



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

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Abstract

Aim: The aim was 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 studied: Fungi, invertebrates, phytoplankton, plants, seaweed, soil microbes and 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. The local and regional inventory diversity remain unaltered, whereas species composition across temperature gradients and the patterns of species dominance change with temperature, creating novel communities that might be harder to predict.

KEYWORDS

α -diversity, β -diversity, climate change, habitat fragmentation, manipulative experiments, meta-analysis

1 | 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 (Cahill et al., 2013; Lurgi et al., 2012; Peñuelas et al., 2013; Scheffers et al., 2016). These changes are likely to accelerate extinction rates at the global scale in the coming decades (Urban, 2015), with important consequences for the provision of crucial ecosystem services (Bulling et al., 2010; Pecl et al., 2017; Peñuelas et al., 2017; Scheffers et al., 2016), for local livelihoods and for the global economy (Lee et al., 2015; Stern, 2015).

Our understanding of the effects of warming on the biota is centred primarily on the responses of single species or on various measures of local diversity (i.e., α -diversity; Antão et al., 2020; Araújo & Luoto, 2007; Gruner et al., 2017; Wiens, 2016). Recent syntheses of the impacts of global change on α -diversity have spurred controversy. Some studies suggest declines in local average species richness (e.g., Cardinale et al., 2018; Gonzalez et al., 2016), whereas others suggest that the average number of species is roughly constant over time (e.g., Dornelas et al., 2014; Vellend et al., 2017). The effects of warming on 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 not fully elucidated.

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). A focus on species diversity at the level of 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). Identification of the independent effects of global warming in different components of species diversity is challenging, because warming is likely to be 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 can identify two important and contrasting phenomena, namely 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 et al., 2007). Nestedness can indicate non-random processes of species loss and/or gain across space, representing differences in the sensitivity of species 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). An understanding of 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 et al., 2005). For instance, high levels of nestedness in open patches across a thermal

gradient might indicate that species are being lost systematically 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, might suggest that a particular set of species is being selected to occupy specific sections of the new climatic gradient (e.g., Hillebrand et al., 2010), forming novel communities (Urban et al., 2012; Williams & Jackson, 2007).

The establishment of causal connections between changes in climate and biodiversity poses an extra challenge because non-experimental field studies rely on correlational data, which make 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. Given that the 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, because previous meta-analyses showed that the effects of warming on experimental meta-communities depend on the experimental design itself, including differences in the temperature and time of manipulation and the ecosystem type (Gruner et al., 2017; Marino et al., 2018). Given that habitat fragmentation has been shown to aggravate the effects of climate change in ecological communities (Oliver et al., 2015; Opdam & Wascher, 2004), 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, because individuals from resident species are able to migrate and (re)colonize open patches.

2 | MATERIALS AND METHODS

2.1 | 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 as the one 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 world-wide. We contacted authors to request raw community data, in order that 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; a list of the data sources is given in Supporting Information Appendix S1) that were used in our analyses. We excluded datasets that used a temperature manipulation (ΔT) of $> 6^\circ\text{C}$, because this exceeds 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 $\Delta T < 6^\circ\text{C}$. If ΔT was $> 6^\circ\text{C}$ in one of the treatments, we used only data from sampling units with experimental temperatures $< 6^\circ\text{C}$. We also excluded studies that we were not able to reconstruct local communities (at the replicate level) from the original data. In the 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.

2.2 | Measures of diversity across scales

Firstly, we computed two measures of α -diversity, namely 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; McGlenn et al., 2019). ENS.pie represents the number of equally abundant species in a perfectly even community (Chase & Knight, 2013; McGlenn et al., 2019). It offers many advantages over other diversity indices in meta-analytical approaches, because ENS.Pie is scale independent (i.e., relative insensitivity 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 mechanisms of coexistence of species in the experiment (Schuler et al., 2017).

Secondly, we calculated the β -diversity among replicates within any given study and partitioned it into species turnover and nestedness components using two different approaches: (a) based on qualitative data (i.e., species presence/absence; see Baselga et al., 2007); and (b) 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 β -diversity, separating two components of abundance-based dissimilarity: (a) balanced variation in abundance, in which individuals of some species in one site are substituted by the same number of individuals of different species in another site; and (b) abundance gradients, in which some individuals are lost from one site to the other (Baselga, 2013). Metrics of β -diversity range from zero (lowest dissimilarity) to one (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 the control, by counting the total number of species or OTUs at the end point of each experiment.

2.3 | Meta-analysis

We calculated the logarithmic response ratio (lnRR; Borenstein et al., 2009) as our measure of effect size for all indices of α - and β -diversity. The lnRR is a measure of the relative effect size (i.e., the proportional change in the response variable relative to the controls). Given that 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 ($\Delta\gamma$) as a measure of the effect size (Borenstein et al., 2009) at the meta-community level. We evaluated differences in γ -diversity using ANOVA, logln-transforming species richness values.

