



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

4 Vinicius A. G. Bastazini¹, Núria Galiana¹, Helmut Hillebrand^{2,3,4}, Marc Estiarte^{5,6}, Romá Ogaya^{5,6},
5 Josep Peñuelas^{5,6}, Ulrich Sommer⁷, José M. Montoya¹

6

7 ¹ Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station,
8 French National Center for Scientific Research and Paul Sabatier University, Moulis, France.

9 ² Institute for Chemistry and Biology of Marine Environments [ICBM], Carl-von-Ossietzky Univer-
10 sity Oldenburg, Schleusenstrasse 1, 26382 Wilhelmshaven

11 ³ Helmholtz-Institute for Functional Marine Biodiversity at the University of Oldenburg [HIFMB],
12 Ammerländer Heerstrasse 231, 26129 Oldenburg

13 ⁴ Alfred Wegener Institute, Helmholtz-Centre for Polar and Marine Research [AWI], Bremerhaven

14 ⁵ CSIC, Global Ecology Unit CREAM-CSIC-UAB, 08913 Bellaterra, Catalonia, Spain.

15 ⁶ CREAM, 08913 Cerdanyola del Vallès, Catalonia, Spain.

16 ⁷GEOMAR Helmholtz Zentrum für Ozeanforschung Kiel,
17 Düsternbrooker Weg 20, 24105 Kiel, Germany

18

19 **Aim:** To evaluate the effects of climate warming on biodiversity across spatial scales (i.e., α -, β -
20 and γ -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 (α -, β - and γ -diversity, partitioning β -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 (α -diversity) but decreased
32 effective numbers of species by affecting species dominance. Warming increased species spatial
33 turnover (β -diversity), although no significant changes were detected at the regional scale (γ -
34 diversity). Site openness and experimental context did not significantly affect our results, despite
35 significant heterogeneity in the effect sizes of α - and β - 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.

2017; Scheffers et al. 2016), to local livelihoods and to the global economy (Lee, Schlemme, Murray & Unsworth 2015; Stern 2015).

Our understanding of the effects of warming on the biota is primarily centered on the responses of single species or on various measures of local diversity, i.e., α -diversity (Araújo & Luoto 2007; Gruner et al. 2017; Wiens 2016; Antão et al. 2020). Recent syntheses of global change impacts on α -diversity have spurred controversy. While some studies suggest declines in local average species richness (e.g., Cardinale, Gonzalez, Allington & Loreau et al. 2018; Gonzalez et al. 2016), others suggest that the average number of species is roughly constant over time (e.g., Dornelas et al. 2014; Vellend et al. 2017). In any case, other important aspects of biodiversity, such as changes in differentiation diversity (i.e., compositional similarity among local communities, such as β -diversity) and higher levels of inventory diversity (i.e., diversity within spatial units, such as γ -diversity) at the regional level, are nevertheless usually neglected.

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

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

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

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

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

diversity should be unaltered, given that richer patches should have levels of species diversity similar to the levels of the regional pool.

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

Material and Methods

Data

We compiled data from published meta-community experiments (mesocosms or microcosms), encompassing ecological communities (individual replicates) subject to warming and their corresponding controls. We used the search engines of the ISI Web of Science and Google Scholar with cross-referencing to find studies published between 1995 and 2017, using the same search string used by Gruner et al. (2017), who conducted an earlier meta-analysis of the effect of warming on α -diversity: “(temperature or warming) AND (diversity or evenness or richness) AND (experiment*or mesocosm*or manipul*)”. We also included additional studies identified in the course of the literature review, following relevant citation tracks. Our search identified 131 studies published worldwide. We contacted authors requesting for raw community data, so we could calculate a standardized measure of β -diversity for each dataset. Based on primary data, we were able to extract 67 datasets (from 28 studies; see Table 1 in Supporting Information) that were used in our analyses. We excluded datasets that used temperature manipulation (ΔT) 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 ΔT was above 6°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 α -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 β -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 β -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 γ -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 α - and β -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 γ -diversity, we estimated the
164 raw difference between control and impact γ -diversity (Δ -gamma) as a measure of effect size
165 (Borenstein et al. 2009) at the meta-community level. We evaluated differences in γ -diversity using
166 anova, log-transforming species richness values.

