

# The impact of climate warming on species diversity across scales: Lessons from experimental meta-ecosystems

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1 **The impact of climate warming on species diversity across scales: lessons from experimental**  
2 **meta-ecosystems**

3

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18

19 **Aim:** To evaluate the effects of climate warming on biodiversity across spatial scales (i.e.,  $\alpha$ -,  $\beta$ -  
20 and  $\gamma$ -diversity) and the effects of patch openness and experimental context on diversity responses.

21 **Location:** Global

22 **Time period:** 1995 - 2017

23 **Major taxa studies:** Fungi, Invertebrates, Phytoplankton, Plants, Sea weed, Soil Microbes, Zoo-  
24 plankton

25 **Methods:** We compiled data from warming experiments and conducted a meta-analysis to evaluate  
26 the effects of warming on different components of diversity (such as species richness and equivalent  
27 numbers) at different spatial scales ( $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity, partitioning  $\beta$ -diversity into species turn-  
28 over and nestedness components). We also investigated how these effects were modulated by sys-  
29 tem openness, defined as the possibility of replicates being colonized by new species, and experi-  
30 mental context (duration, mean temperature change and ecosystem type).

31 **Results:** Experimental warming did not affect local species richness ( $\alpha$ -diversity) but decreased  
32 effective numbers of species by affecting species dominance. Warming increased species spatial  
33 turnover ( $\beta$ -diversity), although no significant changes were detected at the regional scale ( $\gamma$ -  
34 diversity). Site openness and experimental context did not significantly affect our results, despite  
35 significant heterogeneity in the effect sizes of  $\alpha$ - and  $\beta$ - diversity.

36 **Main conclusions:** Our meta-analysis shows that the effects of warming on biodiversity are scale-  
37 dependent. While local and regional inventory diversity remain unaltered, species composition  
38 across temperature gradients and the patterns of species dominance change with temperature, creat-  
39 ing novel communities that might be harder to predict.

40 **Keywords:** Climate change, Alpha and Beta diversity, Habitat fragmentation, Manipulative exper-  
41 iments, Meta-analysis.

42

## 43 **Introduction**

44 Climate change and its consequent increase in average global temperature are already af-  
45 fecting important biological processes, such as rates of species dispersion, phenologies, range dis-  
46 tributions, community assembly and biotic interactions (Cahil et al. 2012; Lurgi, López & Montoya  
47 2012; Peñuelas et al. 2013; Scheffers et al. 2016). These changes will likely accelerate extinction  
48 rates at the global scale in the coming decades (Urban et al. 2015), with important consequences to  
49 the provision of crucial ecosystem services (Bulling et al. 2010; Pecl et al. 2017; Peñuelas et al.

50 2017; Scheffers et al. 2016), to local livelihoods and to the global economy (Lee, Schlemme, Mur-  
51 ray & Unsworth 2015; Stern 2015).

52 Our understanding of the effects of warming on the biota is primarily centered on the re-  
53 sponses of single species or on various measures of local diversity, i.e.,  $\alpha$ -diversity (Araújo & Luoto  
54 2007; Gruner et al. 2017; Wiens 2016; Antão et al. 2020). Recent syntheses of global change im-  
55 pacts on  $\alpha$ -diversity have spurred controversy. While some studies suggest declines in local average  
56 species richness (e.g., Cardinale, Gonzalez, Allington & Loreau et al. 2018; Gonzalez et al. 2016),  
57 others suggest that the average number of species is roughly constant over time (e.g., Dornelas et al.  
58 2014; Vellend et al. 2017). In any case, other important aspects of biodiversity, such as changes in  
59 differentiation diversity (i.e., compositional similarity among local communities, such as  $\beta$ -diversi-  
60 ty) and higher levels of inventory diversity (i.e., diversity within spatial units, such as  $\gamma$ -diversity) at  
61 the regional level, are nevertheless usually neglected.

62 Measures of  $\alpha$ -diversity, especially species richness, are insensitive to many possible  
63 changes within communities in response to environmental change (Hekkala & Roberge 2018; Hil-  
64 lebrand et al. 2018). Focusing on species diversity at individual local communities limits our ability  
65 to understand spatial and temporal changes of ecosystems in response to both natural and anthropo-  
66 genic factors (Chase et al. 2018). Identifying the independent effects of global warming in different  
67 components of species diversity is challenging, because warming is likely confounded with other  
68 environmental stressors, such as habitat loss and fragmentation.