To evaluate the effect of warming on α - and β -diversity, we first fitted random-effect models using the lnRR as response variable, with the dataset identity as a random intercept. We measured heterogeneity (I^2) of this random model as a means to access the total variance component that was not explained by sampling variance (i.e., the percentage of total variation across studies that is attributable to heterogeneity rather than to chance itself; Higgins et al., 2003).

To answer the remaining questions (the effect of site openness and experimental context), we then fitted meta-regression models, using four experimental moderators: ΔT (difference between control and warming treatments, in degrees Celsius; range: 0.23 – 5°C), study length (in days; range: 15 – $7,300$ days), ecosystem type (categorical, coded as dummy variables: freshwater, terrestrial and 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-theoretical framework (Burnham & Anderson, 2002). To evaluate model plausibility, we used the Bayesian information criterion (BIC) and BIC weight (BICw_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 the BIC for all possible models. The information-theoretical approach taken 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 took 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 the 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 $\Delta\gamma$ as the response variable. All analyses were conducted in the R environment (R Core Team, 2012).

3 | RESULTS

3.1 | Effects of warming on diversity

Experimental warming had no significant effect on species richness locally, but significantly reduced the effective number of species (ENS.Pie), which decreased on average by 4.4% in warming replicates when compared with controls ($\ln RR \pm SE = -0.0450 \pm 0.02$; z -value = -2.2456 ; $p = .02$; Figure 1). For both controls and warming replicates, ENS.Pie was smaller than the observed richness. 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 $I^2 \pm SD = 79.73 \pm 1.22$; Figure 1).

Species turnover (or the balanced gradient in species abundance in the case of quantitative data) was the main component of total β -diversity (ANOVA p -values < .001; Figure 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 ; $p = .007$; Figure 3) when compared with controls. The overall mean effect size for all other measures of β -diversity was not different from zero (Figure 3). All models for β -diversity presented significant heterogeneity (mean $I^2 \pm SD = 46.53 \pm 17.45$; Figure 3), with nestedness components being more heterogeneous than turnover components (Figure 3).

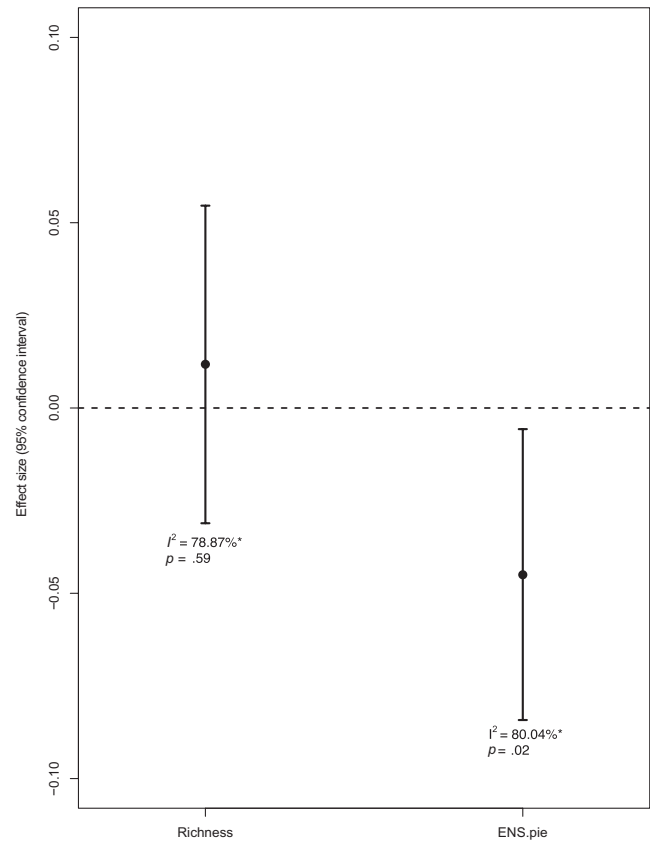


FIGURE 1 Mean effect size \pm 95% confidence intervals from temperature-change experiments on both components of community α -diversity, namely species richness and the effective number of species (ENS.Pie). I^2 represents the amount of heterogeneity (i.e., variation in effect sizes) that is not accounted for by the sampling error variance. Confidence intervals above (or below) the dashed line show significant positive (or negative) effect sizes. Asterisks indicate a significant ($p < .05$) I^2

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 ($F_{1,132} = 0.008$; $p = .93$). The average raw difference showed that 40.3% of the meta-ecosystems lost species at the species pool level, whereas 37.31% gained species, with the remaining 22.39% of the datasets showing constant species richness ($\chi^2 = 5.52$, d.f. = 2; p -value = .06).

