decreasing species evenness with increasing environmental
322 dissimilarity (*Supplementary materials, Fig. S4*)

323

324 **Discussion**

325 We provide evidence that as landscape-level environmental heterogeneity increases, β increases,
326 which in turn is significantly associated with differences in landscape-level expressions of two
327 ecosystem functions. In addition, while primary production and decomposition were primarily
328 controlled by environmental conditions, at the highest levels of environmental dissimilarity, β
329 appeared to explain a greater proportion of the variation in decomposition than either α or γ . This
330 relatively large impact of β compared to α or γ suggests that in landscapes with a high level of
331 spatial heterogeneity, the turnover of species among ecosystems is a more important driver of
332 this basal ecosystem process than the actual composition of species. Relationships between
333 biodiversity and ecosystem function have been investigated across a wide variety of systems
334 (Tilman and Downing 1994, Bellwood et al. 2003, Girvan et al. 2005, Hattenschwiler et al. 2005,
335 Atwood et al. 2015), but the majority of these previous studies focus on how biodiversity and
336 community composition affects the processes within a specific ecosystem (Tilman and Downing
337 1994, Reich et al. 2005), or rates of flux to neighboring ecosystems (Atwood et al. 2014b).
338 Recent experiments show that α , β , and γ can alter landscape-level patterns of ecosystem
339 function (Pasari et al. 2013, Hautier et al. 2018, Winfree et al. 2018). Our results build on those
340 studies by showing that the importance of β as a driver of ecosystem functions may depend on
341 the level of environmental dissimilarity among ecosystems in a landscape.

342 Our results revealed that as landscape-level environmental dissimilarity increased,
343 landscape-level β also increased, but we observed no concurrent changes in α . This relationship
344 between environmental dissimilarity and β is consistent with ecological niche theory (species
345 sorting), which proposes that different species are better adapted to different conditions
346 (Vandermeer 1972, Chase and Leibold 2003), and aligns with recent findings from temperate
347 forest (Barnes et al. 2016) and pollination systems (Winfree et al. 2018). Recent theory has
348 shown that as environmental dissimilarity increases, increased β becomes increasingly important
349 for stabilizing ecological communities (Wang and Loreau 2014, 2016). The positive relationship
350 we observed between environmental dissimilarity and β may therefore mean that community
351 stability is being maintained by increased species turnover as conditions across the landscape
352 become increasingly heterogeneous. In addition β and γ increased as the number of elevated
353 nutrient mesocosms in the landscape increased, while α decreased. Many studies have reported a
354 unimodal, hump-shaped relationship between nutrient concentrations and biodiversity (Barnett
355 and Beisner 2007, Cardinale et al. 2012b). Our finding of decreased alpha diversity with
356 increased numbers of elevated nutrient landscapes suggest that nutrient levels in the experiment
357 pass the threshold at which nutrients increase taxon dominance and reduce species richness
358 (Nygaard and Ejrnæs 2009). The decrease in α associated with increased temperature suggest
359 that this abiotic factor may represent a stressor on the ecosystem, reducing the diversity present.
360 The increase in β associated with elevated nutrients and temperature suggests that as nutrients
361 and temperature increase, stochastic determinants of community composition such as priority
362 effects become stronger (Chase 2010), enhancing dissimilarity among ecosystems.

363 The positive relationships between NEP and α and β at environmental dissimilarity
364 greater than 0 would suggest that high primary production is providing a resource that can lead to

365 high consumer diversity (Tilman et al. 1982, Chase and Leibold 2002). In addition, the greatest
366 driver of primary production within the experiment was the number of elevated nutrient
367 mesocosms within a landscape. Previous continental scale studies have also demonstrated that
368 the majority of variation in primary productivity is driven by abiotic conditions, with diversity
369 contributing far less (Burley et al. 2016). The combination of the positive relationship between α
370 and β and primary production, together with the high proportion of variation associated with
371 elevated nutrients suggests that, in our system, primary production and the invertebrate consumer
372 community it supports is strongly influenced by bottom-up processes.

373 Rates of leaf litter decomposition were not associated with either α or β when
374 environmental dissimilarity was 0, influenced by γ , but primarily controlled by elevated
375 temperature and nutrients. The positive effect of elevated temperature on decomposition rates
376 likely stems from higher temperatures increasing rates of microbial metabolism (Geraldine et al.
377 2012, Follstad Shah et al. 2017). The positive effects of elevated nutrients on decomposition may
378 have occurred through a priming effect, as increased primary producer biomass leads to the
379 production of algal-based C exudates that can stimulate bacterial growth (Danger et al. 2016).
380 Unlike primary production, which can be influenced by both consumption and algal growth,
381 litter standing stocks can only be influenced by consumption as there was no leaf litter addition.
382 This lack of an addition mechanism could potentially explain why diversity had a stronger
383 general impact on decomposition than primary productivity, where elevated nutrients are likely
384 to promote algal growth and counteract the effects of consumption.