69 The consequences of warming across local communities can be measured by metrics of  $\beta$ -  
70 diversity. Changes in  $\beta$ -diversity may identify two important and contrasting phenomena: nested-  
71 ness (communities with fewer species are subsets of richer communities) and spatial turnover (the  
72 replacement of species in one community by different species in another community; Baselga 2010;  
73 Baselga, Jiménez-Valverde & Niccolini. 2007). Nestedness can indicate non-random processes of  
74 species loss and/or gain across space, representing differences in species sensitivity to environmen-  
75 tal gradients or disturbances. Turnover implies that the replacement of a set of species across a gra-

76 dient is driven by differences in the optimal niche, leading to environmental sorting or historical  
77 constraints (Baselga 2010; Baselga et al. 2007). Understanding the processes driving changes in  $\beta$ -  
78 diversity provides crucial information to understand the impact of warming, assisting decision mak-  
79 ers to choose relevant spatial scales for conservation (Bergamin et al. 2017; Legendre, Borcard, &  
80 Peres-Neto 2005). For instance, high levels of nestedness in open patches across a thermal gradient  
81 may indicate that species are being systematically lost at higher temperatures, and this loss cannot  
82 be compensated by dispersal or recolonization across the patches of habitat. High levels of species  
83 turnover, in contrast, may suggest that a particular set of species is being selected to occupy specific  
84 sections of the new climatic gradient (e.g., Hillebrand, Soininen & Snoeijs 2010) forming novel  
85 communities (Urban et al. 2012; Williams & Jackson 2007).

86           Establishing causal connections between changes in climate and biodiversity pose an extra  
87 challenge because non-experimental field studies rely on correlational data, which makes inferential  
88 interpretation troublesome (Stewart et al. 2013). Experimental meta-ecosystems offer a solution to  
89 this limitation, because they provide a unique opportunity to comprehend and predict responses of  
90 biodiversity to warming (Stewart et al. 2013), mimicking climatically induced changes in meta-  
91 ecosystems with different levels of habitat patchiness and isolation.

92           Here, we present the results of a meta-analysis devised to evaluate the effects of increas-  
93 ing average temperatures on biodiversity across spatial scales (i.e.,  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity). Recent  
94 syntheses on the effects of experimental warming have evaluated its effects on species diversity at  
95 local scales (Gruner et al. 2017). Thus, the knowledge of how warming affects biodiversity across  
96 spatial scales is an open and crucial question to be answered, in order to improve our ability to an-  
97 ticipate and mitigate its effects. As processes that shape diversity patterns are spatially structured  
98 (Chase et al. 2018), we expect that responses at the local scale ( $\alpha$ -diversity within replicates) will  
99 differ from responses at larger spatial scales ( $\gamma$ -diversity of the experimental system), and that  
100 warming will have a deleterious effect on  $\alpha$ -diversity and increase rates of nestedness in  $\beta$ -diversity  
101 through a systematic loss of species less adapted to the new climatic conditions. This implies that  $\gamma$ -

102 diversity should be unaltered, given that richer patches should have levels of species diversity simi-  
103 lar to the levels of the regional pool.

104 Our meta-analysis also evaluates the effect of important moderators, as previous meta-  
105 analyses showed that the effects of warming on experimental meta-communities depend on experi-  
106 mental design itself, including differences in temperature and time of manipulation and ecosystem  
107 type (Gruner et al. 2017; Marino et al. 2018). As habitat fragmentation has been shown to aggravate  
108 the effects of climate change in ecological communities (Opdam & Wascher 2004; Oliver et al.  
109 2015), we expect open patches, defined as the possibility of replicates being colonized by new spe-  
110 cies, to be less prone to lose species, or at least, more likely to recover from species loss, as individ-  
111 uals from resident species are able to migrate and (re) colonize open patches.