167 To evaluate the effect of warming on α - and β -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: Δ 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 γ -diversity, we used
197 linear models within the same multi-model inference approach, using Δ -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 =

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

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

Openness and experimental context as mediators of the effects of warming

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

231 imental ΔT had a significant effect on explaining variation in species richness. On average, ΔT was
232 among the top moderators explaining differences in effect sizes for β -diversity (Fig. S1.2), although
233 no slope differed from zero. Study duration had no significant effect on α -, β - and γ -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 γ -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 β -diversity (Hillebrand et al. 2008), this effect was not
250 strong enough to be detected by abundance-based measures of β -diversity.

251 Our results for α -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 α -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 β -

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 β -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. β -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 α -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 β -diversity values. In agreement with our results, species turnover
302 has been shown to be the dominant component of total β -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, Zeddiam, & 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 α -diversity analyses, which were more het-
355 erogeneous than those for β -diversity. Heterogeneity on the effects of warming on diversity depends
356 on the experimental system for different components of inventory diversity (both α - and γ -
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 ΔT 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 β -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 α -diversity. Despite the relative importance of study duration for γ -diversity, our results for α -
368 and β -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-

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

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References

- Angeler, D. G. (2013). Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. *Diversity and Distributions*, 19(7), 772-781.
- Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., ... & Schipper, A. M. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology & Evolution*, 1-7.
- Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16(6), 743-753.
- Årevall, J., Early, R., Estrada, A., Wennergren, U., & Eklöf, A. C. (2018). Conditions for successful range shifts under climate change: The role of species dispersal and landscape configuration. *Diversity and Distributions*, 24(11), 1598-1611.

411 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity.
412 *Global Ecology and Biogeography*, 19(1), 134-143.

413 Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among
414 several sites, while average pairwise dissimilarity may be misleading. *Ecography*, 36(2), 124-128.

415 Baselga, A., Jiménez-Valverde, A., & Niccolini, G. (2007). A multiple-site similarity measure
416 independent of richness. *Biology Letters*, 3(6), 642-645.

417 Bergamin, R. S., Bastazini, V. A. G., Vélez-Martin, E., Debastiani, V., Zanini, K. J., Loyola, R.,
418 & Müller, S. C. (2017). Linking beta diversity patterns to protected areas: Lessons from the Brazili-
419 an Atlantic Rainforest. *Biodiversity and Conservation*, 26(7), 1557-1568.

420 Borenstein, M., Hedges, L. V., Higgins, J. P., & Rothstein, H. R. (2009). *Introduction to meta-*
421 *analysis*. John Wiley & Sons.

422 Buckley, L. B., & Roughgarden, J. (2006). Climate, competition, and the coexistence of island
423 lizards. *Functional Ecology*, 20(2), 315-322.

424 Bulling, M. T., Hicks, N., Murray, L., Paterson, D. M., Raffaelli, D., White, P. C., & Solan, M.
425 (2010). Marine biodiversity–ecosystem functions under uncertain environmental fu-
426 tures. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2107-
427 2116.

428 Burnham K. P., Anderson D. R. 2002. Model selection and multimodel inference: a practical in-
429 formation-theoretic approach. Springer, New York.

430 Cadotte, M. W. (2006). Dispersal and species diversity: a meta-analysis. *The American Natural-*
431 *ist*, 167(6), 913-924.

432 Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong
433 Ryu, H., ... & Wiens, J. J. (2013). How does climate change cause extinction?. *Proceedings of the*
434 *Royal Society B: Biological Sciences*, 280(1750), 20121890.

