SYNTHESIS

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Biodiversity promotes ecosystem functioning despite environmental change

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Abstract

Three decades of research have demonstrated that biodiversity can promote the functioning of ecosystems. Yet, it is unclear whether the positive effects of biodiversity on ecosystem functioning will persist under various types of global environmental change drivers. We conducted a meta-analysis of 46 factorial experiments manipulating both species richness and the environment to test how global change drivers (i.e. warming, drought, nutrient addition or CO_2 enrichment) modulated the effect of biodiversity on multiple ecosystem functions across three taxonomic groups (microbes, phytoplankton and plants). We found that biodiversity increased ecosystem functioning in both ambient and manipulated environments, but often not to the same degree. In particular, biodiversity effects on ecosystem functioning were larger in stressful environments induced by global change drivers, indicating that high-diversity communities were more resistant to environmental change. Using a subset of studies, we also found that the positive effects of biodiversity were

mainly driven by interspecific complementarity and that these effects increased over time in both ambient and manipulated environments. Our findings support biodiversity conservation as a key strategy for sustainable ecosystem management in the face of global environmental change.

INTRODUCTION

Global environmental changes are reshaping the structure and processes of ecosystems, potentially threatening the functioning and services that ecosystems provide to human society (Jiang et al., 2020; Song et al., 2019; Zhou et al., 2012). In the face of environmental change, biodiversity is a key factor maintaining (Cardinale et al., 2012; Hooper et al., 2012; Naeem et al., 2009) and buffering ecosystem functioning (Hisano et al., 2018; Pires et al., 2018; Yachi & Loreau, 1999). However, environmental change also alters species dynamics and interactions, causing rapid changes in biodiversity at various spatial scales (Blowes et al., 2019; Dornelas et al., 2014; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2019; Urban, 2015; Vellend et al., 2013). Therefore, changing environments can affect ecosystem functioning both directly, via altering rates of ecosystem processes (Spaak et al., 2017), and indirectly, via changing biodiversity (Giling et al., 2019; Hautier et al., 2015). Furthermore, environmental changes can interact with biodiversity in regulating ecosystem functioning, such that the effects of biodiversity on ecosystem functioning may be enhanced or weakened under altered environmental conditions, even if biodiversity itself does not change (Benkwitt et al., 2020; Eisenhauer et al., 2019). However, the potential interactions between environmental changes and biodiversity are much less understood compared with the direct and indirect effects of environmental change on ecosystems, leaving it unclear whether the positive effects of biodiversity will persist in future environments impacted by global change drivers (De Laender et al., 2016).

While existing biodiversity experiments have mostly manipulated species richness under ambient environmental conditions, a growing number of experiments examine how environmental change (or global change drivers) may alter the effects of biodiversity on ecosystem functioning across different taxonomic groups, such as terrestrial plants, microbes, or phytoplankton (Bestion et al., 2020; Craven et al., 2016; García et al., 2018; Hautier et al., 2014). Using factorial designs in which biodiversity and environmental manipulations were combined, these studies revealed strengthened (García et al., 2018; Reich et al., 2001; Steudel et al., 2011), constant (Eisenhauer et al., 2018; Thakur et al., 2015), or weakened (De Boeck et al., 2008) biodiversity effects impacted by various types of global change drivers. Such mixed results may be explained by the context dependency of biodiversity effects, which vary in strength across different types and magnitudes of environmental manipulations, different taxonomic groups, or different aspects of ecosystem functions being measured. For instance, experimental warming in microbial and phytoplankton communities has been found to either dampen or enhance ecosystem productivity (Bestion et al., 2020; García et al., 2018; Tabi et al., 2019; Yvon-Durocher et al., 2015). Currently, we lack a synthetic understanding of both how different types of environmental change may influence biodiversity effects on ecosystem functioning, and how these interactive effects depend on the experimental context (e.g. taxonomic group, experimental time, etc.) (Eisenhauer et al., 2019).