112

## 113 **Material and Methods**

### 114 *Data*

115 We compiled data from published meta-community experiments (mesocosms or micro-  
116 cosms), encompassing ecological communities (individual replicates) subject to warming and their  
117 corresponding controls. We used the search engines of the ISI Web of Science and Google Scholar  
118 with cross-referencing to find studies published between 1995 and 2017, using the same search  
119 string used by Gruner et al. (2017), who conducted an earlier meta-analysis of the effect of warming  
120 on  $\alpha$ -diversity: “(temperature or warming) AND (diversity or evenness or richness) AND (experi-  
121 ment\*or mesocosm\*or manipul\*)”. We also included additional studies identified in the course of  
122 the literature review, following relevant citation tracks. Our search identified 131 studies published  
123 worldwide. We contacted authors requesting for raw community data, so we could calculate a  
124 standardized measure of  $\beta$ -diversity for each dataset. Based on primary data, we were able to extract  
125 67 datasets (from 28 studies; see Table 1 in Supporting Information) that were used in our analyses.  
126 We excluded datasets that used temperature manipulation ( $\Delta T$ ) in excess of 6°C, as these exceed the

127 most extreme projections for global temperature increase by the end of the 21st century (Stocker et  
128 al. 2013). When studies reported manipulations at multiple temperatures, we averaged the experi-  
129 mental temperature, as long as  $\Delta T < 6^\circ\text{C}$ . If  $\Delta T$  was above  $6^\circ\text{C}$  in one of the treatments, we only  
130 used data from sampling units with experimental temperatures  $< 6^\circ\text{C}$ . In case of studies with multi-  
131 ple factors besides warming we partitioned the data into independent subsets within the levels of the  
132 other factors in order to estimate biodiversity metrics and effect sizes.

### 133 *Measures of diversity across scales*

134 Firstly, we computed two measures of  $\alpha$ -diversity: species richness, i.e., the total number  
135 of identified taxa or operational taxonomic units (OTUs) and the effective number of species de-  
136 rived from Hurlbert's Probability of Interspecific Encounter (ENS.Pie; Chase & Knight 2013;  
137 McGlinn et al. 2019). ENS.pie represents the number of equally abundant species in a perfectly  
138 even community (Chase & Knight 2013; McGlinn et al. 2019). It offers many advantages over other  
139 diversity indices in meta-analytical approaches, as ENS.Pie is scale-independent (i.e. insensitive to  
140 sample grain and extent) when communities are distributed randomly (Chase & Knight 2013), and  
141 it is an unambiguous metric of effect size (Chase & Knight 2013). Thus, ENS.pie allows one to dis-  
142 entangle sampling effects, from treatment effects that would alter the coexistence mechanisms of  
143 species in the experiment (Schuler et al. 2017).

144 Secondly, we calculated  $\beta$ -diversity among replicates within any given study, and parti-  
145 tioned it into species turnover and nestedness components using two different approaches: (i) based  
146 on qualitative data (i.e., species presence/absence; see Baselga et al. (2007); (ii) based on quantita-  
147 tive data. For quantitative data, we computed nestedness measuring the abundance gradient and  
148 species turnover as the balanced variation of abundance (Baselga 2010, 2013). This method uses  
149 matching components in terms of species abundances to provide a partition of beta-diversity,  
150 separating two components of abundance-based dissimilarity: balanced variation in abun-  
151 dance. In this case, individuals of some species in one site are substituted by the same number  
152 of individuals of different species in another site, and abundance gradients, in which some

153 individuals are lost from one site to the other (Baselga 2013). Metrics of  $\beta$ -diversity range from  
154 0 (lowest dissimilarity) to 1 (highest dissimilarity), and in both cases, the partition is additive, ena-  
155 bling the measurement of the total dissimilarity of experimental communities (Baselga 2013).

156 Thirdly, we calculated  $\gamma$ -diversity for both warming treatments and control, by counting  
157 the total number of species or OTUs at the end point of each experiment.

158

### 159 *Meta-analysis*

160 We calculated the log response ratio (lnRR; Borenstein, Hedges, Higgins & Rothstein  
161 2009) as our measure of effect size for all indices of  $\alpha$ - and  $\beta$ -diversity. lnRR is a measure of the  
162 relative effect size, i.e. the proportional change in the response variable relative to the controls. As  
163 there is no replication at the study level to estimate the variance for  $\gamma$ -diversity, we estimated the  
164 raw difference between control and impact  $\gamma$ -diversity ( $\Delta$ -gamma) as a measure of effect size  
165 (Borenstein et al. 2009) at the meta-community level. We evaluated differences in  $\gamma$ -diversity using  
166 anova, log-transforming species richness values.