385 Our study provides compelling evidence that β -diversity may increase ecosystem
386 functions across heterogeneous landscapes. Previous investigations using mesocosms observed
387 that increased β generally did not affect mean levels of ecosystem function in landscapes with

388 similar abiotic conditions, although it did substantially increase the variance in rates of functional
389 processes (Pasari et al. 2013). This previous observation is consistent with our results in that we
390 found no significant relationship between β and either decomposition or primary production
391 when all ecosystems within a landscape had the same environmental conditions. However,
392 increased environmental dissimilarity led to both increased β , and an increase in the strength of
393 the relationship between β and ecosystem functions, to the extent that β was more strongly
394 associated with ecosystem functions than either α or γ . The relatively high importance of β as
395 environmental dissimilarity increases agrees with previous field experiments investigating the
396 relationships between diversity and ecosystem functions (Isbell et al. 2017, Winfree et al. 2018).
397 These previous investigations specifically note that as the spatial scale over which ecosystem
398 functions are measured increases, environmental conditions are likely to become increasingly
399 heterogeneous, meaning different species are better suited to performing different functions
400 (Winfree et al. 2018). As anthropogenic stressors affect some ecosystems more than others
401 (Ashcroft et al. 2009), and can homogenize communities (Mondy and Usseglio-Polatera 2014),
402 understanding the relationships between diversity, environmental heterogeneity and ecosystem
403 functions is crucial to estimating the wider impact of human alteration of landscapes.

404

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409

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590 **Figure legends**

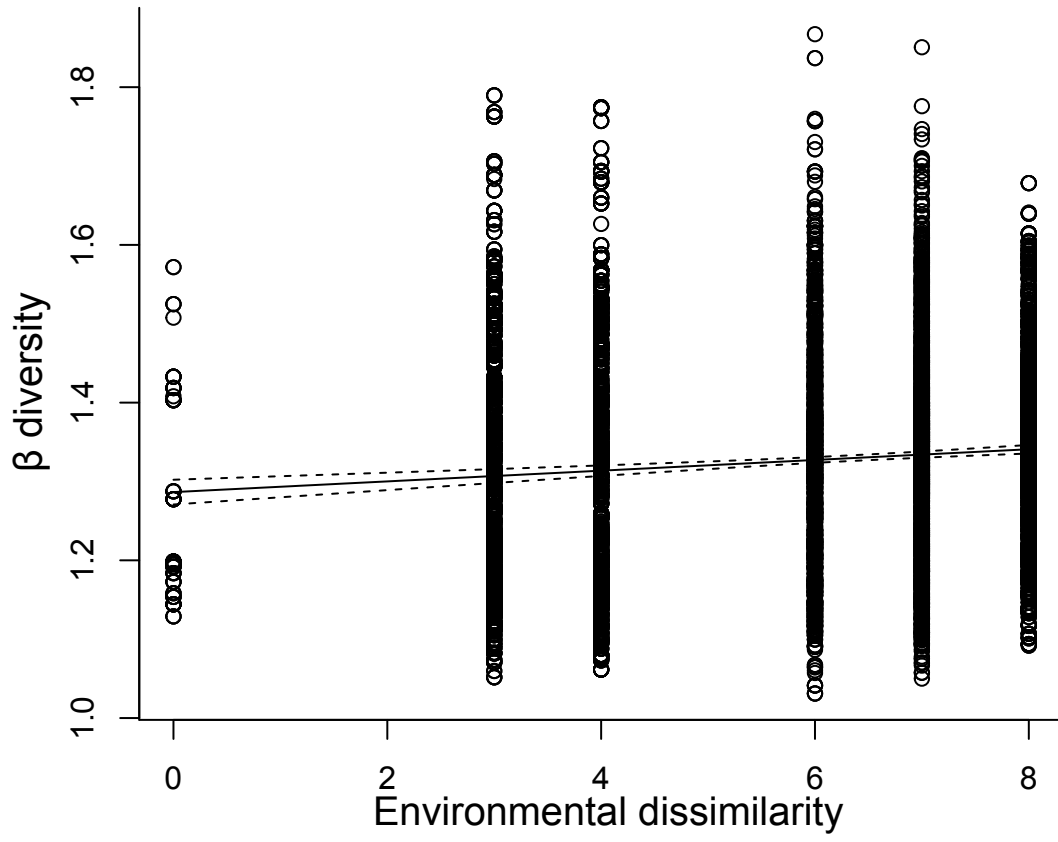
591 **FIG. 1.** β -diversity (measured as effective numbers) increases with increased environmental
592 heterogeneity. Open circles \bullet represent raw data, solid line indicates fit of a linear regression
593 model, dashed lines indicate standard errors estimates.