3.2 | 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; Supporting Information Figures S1–S3). Ecosystem type was amongst the main moderators explaining differences in the effect size for species richness, with terrestrial and marine systems having larger effect

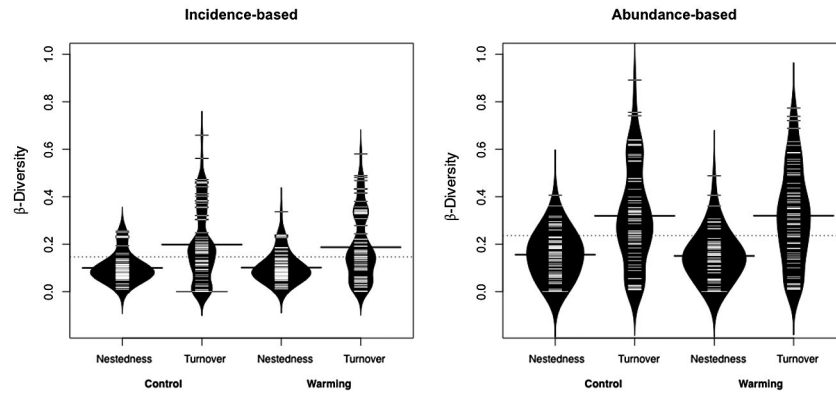


FIGURE 2 Bean plot showing differences in spatial turnover and nestedness for both incidence-based indices and abundance-based indices. Values of β -diversity close to zero represent low dissimilarity, whereas values close to one represent high dissimilarity. Lines represent individual observations. The shaded areas show the distribution density. Thick lines represent the averages within each level. Dotted lines indicate the global average

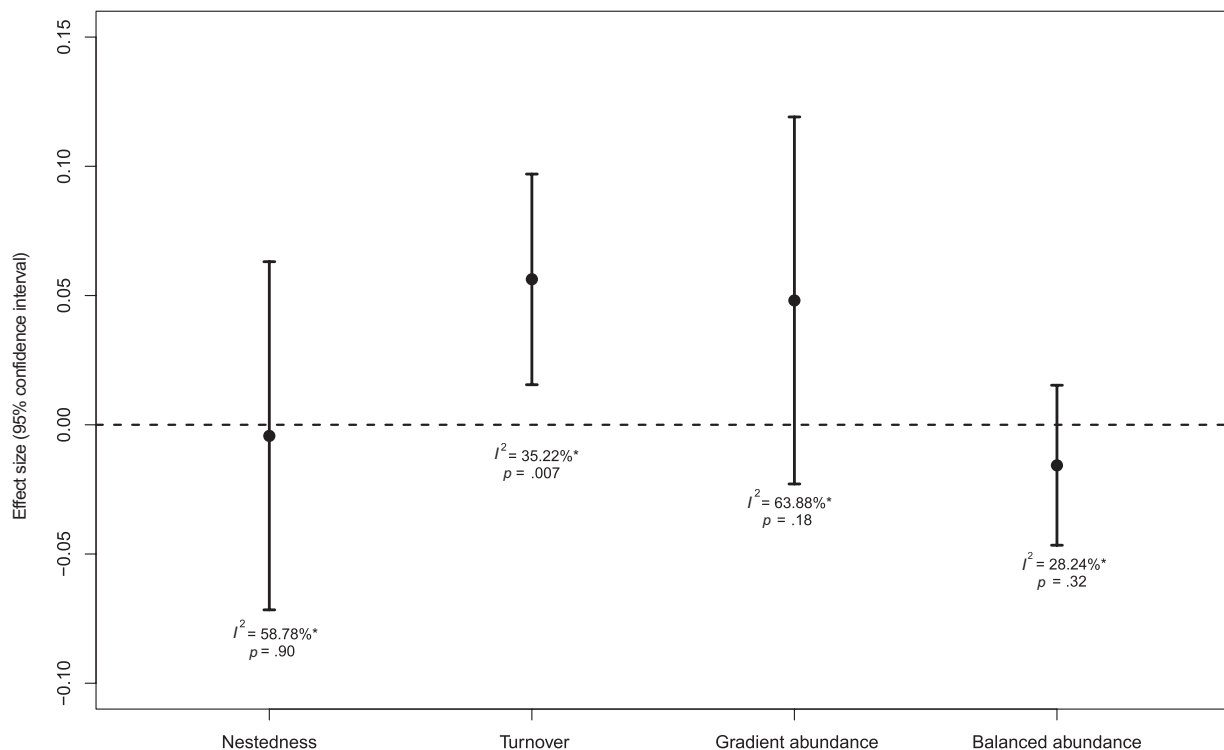


FIGURE 3 Mean effect size \pm 95% confidence intervals from temperature-change experiments on different aspects of community β -diversity. Nestedness and turnover are incidence-based measures, whereas gradient and balanced abundance are abundance-based measures. I^2 represents the amount of heterogeneity (i.e., the variation in effect sizes) that is not accounted for by the sampling error variance. Confidence intervals above (or below) the dashed line show significant positive (or negative) effect sizes. Asterisks indicate a significant ($p < .05$) I^2