167 To evaluate the effect of warming on  $\alpha$ - and  $\beta$ -diversity, we first fitted random-effect  
168 models using lnRR as response variable, with the dataset identity as a random intercept. We meas-  
169 ured heterogeneity ( $I^2$ ) of this random model as a mean to access the total variance component that  
170 was not explained by sampling variance, i.e., the percentage of total variation across studies that is  
171 owed to heterogeneity rather than chance itself (Higgins, Thompson, Deeks, & Altman 2003). To  
172 answer the remaining questions (the effect of site openness and experimental context), we then fit-  
173 ted meta-regression models, using four experimental moderators:  $\Delta$  temperature (difference be-  
174 tween control and warming in Celsius degrees; range: 0.23 – 5 °C), study length (in number of  
175 days; range: 15 - 7,300 days), ecosystem type (categorical coded as dummy variables: freshwater,  
176 terrestrial, marine), and patch openness (binary state: system open or closed to migration of individ-  
177 uals), which measures the potential of individual replicates to receive new species. This moderator  
178 was used as a proxy of patch openness for natural communities.



179 We evaluated the effects of each moderator on each level of diversity using a multi-model  
180 inference approach within an information-theoretic framework (Burnham & Anderson 2002). To  
181 evaluate model plausibility, we used Bayesian Information Criterion (BIC) and BIC weight (BIC-  
182  $w_i$ ), which measures the relative likelihood of the model given the data, normalized across the set of  
183 candidate models to sum to one for all possible models (Burnham & Anderson 2002). We also  
184 evaluated the importance of each moderator by computing its relative importance value based on  
185 BIC for all possible models. The information-theoretic approach used here allows the assessment  
186 and comparison of the support of several competing models, based on the probability of each model  
187 being the best model in the set of candidate models. The relative importance of a moderator (within  
188 the range 0-1) is the probability that a given moderator appears in the best model and it is estimated  
189 by summing the weights of each model where that moderator appears. It is important to stress that  
190 we used this approach in order to extract all the information from the set of possible models, and  
191 not to select the “best” model. This approach also allowed us to estimate the weighted average val-  
192 ue for each model parameter (i.e., slopes and intercepts). We estimated a weighted averaged slope  
193 for each moderator based on all possible nested models and their respective model plausibility,  
194 measured by  $BICw_i$ , (Burnham & Anderson 2002). We evaluated the significance of each modera-  
195 tor building 95% confidence intervals for each averaged model parameter.

196 To estimate the effects of site openness and experimental context on  $\gamma$ -diversity, we used  
197 linear models within the same multi-model inference approach, using  $\Delta$ -gamma as the response  
198 variable. All analyses were conducted in the R environment (R Core Team 2012).

199

## 200 **Results**

### 201 *Effects of warming on diversity*

202 Experimental warming had no significant effect on species richness locally but reduced  
203 significantly the effective number of species (ENS.Pie), which decreased on average by 4.4% in  
204 warming replicates when compared to controls ( $\ln RR \pm se = -0.0450 \pm 0.02$ ; z-value = -2.2456; p =

205 0.02; Fig. 1). For both controls and warming replicates, ENS.Pie was smaller than the observed  
206 richness (Fig S1.3). This reduction suggests that warming has a detrimental effect for rare or less  
207 frequent species, and a beneficial effect for dominant species, resulting in less equitable communi-  
208 ties in warming replicates. Random models for  $\alpha$ -diversity, i.e., richness and ENS.Pie, presented  
209 high and significant heterogeneity (mean  $I^2 \pm SD = 79.73 \pm 1.22$ ; Fig. 1).