594
595 **FIG. 2.** Relationships between different metrics of biodiversity and environmental heterogeneity
596 on rates of net ecosystem production. A, slope coefficients for each factor taken from a linear
597 model incorporating all factors. B, proportion of the total variation in decomposition explained
598 by each factor. A star symbol (*) indicates a relationship was not significant ($P > 0.008$
599 following a Bonferroni correction), an obelisk symbol (†) indicates there was no variation in a
600 factor, making a coefficient estimate impossible.

601
602 **FIG. 3.** Relationships between different metrics of biodiversity and environmental heterogeneity
603 on rates of leaf litter decomposition. A, slope coefficients for each factor taken from a linear
604 model incorporating all factors. B, proportion of the total variation in decomposition associated
605 with each factor. A star (“*”) indicates a relationship was not significant ($P > 0.008$ following a
606 Bonferroni correction), an obelisk (“†”) indicates there was no variation in a factor making
607 obtaining a coefficient impossib

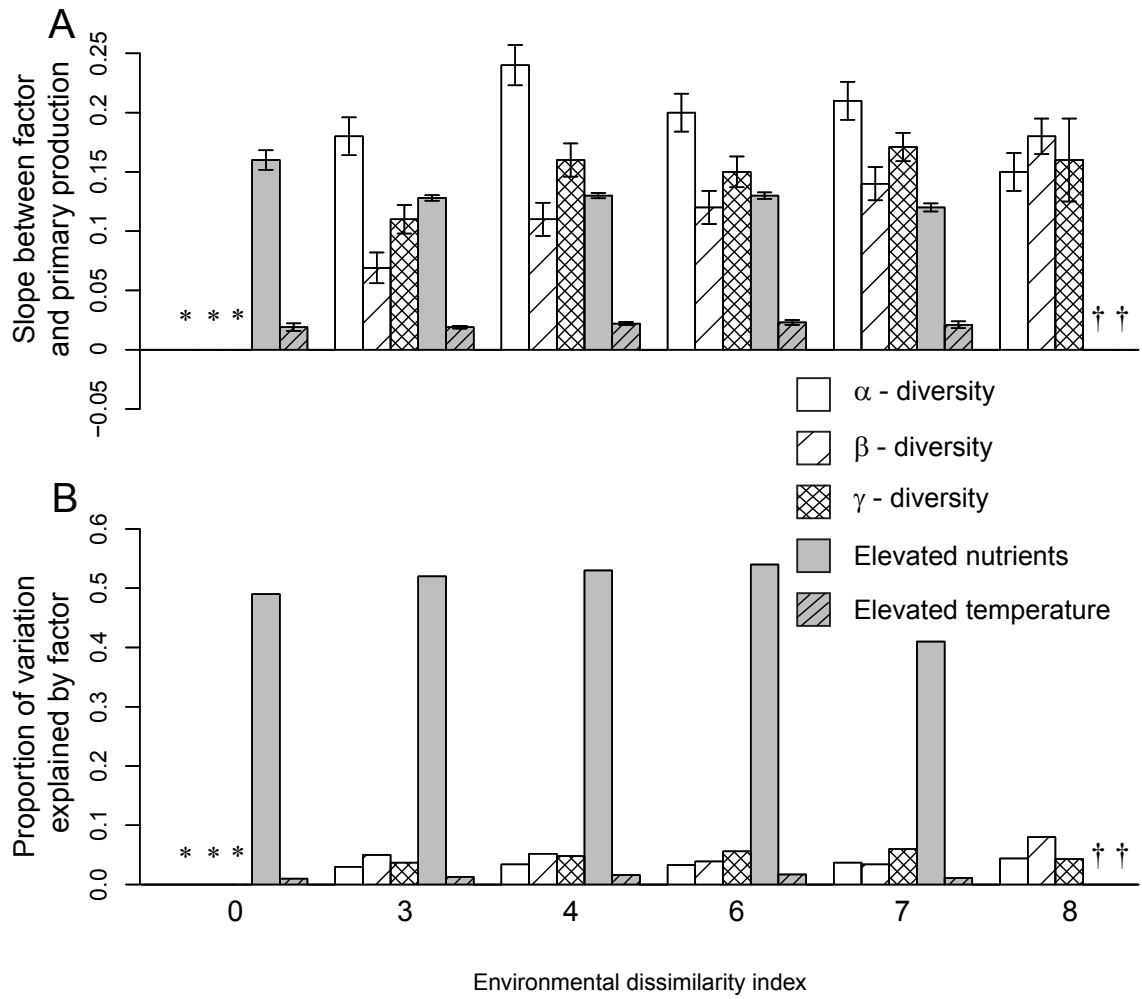
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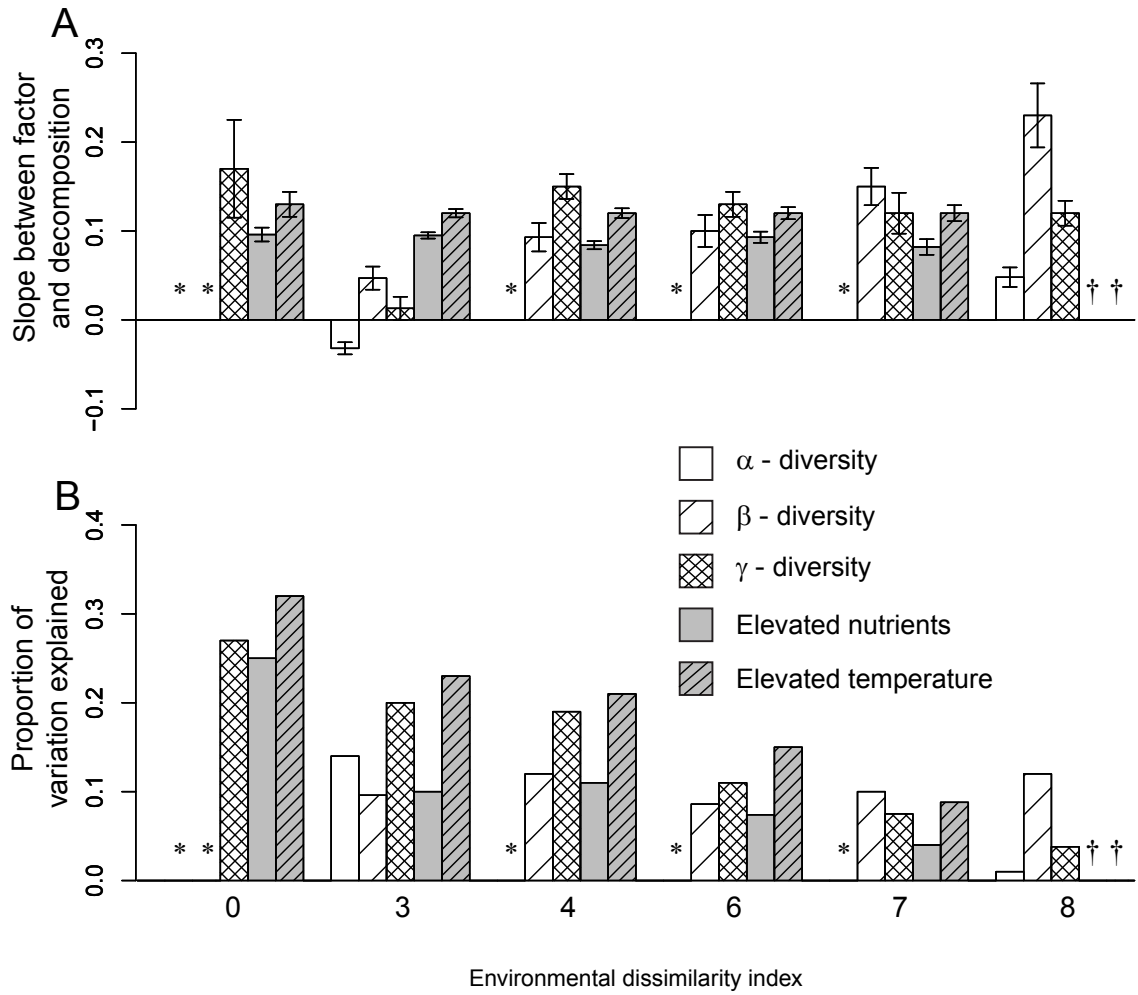
610

611 **FIG. 1.**



612

613 **FIG. 2.**



614

615 **FIG. 3.**