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

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Aim: To evaluate the effects of climate warming on biodiversity across spatial scales (i.e., *α-, β- and γ*-diversity) and the effects of patch openness and experimental context on diversity responses.

Location: Global

Time period: 1995 - 2017

Major taxa studies: Fungi, Invertebrates, Phytoplankton, Plants, Sea weed, Soil Microbes, Zooplankton

Methods: We compiled data from warming experiments and conducted a meta-analysis to evaluate the effects of warming on different components of diversity (such as species richness and equivalent numbers) at different spatial scales (*α-, β- and γ*-diversity, partitioning *β*-diversity into species turnover and nestedness components). We also investigated how these effects were modulated by system openness, defined as the possibility of replicates being colonized by new species, and experimental context (duration, mean temperature change and ecosystem type).

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

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

Keywords: Climate change, Alpha and Beta diversity, Habitat fragmentation, Manipulative experiments, Meta-analysis.

Introduction

Climate change and its consequent increase in average global temperature are already affecting important biological processes, such as rates of species dispersion, phenologies, range distributions, community assembly and biotic interactions (Cahil et al. 2012; Lurgi, López & Montoya 2012; Peñuelas et al. 2013; Scheffers et al. 2016). These changes will likely accelerate extinction rates at the global scale in the coming decades (Urban et al. 2015), with important consequences to 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 gradient 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 most extreme projections for global temperature increase by the end of the 21st century (Stocker et al. 2013). When studies reported manipulations at multiple temperatures, we averaged the experimental temperature, as long as $\Delta T < 6°C$. If ΔT was above 6°C in one of the treatments, we only used data from sampling units with experimental temperatures < 6°C. In case of studies with multiple factors besides warming we partitioned the data into independent subsets within the levels of the other factors in order to estimate biodiversity metrics and effect sizes.

Measures of diversity across scales

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

Secondly, we calculated β-diversity among replicates within any given study, and partitioned it into species turnover and nestedness components using two different approaches: (i) based on qualitative data (i.e., species presence/absence; see Baselga et al. (2007); (ii) based on quantitative data. For quantitative data, we computed nestedness measuring the abundance gradient and species turnover as the balanced variation of abundance (Baselga 2010, 2013). This method uses matching components in terms of species abundances to provide a partition of beta-diversity, separating two components of abundance-based dissimilarity: balanced variation in abundance. In this case, individuals of some species in one site are substituted by the same number of individuals of different species in another site, and abundance gradients, in which some individuals are lost from one site to the other (Baselga 2013). Metrics of β-diversity range from 0 (lowest dissimilarity) to 1 (highest dissimilarity), and in both cases, the partition is additive, enabling the measurement of the total dissimilarity of experimental communities (Baselga 2013).

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

Meta-analysis

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

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

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

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

Results

Effects of warming on diversity

Experimental warming had no significant effect on species richness locally but reduced significantly the effective number of species (ENS.Pie), which decreased on average by 4.4% in warming replicates when compared to controls (lnRR ± se = -0.0450 ± 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 ± SD = 79.73 ± 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% (lnRR ± se = 0.0563 ± 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 ± SD= 46.53 ± 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 ($x^2 = 5.52$, 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). Experimental ΔT had a significant effect on explaining variation in species richness. On average, ΔT was among the top moderators explaining differences in effect sizes for *β*-diversity (Fig. S1.2), although no slope differed from zero. Study duration had no significant effect on *α*-, *β*- and γ-diversity results and (Table 1; Fig. S1.1, Fig. S1.2, Fig. S1.3).

Discussion

Effects of warming on components of diversity

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

Our results for *α*-diversity contrast with those reported in the meta-analysis by Gruner et al. (2017), in which warming decreased species richness while it had no effect on species evenness (although evenness decreased significantly in terrestrial systems). The difference between our results and those of Gruner and colleagues could be a consequence of the methodological approach used in our work, as we estimated *α*-diversity from raw data for each dataset, and not from published values. Our methodological choice was due to the need to have standardized measures of *β*-

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

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

Our meta-analysis provides critical information for understanding the consequences of climate change on meta-ecosystems, showing that spatial turnover becomes more common under warming scenarios. Understanding changes in community composition across local communities as a consequence of warming is crucial for choosing relevant spatial scales for conservation and the planning of protected areas (Bergamin, et al. 2017; Legendre et al. 2005). An important practical aspect to consider for conservation is that changes in community composition (i.e. β-diversity) provide information more relevant for conservation than less informative measures, such as indices of species richness and community diversity, which cannot account for differences among ecological communities or functional and evolutionary differences among species (Hekkala & Roberge 2018; Hillebrand et al. 2018). This aspect also applies to shifts in species dominance within communities, which respond faster to anthropogenic pressures than α-richness (Hillebrand et al. 2008, 2018), as we observed for ENS.Pie.