210

211 Species turnover (or balanced gradient in species abundance in the case of quantitative  
212 data) was the main component of total  $\beta$ -diversity (Anova p-values  $< 0.001$ ; Fig. 2). Overall, exper-  
213 imental warming had no consistent effect on  $\beta$ -diversity, except for qualitative species turnover,  
214 which increased on average by 5.8% ( $\ln RR \pm se = 0.0563 \pm 0.0208$ ; z-value = 2.7066; p = 0.007;  
215 Fig. 3) when compared to controls. The overall mean effect size for all other measures of  $\beta$ -  
216 diversity was not different from zero (Fig. 3). All models for  $\beta$ -diversity presented significant hetero-  
217 geneity (mean  $I^2 \pm SD = 46.53 \pm 17.45$ ; Fig. 3), with nestedness components being more heteroge-  
218 neous than turnover components (Fig. 3). The increase of species turnover implies that warming is  
219 not causing net species gain or loss at the replicate level, with more tolerant species persisting in  
220 warming environments. This increase in species turnover did not affect the total number of species  
221 at the regional level (i.e.,  $\gamma$ -diversity) in warmed meta-ecosystems ( $F_{1,132} = 0.008$ ; p = 0.93). The  
222 average raw difference shows that 40.3% of the meta-ecosystems lost species at the species pool  
223 level, while 37.31% gained species, with the remaining 22.39% of the datasets showing constant  
224 species richness ( $\chi^2 = 5.52$ , df = 2; p-value = 0.06).

225

226 *Openness and experimental context as mediators of the effects of warming*

227 Contrary to our initial expectations, patch openness had no significant effect on any com-  
228 ponent of diversity (Table 1; Fig. S1.1, Fig. S1.2, Fig. S1.3). Ecosystem type was amongst the main  
229 moderators explaining differences in the effect size for species richness, with terrestrial and marine  
230 systems having larger effect sizes for richness than freshwater systems (Table 1; Fig. S1.1). Exper-

231 imental  $\Delta T$  had a significant effect on explaining variation in species richness. On average,  $\Delta T$  was  
232 among the top moderators explaining differences in effect sizes for  $\beta$ -diversity (Fig. S1.2), although  
233 no slope differed from zero. Study duration had no significant effect on  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity results  
234 and (Table 1; Fig. S1.1, Fig. S1.2, Fig. S1.3).

235

## 236 **Discussion**

### 237 *Effects of warming on components of diversity*

238 We know little about the effects of climate change on biodiversity across spatial scales.  
239 Our meta-analysis found that experimental warming did not affect local species richness but altered  
240 the patterns of species dominance at the local scale and species turnover across space. Warming  
241 decreased the effective number of species (ENS.Pie) and increased spatial turnover, which in turn  
242 led to small increases in  $\gamma$ -diversity in some ecosystems. Chase & Knight (2013) have demonstrated  
243 that ENS.Pie should become increasingly lower than richness as the level of equitability decreases.  
244 Decreases in ENS.Pie respond to decreases in species evenness and not richness, suggesting a con-  
245 sistent effect on relative species abundance, with some species becoming more dominant in warmed  
246 systems. Changes in dominance seem to be a recurrent response to warming (Harte & Shaw 1995;  
247 Hillebrand, Bennett, & Cadotte 2008; Kosten et al. 2012; Yvon-Durocher et al. 2015). Although  
248 increased local species dominance may lead to an increment of cascading extinctions (Zarnetske,  
249 Skelly & Urban 2012) and higher levels of  $\beta$ -diversity (Hillebrand et al. 2008), this effect was not  
250 strong enough to be detected by abundance-based measures of  $\beta$ -diversity.

251 Our results for  $\alpha$ -diversity contrast with those reported in the meta-analysis by Gruner et  
252 al. (2017), in which warming decreased species richness while it had no effect on species evenness  
253 (although evenness decreased significantly in terrestrial systems). The difference between our re-  
254 sults and those of Gruner and colleagues could be a consequence of the methodological approach  
255 used in our work, as we estimated  $\alpha$ -diversity from raw data for each dataset, and not from pub-  
256 lished values. Our methodological choice was due to the need to have standardized measures of  $\beta$ -

257 diversity, which were not directly available from published values. Our sample size was sufficiently  
258 large to detect regional changes in species diversity but may have not provided enough power to  
259 detect changes in local species richness. The partition of multifactorial data, i.e. studies with more  
260 factors than only warming, into independent subsets reduces sample size within data sets, and het-  
261 erogeneity is larger between smaller than larger studies (IntHout, Ioannidis, Borm, & Goeman  
262 2015), which may have reduced our ability to detect changes in local species richness. Our ap-  
263 proach, however, allowed us to analyze data consistently, producing comparable estimates of effect  
264 sizes, especially for  $\beta$ -diversity across studies.