435 Cardinale, B. J., Gonzalez, A., Allington, G. R., & Loreau, M. (2018). Is local biodiversity de-
436 clining or not? A summary of the debate over analysis of species richness time trends. *Biological*
437 *Conservation*, 219, 175-183.

438 Chase, J. M., & Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on bi-
439 odiversity: why standardised sampling is not enough. *Ecology Letters*, 16, 17-26.

440 Chase, J. M., McGill, B. J., McGlinn, D. J., May, F., Blowes, S. A., Xiao, X., ... & Gotelli, N. J.
441 (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its
442 change across communities. *Ecology letters*, 21(11), 1737-1751.

443 Dangles, O., Carpio, C., Barragan, A. R., Zeddiam, J. L., & Silvain, J. F. (2008). Temperature as
444 a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological*
445 *Applications*, 18(7), 1795-1809.

446 Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A.
447 E. (2014). Assemblage time series reveal biodiversity change but not systematic
448 loss. *Science*, 344(6181), 296-299.

449 Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T.
450 V., ... & Fosaa, A. M. (2012). Global assessment of experimental climate warming on tundra vege-
451 tation: heterogeneity over space and time. *Ecology letters*, 15(2), 164-175.

452 Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecol-*
453 *ogy, Evolution, and Systematics*, 48, 1-23.

454 Fahrig, L. (2018). Forty years of bias in habitat fragmentation research. *Chapter 5 in: Kareiva*
455 *P, Silliman B, Marvier M. Effective conservation science: Data not dogma*. Oxford. Pages 32-38.

456 Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Guégan, J. F., ...
457 & O'Brien, E. M. (2009). Spatial species-richness gradients across scales: a meta-
458 analysis. *Journal of Biogeography*, 36(1), 132-147.

459 Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., ... & Foldvik,
460 A. (2011). Competitive exclusion along climate gradients: energy efficiency influences the distribu-
461 tion of two salmonid fishes. *Global Change Biology*, 17(4), 1703-1711.

462 Fletcher Jr, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., ... &
463 Melo, F. P. (2018). Is habitat fragmentation good for biodiversity?. *Biological conservation*, 226, 9-
464 15.

465 Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M.
466 M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communi-
467 ties. *Proceedings of the National Academy of Sciences*, 114(46), 12202-12207.

468 Gibson□Reinemer, D. K., Sheldon, K. S., & Rahel, F. J. (2015). Climate change creates rapid
469 species turnover in montane communities. *Ecology and evolution*, 5(12), 2340-2347.

470 Gonzalez, A., Cardinale, B. J., Allington, G. R., Byrnes, J., Arthur Endsley, K., Brown, D. G.,
471 ... & Loreau, M. (2016). Estimating local biodiversity change: a critique of papers claiming no net
472 loss of local diversity. *Ecology*, 97(8), 1949-1960.

473 Gruner, D. S., Bracken, M. E., Berger, S. A., Eriksson, B. K., Gamfeldt, L., Matthiessen, B., ...
474 & Hillebrand, H. (2017). Effects of experimental warming on biodiversity depend on ecosystem
475 type and local species composition. *Oikos*, 126(1), 8-17.

476 Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Cook,
477 W. M. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advanc-*
478 *es*, 1(2), e1500052.

479 Harte, J., & Shaw, R. (1995). Shifting dominance within a montane vegetation community: re-
480 sults of a climate-warming experiment. *Science*, 267(5199), 876-880.

481 Hekkala, A. M., & Roberge, J. M. (2018). The use of response measures in meta-analyses of
482 land-use impacts on ecological communities: a review and the way forward. *Biodiversity and Con-*
483 *servation*, 27(11), 2989-3005.

484 Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: a re-
 485 view of evenness effects on local and regional ecosystem processes. *Ecology*, 89(6), 1510-1520.