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

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

Explaining heterogeneous effects of warming on components of diversity

Physiological responses to environmental temperature, such as thermal scaling of performance, i.e., changes in species growth, energy gain and activity patterns as a function of temperature, can determine the result of competitive interactions among species (Buckley & Roughgarden 2006; Finstad et al. 2011). Thermal scaling might ultimately cause competitive exclusion due to niche retractions (Finstad et al. 2011). Competitive displacement is also an important mechanism changing community composition and turnover, which act in consonance with environmental filtering (Leibold & Chase 2017). Besides changes in community composition itself, warming has also an effect on community structure, by altering competitive dominance, and consequently species abundance (Harte & Shaw 1995; Hillebrand et al. 2018), which may also explain the decreases in ENS.Pie we have observed in our results. As we mentioned before, warming seems to promote species sorting, selecting species with new set of traits and adaptations, which might be suboptimal at control temperatures. This new set of traits might lead to competitive advantages and boost the dominance of new species (Dangles, Carpio, Barragan, Zeddam, & Silvain 2008; Kosten et al 2012).

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

Average I^2 values suggest that most of the variability across studies is due to heterogeneity rather than chance alone, especially for results from *α*- diversity analyses, which were more heterogeneous than those for *β*-diversity. Heterogeneity on the effects of warming on diversity depends on the experimental system for different components of inventory diversity (both *α- and γ*-diversity). It has been shown that experimental marine systems tend to have higher average losses of species at the local level, compared to terrestrial and freshwater systems (Gruner et al. 2017), which differs from our results, as marine and terrestrial systems tended to gain more species than freshwater systems. However, time series from non-experimental marine communities show that species richness tend to increase with warming (Antão et al 2020).

Contrary to our initial expectation, longer studies with higher ΔT did not have larger losses of species nor more nested communities as a consequence of sequential loss of diversity, despite evidence that both components of *β*-diversity change monotonically over time (Angeler 2013). Our results for the effects of study length on local species richness and ENS.Pie are in agreement with the meta-analysis of Gruner et al. (2017), who also reported that study duration had no effect on *α*-diversity. Despite the relative importance of study duration for *γ*-diversity, our results for *α*- and *β*- diversity reinforce the notion that temperature change can be the main driver of changes in species composition, creating rapid changes and novel assembled communities across the warming gradient (Gibson□Reinemer et al. 2015), regardless of the duration of exposition.

Conclusions and way forward

Despite decades of research on the effects of warming on species diversity, only recently we have started to have robust syntheses of its effects in experimental meta-ecosystems (e.g., Gruner et al. 2017; Marino et al. 2018). However, most of the information available focused on local communities, with warming effects at the regional scale commonly neglected. Despite the acknowledged limitations of our meta-analysis, and the inherent difficulties in translating lessons learned from experimental to real meta-ecosystems, our results support the need for a refocus of the agenda on global change consequences for biodiversity. The focus should shift from effects on local richness only to the full understanding of the effects on biodiversity at the regional scale. This poses important challenges for both experimental and observational designs. Although warming experiments have become more complex over the past years, with an ever-increasing number of factors considered, we still lack appropriate protocols to detect changes in communities across spatial scales and across a large number of taxa and ecosystem types. Although our results showed that patch isolation *per se* might not be as deleterious as it is generally assumed, improving our understanding 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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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 (*α* = 0.05). Bold values represent significant slopes.

			Incidence		Abundance		
	Richness	ENS.Pie	Nestedness	Turnover	Nestedness	Turnover	Gamma
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 ±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 ± 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. Confidence Intervals above (or below) the dashed line show significant positive (or negative) effect sizes. Asterisks: significant ($p < 0.05$) I^2.