One hypothesis about the interactive effects of biodiversity and environmental change is that global change drivers alter the strength and even the type of interspecific interactions (Baert et al., 2018; He et al., 2013; Hoek et al., 2016), which underlie the effects of biodiversity on ecosystem functioning. Two classes of processes have been proposed to explain biodiversity effects, namely complementarity (CE) and selection (SE) effects (Loreau & Hector, 2001; Tilman et al., 2014). CE arises from interspecific niche partitioning or facilitation, and SE arises from a disproportionally high contribution of one or few species to ecosystem functioning. Many studies suggest that the strength and type of species interactions may shift as the environment changes (He et al., 2013; Hoek et al., 2016; Maestre et al., 2009; Olsen et al., 2016). In particular, the stress-gradient hypothesis predicts that species interactions can switch from higher competition in favourable environments to lower competition or even facilitation in stressful environments (Bertness & Callaway, 1994; He et al., 2013; Hoek et al., 2016; but see Metz & Tielbörger, 2016). Such a switch may enhance CE and hence overall biodiversity effects in stressful environments. On the other hand, SE may also increase with environmental stress because more diverse communities may have a higher probability of including stress-tolerant species and such species may be expected to outcompete stress-intolerant ones and dominate in stressful environments (Baert et al., 2018; Bestion et al., 2020; Maestre et al., 2009). Thus, stress intensity induced by environmental changes may provide a useful indicator to predict the influence of environmental changes on the magnitude of biodiversity effects on ecosystem functioning (Baert et al., 2018).

Previous experiments also suggested that biodiversity effects, particularly CE, increased over time (Cardinale et al., 2007; Huang et al., 2018; Reich et al., 2012). Such enhanced biodiversity effects were at least in part due to character displacement during the succession of experimental communities (van Moorsel et al., 2018; Zuppinger-Dingley et al., 2014). In stressful environments, interspecific facilitation and the compensation of more resistant species may allow high-diversity communities to cope better with stress through time and maintain ecosystem functions at higher levels than less diverse communities (Hisano et al., 2018; Wright et al., 2021). In such cases, the influence of environmental changes on biodiversity effects may strengthen over time, but the magnitude of these effects is uncertain.

In this study, we performed a meta-analysis of 46 factorial experiments in which species richness was manipulated together with at least one of four types of global change drivers (namely warming, drought, nutrient addition or CO_2 enrichment) to systematically assess how environmental change may modify biodiversity effects on ecosystem functioning across three taxonomic groups (namely microbes, phytoplankton, and terrestrial plants [plants for short]). These four global change drivers capture common anthropogenic impacts on ecosystems and are most frequently investigated in the literature (e.g. Hooper et al., 2012; Song et al., 2019). That said, only warming could be assessed in all three taxonomic groups (i.e. microbes, phytoplankton, and plants, with 4, 3, and 6 studies, respectively), and drought, nutrient and CO_2 enrichment were only assessed in plants (with 14, 11, and 8 studies, respectively). Using these data, we asked two questions: (i) does biodiversity promote ecosystem functioning under both ambient and manipulated environmental conditions? (ii) do global change drivers influence the magnitude of biodiversity effects, and do such influences vary through time and depend on the stress intensity induced by environmental changes? Our hypothesis is that biodiversity promotes ecosystem functioning across a range of environmental conditions, but its effect size can be modulated by global change drivers. In stressful environments, mixtures may be less influenced than monocultures if CE increases with stress intensity as predicted by the stress gradient hypothesis (Bertness & Callaway, 1994), or if SE increases with stress intensity due to the presence of stress-tolerant species (Baert et al., 2018; Bestion et al., 2020). In such cases, biodiversity effects increase with stress intensity (H_1 in Figure 1). Otherwise, biodiversity effects can decrease with stress intensity if mixtures are more sensitive to environmental stress (H_2 in Figure 1). Finally, biodiversity effects will not change with stress intensity if mixtures and monocultures are similarly sensitive to environmental stress (H_0 in Figure 1).

METHODS

Data collection

We searched the literature and extracted all factorial experiments that manipulated species richness and at least one of the four focal types of global change drivers, i.e. warming, drought, nutrient addition or CO_2 enrichment (see Appendix B: Table B1 for search terms). We performed the search on 17 February 2020 in the Web of Science and retrieved 2386 papers in total. We then selected studies using the following criteria (See PRISMA diagram, Appendix B: Fig. B1): (i) the experiment includes monocultures and mixtures under both ambient and manipulated environmental conditions; (ii) the study provides measures of at least one ecosystem function under different treatments. In total, 35 experimental studies were selected based on our criteria, and we added 11 experimental studies from cross-referencing that met our criteria (Appendix B: Table B7). This led to a total of 46 experimental studies, including 7582 experimental units (ranging from a culture dish to a field plot) covering different taxonomic groups and types of global change drivers. Note that the 46 experimental studies were treated as independent in our meta-analysis, although some of them came from the same site but involved different types of environmental manipulations (e.g. BioCON experiment with nutrient addition or CO_2 enrichment; Reich et al., 2001). This simplification was justified by a likelihood ratio test which reported no significant difference between models including and excluding the non-independence between studies (see Appendix A).