486 Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., ... &
 487 Lewandowska, A. M. (2018). Biodiversity change is uncoupled from species richness trends: Con-
 488 sequences for conservation and monitoring. *Journal of Applied Ecology*, 55(1), 169-184.

489 Hillebrand, H., Soininen, J., & Snoeijs, P. (2010). Warming leads to higher species turnover in a
 490 coastal ecosystem. *Global Change Biology*, 16(4), 1181-1193.

491 Higgins, J. P., Thompson, S. G., Deeks, J. J., & Altman, D. G. (2003). Measuring inconsistency
 492 in meta-analyses. *Bmj*, 327(7414), 557-560.

493 IntHout, J., Ioannidis, J. P., Borm, G. F., & Goeman, J. J. (2015). Small studies are more heter-
 494 ogeneous than large ones: a meta-meta-analysis. *Journal of Clinical Epidemiology*, 68(8), 860-869.

495 Kosten, S., Huszar, V. L., Bécares, E., Costa, L. S., Van Donk, E., Hansson, L. A., ... & De
 496 Meester, L. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global*
 497 *Change Biology*, 18(1), 118-126.

498 Lee, C., Schlemme, C., Murray, J., & Unsworth, R. (2015). The cost of climate change: Ecosys-
 499 tem services and wildland fires. *Ecological Economics*, 116, 261-269.

500 Legendre, P., Borcard, D., & Peres-Neto, P. R. (2005). Analyzing beta diversity: partitioning the
 501 spatial variation of community composition data. *Ecological Monographs*, 75(4), 435-450.

502 Leibold, M. A., & Chase, J. M. (2017). *Metacommunity ecology*. Princeton University Press.

503 Loeuille, N., & Leibold, M. A. (2008). Evolution in metacommunities: on the relative im-
 504 portance of species sorting and monopolization in structuring communities. *The American Natural-*
 505 *ist*, 171(6), 788-799.

506 Lurgi, M., López, B. C., & Montoya, J. M. (2012). Novel communities from climate
 507 change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2913-
 508 2922.

509 Marino, N. D. A. C., Romero, G. Q., & Farjalla, V. F. (2018). Geographical and experimental
510 contexts modulate the effect of warming on top-down control: a meta-analysis. *Ecology Let-*
511 *ters*, 21(3), 455-466.

512 McGlinn, D. J., Xiao, X., May, F., Gotelli, N. J., Engel, T., Blowes, S. A., ... & McGill, B. J.
513 (2019). Measurement of Biodiversity (MoB): A method to separate the scale-dependent effects of
514 species abundance distribution, density, and aggregation on diversity change. *Methods in Ecology*
515 *and Evolution*, 10(2), 258-269.

516 Oliver, T., Marshall, H., Morecroft, M. *et al.* (2015) Interacting effects of climate change and
517 habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* 5, 941–945 (2015).

518 Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: linking land-
519 scape and biogeographical scale levels in research and conservation. *Biological Conserva-*
520 *tion*, 117(3), 285-297.

521 Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Fal-
522 coni, L. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and hu-
523 man well-being. *Science*, 355(6332), eaai9214.

524 Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., ... & Filella, I. (2013).
525 Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global*
526 *change biology*, 19(8), 2303-2338.

527 Peñuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusà, J., Ogaya, R., ... & Peguero, G. (2017).
528 Impacts of global change on Mediterranean forests and their services. *Forests*, 8(12), 463.

529 Quinn, J. F., & Harrison, S. P. (1988). Effects of habitat fragmentation and isolation on species
530 richness: evidence from biogeographic patterns. *Oecologia*, 75(1), 132-140.

531 R Core Team (2012). R: A language and environment for statistical computing. R Foundation
532 for Statistical Computing, Vienna, Austria.

533 Scheffers, B. R., De Meester, L., Bridge, T. C., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T.,
 534 ... & Pacifici, M. (2016). The broad footprint of climate change from genes to biomes to peo-
 535 ple. *Science*, 354(6313), aaf7671.