265         Despite these differences between our results and those of Gruner et al. (2017), it is im-  
266 portant to note that the effects of different components of global change on local species richness  
267 have been largely debated in the past years, with some proponents suggesting that, on average, spe-  
268 cies richness is not declining at local scales (e.g., Dornelas et al. 2014; Hillebrand et al. 2018; Vel-  
269 lend et al. 2017), and others suggesting that these claims may be based on poor or incomplete data  
270 and on the lack of well-defined temporal baselines for detecting changes in local species richness  
271 (e.g. Cardinale et al. 2018; Gonzalez et al. 2016). Recent syntheses have also shown that species  
272 richness does not decrease with warming (Suggitt, Lister & Thomas 2019; Antão et al. 2020; Yue et  
273 al. 2020). Observational studies have similarly demonstrated that climate has an important role in  
274 determining species richness at large scales but cannot account for the variation in species richness  
275 at finer scales (Field et al. 2009). Our results support this notion that the lack of effect on average  
276 local species richness and the increase in spatial turnover of species composition seems to be a  
277 common consequence of numerous human-induced disturbances (Dornelas et al. 2014; Hillebrand  
278 et al. 2018), including climate warming (Dornelas et al. 2014; Hillebrand et al. 2010).

279         Our meta-analysis provides critical information for understanding the consequences of  
280 climate change on meta-ecosystems, showing that spatial turnover becomes more common under  
281 warming scenarios. Understanding changes in community composition across local communities as  
282 a consequence of warming is crucial for choosing relevant spatial scales for conservation and the

283 planning of protected areas (Bergamin, et al. 2017; Legendre et al. 2005). An important practical  
284 aspect to consider for conservation is that changes in community composition (i.e.  $\beta$ -diversity) pro-  
285 vide information more relevant for conservation than less informative measures, such as indices of  
286 species richness and community diversity, which cannot account for differences among ecological  
287 communities or functional and evolutionary differences among species (Hekkala & Roberge 2018;  
288 Hillebrand et al. 2018). This aspect also applies to shifts in species dominance within communities,  
289 which respond faster to anthropogenic pressures than  $\alpha$ -richness (Hillebrand et al. 2008, 2018), as  
290 we observed for ENS.Pie.

291           Contrary to our initial expectation that experimental warming would create higher levels  
292 of nestedness due to a systematic loss of species at the local scale, our results support the notion that  
293 warming promotes turnover in species composition by selecting species with distinct set of traits  
294 when compared to initial and/or control communities. This can correspond to two phenomena. In  
295 closed systems, the expansion of the upper bound of the temperature range in warmed treatments  
296 imposes a selection effect that seems idiosyncratic at the replicate level. In other words, warming  
297 seems to facilitate the establishment of different thermal-tolerant species in different replicates. In  
298 open systems, a wider range of temperature conditions is available, i.e., both control and warmed  
299 replicates can be colonized by species from the “regional” pool. This allows species to inhabit dif-  
300 ferent parts of the thermal gradient. Such differential species sorting across the extended tempera-  
301 ture gradient can lead to larger  $\beta$ -diversity values. In agreement with our results, species turnover  
302 has been shown to be the dominant component of total  $\beta$ -diversity in most ecological systems, inde-  
303 pendent of taxonomic group or geographical region (Soininen, Heino & Wang 2017). Under in-  
304 creasing temperatures, taxonomic and functional turnover seems also to be a recurrent pattern  
305 (Frainer et al. 2017; Hillebrand et al. 2010; Gibson & Reinemer, Sheldon & Rahel. 2015; Yvon-  
306 Durocher et al. 2017), creating novel communities (Lurgi et al. 2012; Urban et al. 2012; Williams &  
307 Jackson 2007).

308 Numerous mechanisms, such as random reshuffling, species invasion and idiosyncratic  
309 rates of range shift, have been proposed as explanations for climate-driven spatial turnover (Gib-  
310 son & Reinemer et al. 2015). However, increase in species turnover suggests that experimental  
311 communities are undergoing a process of species sorting, where warming changes the amplitude of  
312 temperature niches of species within communities, with pre-adapted species replacing resident ones  
313 along the temperature gradient (Loeuille & Leibold 2008). Species sorting has been suggested as a  
314 major mechanism in experimental warming studies for a broad range of taxa, inducing shifts in the  
315 selection of traits across the gradient (Elmendorf et al. 2012; Gibson & Reinemer et al. 2015; Frainer  
316 et al. 2017; Yvon-Durocher et al. 2017). Higher spatial turnover and its consequent novel assem-  
317 blages nevertheless impose an extra and critical implication for climate scientists and policy-  
318 makers, because they suggest that ecological communities may not be able to track climate change  
319 by shifting their ranges, even though species can (Gibson & Reinemer et al. 2015).