We categorised our dataset by taxonomic groups (microbes, phytoplankton, and plants), types of global change drivers (warming, drought, nutrient addition, and CO_2 enrichment) and two categories of ecosystem functions (biomass production and biogeochemical process) (Appendix B: Table B2; Chapin et al., 2011). In our study, microbes referred to non-photosynthetic microorganisms, such as bacteria, fungi and protozoans. Because only the warming treatment was found for microbes and phytoplankton, we have in total six combinations of taxonomic groups and global change drivers, that is warming in all three taxonomic groups, as well as drought, nutrient and CO_2 enrichment in plants. The 46 studies included 3, 4 and 39 experimental studies on microbes, phytoplankton, and plants, respectively (Appendix B: Table B7). For studies on plants, 10 studies were from pots in the greenhouse, and 29 studies were from field experiments. Experimental duration ranged from 6 to 40 days in microbial studies, from 7 to 19 days in phytoplankton studies, and from 1 to 15 years in plant studies. The highest species richness varied among studies on microbes (6~24), phytoplankton (12–64), and plants (2–60). For each type of global change drivers, we recorded the level(s) of experimental manipulation, for example the degree of temperature increase, the proportion of water reduction, the
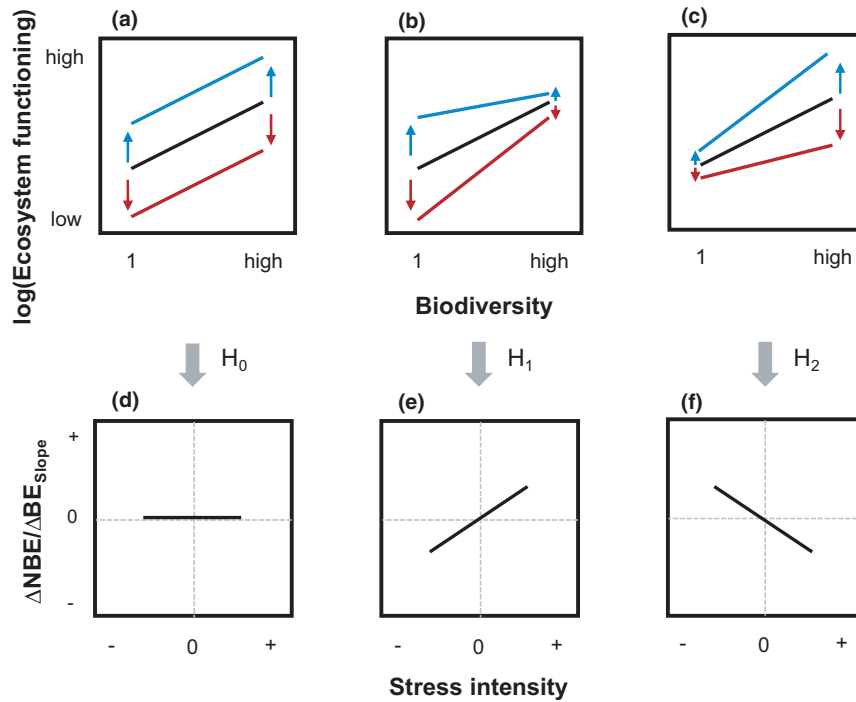
FIGURE 1 Scenarios underlying the responses of biodiversity-ecosystem functioning relationships to stress intensity (a–c) and the resulting relationship between changes in biodiversity effects (ΔNBE, ΔBE$_{Slope}$) and stress intensity (d–f). Global change drivers can either increase or decrease ecosystem functioning and thus result in a more favourable or stressful environment for ecological communities. Under the null scenario (H_0) where mixtures are similarly influenced by global change drivers as monocultures, biodiversity effects are not altered by global change drivers and we will observe no relationship between stress intensity and ΔNBE or ΔBE$_{Slope}$. Under the scenario (H_1) where mixtures are less influenced by global change drivers compared with monocultures, biodiversity effects are enhanced in more stressful environments but weakened in more favourable environments, and we will observe a positive relationship between ΔNBE or ΔBE$_{Slope}$ and stress intensity. Under the scenario (H_2) where mixtures are more influenced by global change drivers compared with monocultures, biodiversity effects are weakened in more stressful environments but enhanced in more favourable environments, and we will observe a negative relationship between ΔNBE or ΔBE$_{Slope}$ and stress intensity