sizes for richness than freshwater systems (Table 1; Supporting Information Figure S1). Experimental ΔT had a significant effect on explaining the variation in species richness. On average, ΔT was among the top moderators explaining differences in effect sizes for β -diversity (Supporting Information Figure S2), although no slope differed from zero. Study duration had no significant effect on α -, β - and γ -diversity results (Table 1; Supporting Information Figures S1–S3).

4 | DISCUSSION

4.1 | 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

TABLE 1 Model-averaged parameter estimates of moderators of α -, β - and γ -diversity, based on all possible models

Moderator			Incidence		Abundance		Gamma
	Richness	ENS.Pie	Nestedness	Turnover	Nestedness	Turnover	
ΔT	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)	

Note: Values in parentheses represent the alpha risk for confidence intervals ($\alpha = .05$). Bold values indicate significant slopes.

ENS.Pie = effective number of species; ΔT = temperature manipulation.

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 and 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 et al., 2008; Kosten et al., 2012; Yvon-Durocher et al., 2015). Although increased local species dominance can lead to an increment of cascading extinctions (Zarnetske et al., 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, whereas 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, because we estimated α -diversity from raw data for each dataset, and not from published values. Our methodological choice was determined by 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 might not have provided enough power to detect changes in local species richness. The partitioning of multifactorial data (i.e., studies with more factors than warming alone) into independent subsets reduces the sample size within datasets, and heterogeneity is larger between smaller studies than larger studies (Int'Hout et al., 2015), which might have reduced our ability to detect changes in local species richness. Our approach, however, allowed us to analyse 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 widely debated in recent 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 might 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 (Antão et al., 2020; Suggitt et al., 2019; Yue et al., 2020). Observational studies have also 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 crucial information for understanding the consequences of climate change on meta-ecosystems, showing that spatial turnover becomes more common under warming scenarios. An understanding of changes in community composition across local communities as a consequence of warming is crucial to the choice of 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 owing 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 sets of traits when compared with 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 et al., 2018). Under increasing temperatures, taxonomic and functional turnover seems also to be a recurrent pattern (Frainer et al., 2017; Hillebrand et al., 2010; Gibson-Reinemer et al., 2015), 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, an increase in species turnover suggests that experimental communities are undergoing a process of species sorting, whereby 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; Frainer et al., 2017; Gibson-Reinemer et al., 2015). Higher spatial turnover and its consequent novel assemblages nevertheless impose an extra and crucial implication for climate scientists and policy-makers, because they suggest that ecological communities might not be able to track climate change by shifting their ranges, even though species can (Gibson-Reinemer et al., 2015).

4.2 | 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 owing 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 also has an effect on community structure, by altering competitive dominance and, consequently, species abundance (Harte & Shaw, 1995; Hillebrand et al., 2018), which might 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 sets 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 et al., 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). The relationship between dispersal and species diversity can 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 for habitat isolation, which, together with habitat fragmentation, has been considered historically as one of the main threats to biodiversity (Haddad et al., 2015; Quinn & Harrison, 1988). However, it has recently been pointed out that fragmentation alone might 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 et al., 2018). This calls attention to the necessity of evaluating other habitat-related issues in warming experiments, such as habitat availability and configuration, in addition to the inherent ability of species to disperse.

Average I^2 values suggest that most of the variability across studies is attributable to heterogeneity rather than chance alone, especially for results from α -diversity analyses, which were more heterogeneous than those for β -diversity. Heterogeneity in 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 with terrestrial and freshwater systems (Gruner et al., 2017), which differs from our results, in which marine and terrestrial systems tended to gain more species than freshwater systems. However, time series from non-experimental marine communities show that species richness tends 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 exposure.

4.3 | Conclusions and way forward

Despite decades of research on the effects of warming on species diversity, only recently have we 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 has been focused on local communities, with warming effects at the regional scale commonly being 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 refocusing of the agenda on the consequences of global change 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 in recent 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, an improvement in 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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DATA AVAILABILITY STATEMENT

No primary data were originated by our study. All data are third-party datasets and are available in the published literature and listed in the Supporting Information (Appendix S1, Data sources). R codes are available at GitHub (<https://github.com/bastazini/-The-impac>

t-of-climate-warming-on-species-diversity-across-scales/blob/main/README.md).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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