320  
321 *Explaining heterogeneous effects of warming on components of diversity*

322 Physiological responses to environmental temperature, such as thermal scaling of perfor-  
323 mance, i.e., changes in species growth, energy gain and activity patterns as a function of tempera-  
324 ture, can determine the result of competitive interactions among species (Buckley & Roughgarden  
325 2006; Finstad et al. 2011). Thermal scaling might ultimately cause competitive exclusion due to  
326 niche retractions (Finstad et al. 2011). Competitive displacement is also an important mechanism  
327 changing community composition and turnover, which act in consonance with environmental filter-  
328 ing (Leibold & Chase 2017). Besides changes in community composition itself, warming has also  
329 an effect on community structure, by altering competitive dominance, and consequently species  
330 abundance (Harte & Shaw 1995; Hillebrand et al. 2018), which may also explain the decreases in  
331 ENS.Pie we have observed in our results. As we mentioned before, warming seems to promote spe-  
332 cies sorting, selecting species with new set of traits and adaptations, which might be suboptimal at  
333 control temperatures. This new set of traits might lead to competitive advantages and boost the

334 dominance of new species (Dangles, Carpio, Barragan, Zeddami, & Silvain 2008; Kosten et al  
335 2012).

336 Patch openness had no significant effect on any component of diversity. Although rescue  
337 from deleterious disturbance, such as warming, depends on the potential for species to disperse and  
338 recolonize previously occupied patches, the relationship between dispersal and species diversity is  
339 complex, spatially contingent (Cadotte 2006) and strongly dependent on other biotic and abiotic  
340 factors (Shanafelt et al. 2018). Dispersal and species diversity relationship may display a unimodal  
341 curve, with diversity being maximized at intermediate levels of dispersal, and not at higher dispersal  
342 levels (Cadotte 2006; Shanafelt et al. 2018). Consequently, open systems with higher rates of immi-  
343 gration do not necessarily retain more diversity than closed systems, and system openness might  
344 even have negative effects on local species richness in warmed systems (Gruner et al. 2017). We  
345 used patch openness as a proxy to habitat isolation, which together with habitat fragmentation has  
346 been historically considered one of the main threats to biodiversity (Haddad et al. 2015; Quinn &  
347 Harrison 1998). However, it has been recently pointed out that fragmentation alone may not be as  
348 deleterious as previously thought (Fahrig 2017, 2018, but see Fletcher et al. 2018), and habitat con-  
349 figuration might be more important than fragmentation *per se* (Årevall, Early, Estrada, Wennergren,  
350 & Eklöf 2018). This calls the attention to the necessity of evaluating other habitat related issues in  
351 warming experiments, such as habitat availability and configuration, as well as species inherent  
352 ability to disperse.

353 Average  $I^2$  values suggest that most of the variability across studies is due to heterogenei-  
354 ty rather than chance alone, especially for results from  $\alpha$ -diversity analyses, which were more het-  
355 erogeneous than those for  $\beta$ -diversity. Heterogeneity on the effects of warming on diversity depends  
356 on the experimental system for different components of inventory diversity (both  $\alpha$ - and  $\gamma$ -  
357 diversity). It has been shown that experimental marine systems tend to have higher average losses  
358 of species at the local level, compared to terrestrial and freshwater systems (Gruner et al. 2017),  
359 which differs from our results, as marine and terrestrial systems tended to gain more species than

360 freshwater systems. However, time series from non-experimental marine communities show that  
361 species richness tend to increase with warming (Antão et al 2020).

362 Contrary to our initial expectation, longer studies with higher  $\Delta T$  did not have larger  
363 losses of species nor more nested communities as a consequence of sequential loss of diversity, de-  
364 spite evidence that both components of  $\beta$ -diversity change monotonically over time (Angeler 2013).  
365 Our results for the effects of study length on local species richness and ENS.Pie are in agreement  
366 with the meta-analysis of Gruner et al. (2017), who also reported that study duration had no effect  
367 on  $\alpha$ -diversity. Despite the relative importance of study duration for  $\gamma$ -diversity, our results for  $\alpha$ -  
368 and  $\beta$ - diversity reinforce the notion that temperature change can be the main driver of changes in  
369 species composition, creating rapid changes and novel assembled communities across the warming  
370 gradient (Gibson & Reinemer et al. 2015), regardless of the duration of exposition.