type and amount of nutrient added (e.g. N and NPK enrichment), and the amount of CO_2 enrichment. For warming treatments in microbes and phytoplankton, which usually contained several temperature levels in addition to the ambient or long term-culture temperature (as the control, e.g. 15℃ in Pennekamp et al., 2018 and 20℃ in García et al., 2018), we only used temperature levels above this control as warming treatments and excluded data with cooling treatments.

Regarding the two categories of ecosystem functions, biomass production captured the total biomass produced during a given period (e.g. grassland biomass production within a year), which has been the most commonly used metric of ecosystem functioning; biogeochemical processes captured soil characteristics (e.g. the concentration of key elements or organic materials in the soil), soil microbial functions (e.g. microbial biomass, microbial growth and abundance) and nutrient cycling (e.g. ectoenzyme activity and organic phosphorus). We considered soil microbial growth and abundance as functions, because soil microbial community composition and activity play key roles in mediating biogeochemical cycling (Cavicchioli et al., 2019) and have been used to indicate belowground secondary productivity (Eisenhauer et al., 2018).

Biodiversity effects under ambient and manipulated environments

We first quantified the net biodiversity effect (NBE) on ecosystem functioning by calculating the bias-corrected estimation of the log response ratio (Koricheva et al., 2013; Lajeunesse, 2015):

$$\text{NBE} = \ln\left(\frac{\overline{X}_{\text{mix}}}{\overline{X}_{\text{mono}}}\right) + \frac{1}{2}\left(\frac{\text{SD}_{\text{mix}}^2}{n_{\text{mix}}\overline{X}_{\text{mix}}^2} - \frac{\text{SD}_{\text{mono}}^2}{n_{\text{mono}}\overline{X}_{\text{mono}}^2}\right) \quad (1)$$

where $\overline{X}_{\text{mix}}$, SD_{mix} and n_{mix} represent the average, standard deviation and sample size (i.e. number of replicates) of ecosystem function, respectively, in mixtures at a given biodiversity level. $\overline{X}_{\text{mono}}$, SD_{mono} and n_{mono} represent similar metrics in monocultures. A positive value of NBE indicates a higher ecosystem functioning in mixtures compared with that in monocultures, and vice versa. We calculated NBE under both ambient (NBE$_A$) and manipulated (NBE$_M$) environments, for each type and level of global change drivers, each taxonomic group, each ecosystem function, each level of species richness in mixtures, and each time point (if the experiment contained multiple observations). Overall,

we obtained 1997 NBE values, including 508, 74 and 146 pairs of NBE_A and NBE_M for the warming treatment in microbes, phytoplankton, and plants, respectively, and 170 for drought, 201 for nutrient addition and 136 for CO_2 enrichment in plants (see Appendix B: Table B1).

To quantify the influence of environmental manipulations (i.e. global change drivers) on biodiversity effects, we calculated the difference in biodiversity effects between ambient and manipulated environments (Lajeunesse, 2011, 2015):

$$\Delta NBE = NBE_M - NBE_A \qquad (2)$$

where the subscripts A and M indicate ambient and manipulated environments, respectively. A positive value of ΔNBE indicates a higher biodiversity effect under the manipulated environment, and vice versa. The relative change in biodiversity effects induced by environmental manipulations can be derived by rescaling ΔNBE (Hooper et al., 2012): $e^{\Delta NBE} - 1 = \frac{e^{NBE_M}}{e^{NBE_A}} - 1$.