536 Shanafelt, D. W., Clobert, J., Fenichel, E. P., Hochberg, M. E., Kinzig, A., Loreau, M., ... &
 537 Perrings, C. (2018). Species dispersal and biodiversity in human-dominated metacommuni-
 538 ties. *Journal of theoretical biology*, 457, 199-210.

539 Schuler, M. S., Chase, J. M., & Knight, T. M. (2017). Habitat patch size alters the importance of
 540 dispersal for species diversity in an experimental freshwater community. *Ecology and evolu-*
 541 *tion*, 7(15), 5774-5783.

542 Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover compo-
 543 nents of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27(1),
 544 96-109.

545 Stern, N. 2015. *Why are we waiting?: The logic, urgency, and promise of tackling climate*
 546 *change*. Mit Press.

547 Stewart, R. I., Dossena, M., Bohan, D. A., Jeppesen, E., Kordas, R. L., Ledger, M. E., ... & Sut-
 548 tle, B. (2013). Mesocosm experiments as a tool for ecological climate-change research. In *Advances*
 549 *in ecological research* (Vol. 48, pp. 71-181). Academic Press.

550 Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., ... & Midgley, P.
 551 M. (2013). Climate change 2013: The physical science basis.

552 Suggitt, A. J., Lister, D. G., & Thomas, C. D. (2019). Widespread effects of climate change on
 553 local plant diversity. *Current Biology*, 29(17), 2905-2911.

554 Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234),
 555 571-573.

556 Urban, M. C., Tewksbury, J. J., & Sheldon, K. S. (2012). On a collision course: competition and
557 dispersal differences create no-analogue communities and cause extinctions during climate change.
558 *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1735), 2072-2080.

559 Vellend, M., Dornelas, M., Baeten, L., Beauséjour, R., Brown, C. D., De Frenne, P., ... & Ma-
560 gurran, A. E. (2017). Estimates of local biodiversity change over time stand up to scruti-
561 ny. *Ecology*, 98(2), 583-590.

562 Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and
563 animal species. *PLoS biology*, 14(12), e2001104.

564 Williams, J. W., & Jackson, S. T. (2007). Novel climates, no analog communities, and ecolog-
565 ical surprises. *Frontiers in Ecology and the Environment*, 5(9), 475-482.

566 Yue, K., Jarvie, S., Senior, A. M., Van Meerbeek, K., Peng, Y., Ni, X., ... & Svenning, J. C.
567 (2020). Changes in plant diversity and its relationship with productivity in response to nitrogen ad-
568 dition, warming and increased rainfall. *Oikos*.

569 Yvon-Durocher, G., Allen, A. P., Cellamare, M., Dossena, M., Gaston, K. J., Leita, M., ... &
570 Trimmer, M. (2015). Five years of experimental warming increases the biodiversity and productivi-
571 ty of phytoplankton. *PLoS biology*, 13(12), e1002324.

572 Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate
573 change. *Science*, 336(6088), 1516-1518.

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Tables:

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

	Incidence				Abundance		Gamma
	Richness	ENS.Pie	Nestedness	Turnover	Nestedness	Turnover	
Delta temperature	0.044 (0.040)	-0.002 (0.09)	0.007 (0.027)	-0.025 (0.055)	0.076 (0.057)	-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							3.456 (2.657)
Marine	0.219(0.112)	0.078 (0.160)	-0.001(0.008)	-0.019 (0.076)	0.002(0.008)	-0.016 (0.055)	
Terrestrial	0.268 (0.131)	0.144 (0.246)	-0.002 (0.011)	-0.066(0.166)	0.001(0.009)	-0.009 (0.033)	

Figures:

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

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

Fig 3. Mean effect size $\pm 95\%$ CI from temperature changes experiments on different aspects of community β -diversity. Nestedness and Turnover are incidence-based measures while gradient and balanced abundance are abundance-based measures. I^2 represents the amount of heterogeneity, 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 .