371

### 372 *Conclusions and way forward*

373 Despite decades of research on the effects of warming on species diversity, only recently  
374 we have started to have robust syntheses of its effects in experimental meta-ecosystems (e.g., Grun-  
375 er et al. 2017; Marino et al. 2018). However, most of the information available focused on local  
376 communities, with warming effects at the regional scale commonly neglected. Despite the acknowl-  
377 edged limitations of our meta-analysis, and the inherent difficulties in translating lessons learned  
378 from experimental to real meta-ecosystems, our results support the need for a refocus of the agenda  
379 on global change consequences for biodiversity. The focus should shift from effects on local rich-  
380 ness only to the full understanding of the effects on biodiversity at the regional scale. This poses  
381 important challenges for both experimental and observational designs. Although warming experi-  
382 ments have become more complex over the past years, with an ever-increasing number of factors  
383 considered, we still lack appropriate protocols to detect changes in communities across spatial  
384 scales and across a large number of taxa and ecosystem types. Although our results showed that  
385 patch isolation *per se* might not be as deleterious as it is generally assumed, improving our under-



386 standing of the interaction between environmental perturbations, such as warming and fragmenta-  
387 tion, is crucial to predict the future of our ecosystems in an increasingly modified world.

388

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398

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580 Tables:

581 Table 1. Model-averaged parameter estimates of moderators of  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity, based on  
582 all possible models. Values in parentheses represent the alpha risk for confidence intervals ( $\alpha =$   
583 0.05). Bold values represent significant slopes.

	Incidence				Abundance		
	Richness	ENS.Pie	Nestedness	Turnover	Nestedness	Turnover	Gamma
Delta temperature	<b>0.044 (0.040)</b>	-0.002 (0.09)	0.007 (0.027)	-0.025 (0.055)	<b>0.076 (0.057)</b>	-0.001(0.004)	0.011(0.167)
Openness	-0.003 (0.022)	-0.003 (0.017)	-0.001(0.018)	0.031(0.109)	0.007 (0.039)	-0.003 (0.019)	-0.071 (0.556)
Study duration	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	-0.001(0.001)
System							<b>3.456 (2.657)</b>
Marine	<b>0.219 (0.112)</b>	0.078 (0.160)	-0.001(0.008)	-0.019 (0.076)	0.002(0.008)	-0.016 (0.055)	
Terrestrial	<b>0.268 (0.131)</b>	0.144 (0.246)	-0.002 (0.011)	-0.066(0.166)	0.001(0.009)	-0.009 (0.033)	

584

585 Figures:

586 Fig 1. Mean effect size  $\pm 95\%$  CI from temperature changes experiments on both components of  
587 community  $\alpha$ -diversity, species richness and effective number of species (ENS.Pie).  $I^2$  represents  
588 the amount of heterogeneity (i.e. variation in effect sizes), which is not accounted by the sampling  
589 error variance. Confidence Intervals above (or below) the dashed line show significant positive (or  
590 negative) effect sizes. Asterisks: significant ( $p < 0.05$ )  $I^2$ .

591

592 Fig 2. Bean plot showing differences in spatial turnover and nestedness, for both incidence based  
593 indices and abundance based indices.  $\beta$ -diversity values close to 0 represent low dissimilarity and  
594 values close to 1 represent high dissimilarity). Lines represent individual observations. Shaded area  
595 shows the distribution density. Thick lines represent the averages within each level. Dashed lines  
596 represent global average.

597

598 Fig 3. Mean effect size  $\pm 95\%$  CI from temperature changes experiments on different aspects of  
599 community  $\beta$ -diversity. Nestedness and Turnover are incidence-based measures while gradient and  
600 balanced abundance are abundance-based measures.  $I^2$  represents the amount of heterogeneity,  
601 which is the variation in effect sizes, which is not accounted by the sampling error variance. Confi-

602 dence Intervals above (or below) the dashed line show significant positive (or negative) effect sizes.

603 Asterisks: significant ( $p < 0.05$ )  $I^2$ .