To understand the mechanisms underlying biodiversity effects, we used the additive partition by Loreau and Hector (2001) to derive the complementarity (CE) and selection effect (SE) on biomass production, based on the 12 studies with available raw data of monocultures (Appendix B: Table B7). We first calculated CE and SE for each mixture and then obtained the mean and standard deviation for each species richness level, each level of environmental manipulation and each experimental time point. For comparison among studies, we standardised CE and SE by the average value of ecosystem function in monocultures (Craven et al., 2016; Loreau & Hector, 2001). In doing so, we excluded monocultures with too low biomass (i.e. less than $2.5\ g\,m^{-2}$ in grassland and $0.005\ mg\,ml^{-1}$ in microbes) following Reich et al. (2012) and omitted 100 (out of 1974) CE or SE values accordingly. Specifically, CE and SE were calculated as:

$$CE = T_{sqrt}\left(\frac{N \cdot \overline{\Delta RY} \cdot \overline{X}_{mono}}{\overline{X}_{mono}} \right) \qquad (3)$$

$$SE = T_{sqrt}\left(\frac{N \cdot cov\left(\overline{\Delta RY}, \overline{X}_{mono}\right)}{\overline{X}_{mono}} \right) \qquad (4)$$

where N and ΔRY are the number of species in the mixture and difference between species' observed relative yield in the mixture and expected relative yield, respectively (Loreau & Hector, 2001). $T_{sqrt}(x) = sign(x) \times \sqrt{|x|}$ represented a square-rooted transformation while keeping the original sign, which has commonly been used in previous studies to reduce the influence of skewed distributions of CE and SE (e.g. Isbell et al., 2009). By definition, we can derive the link between different metrics: $e^{NBE} = \frac{N \cdot \overline{\Delta RY} \cdot \overline{X}_{mono}}{\overline{X}_{mono}} + \frac{N \cdot cov\left(\overline{\Delta RY}, \overline{X}_{mono}\right)}{\overline{X}_{mono}} + 1$. We calculated CE and SE in both ambient (CE_A and SE_A) and

manipulated environment (CE_M and SE_M). We then calculated the difference in CE or SE between the manipulated and ambient environments:

$$\Delta CE = CE_M - CE_A \qquad (5)$$

$$\Delta SE = SE_M - SE_A \qquad (6)$$

In addition to NBE, we also quantified biodiversity effects using the regression slope (BE_{Slope}) between ecosystem functioning and species richness (Baert et al., 2018). We calculated the log-log regression slope between species richness and ecosystem functioning in both ambient (BE_{Slope_A}) and manipulated (BE_{Slope_M}) environments, for each type and level of environmental manipulations, each taxonomic group, each ecosystem function, and each time point. We then derived their difference ($\Delta BE_{Slope} = BE_{Slope\_M} - BE_{Slope\_A}$) to characterise the response of biodiversity effects to global change drivers.

Both NBE and BE_{Slope} have been widely used for quantifying biodiversity effects in experimental studies and meta-analyses (e.g. Baert et al., 2018; Balvanera et al., 2006; Duffy et al., 2017; Hautier et al., 2015; Hooper et al., 2012). NBE is more appropriate if ecosystem functioning saturates rapidly, for example from monocultures to two-species mixtures. In comparison, BE_{Slope} is more appropriate if ecosystem functioning exhibits a (quasi-)linear increase with species richness on log–log scales (Appendix A). As the realistic scenarios should occur along the continuum between a rapid saturating curve and a (quasi-)linear trend (Cardinale et al., 2012), our usage of both NBE and BE_{Slope} facilitates a comprehensive picture of biodiversity effects (see Appendix A for more detailed discussion). For brevity, we presented the results of NBE (and its additive partitions into CE and SE) in the main text and those of BE_{Slope} in Appendix B.

Environmental stress intensity and biodiversity effects

For a given taxonomic group and type of global change drivers, experimental communities might respond to environmental manipulations differently across studies. Following Steudel et al. (2012), we defined stress intensity as the response of monoculture functions to environmental manipulations within each study:

$$\text{Stress intensity} = 1 - \left(\frac{\overline{X}_{mono_M}}{\overline{X}_{mono_A}} \right) \qquad (7)$$

where $\overline{X}_{mono_M}$ and $\overline{X}_{mono_A}$ were average functioning of monocultures in manipulated and ambient environments, respectively. A positive (negative) value of stress intensity indicated that global change drivers decreased (increased) monoculture functions and thus provided a stressful (favourable) condition. We

calculated stress intensity for each ecosystem function, level of environmental manipulation, and experimental time in each study. We then derived average stress intensity through time over the experimental duration, and we also tested the robustness of our results using the value of stress intensity at the end of the experiment (Steudel et al., 2012).

We note that in our definition of stress intensity, the responses of mixtures were not taken into account because they involved both the direct effects of global change drivers and the potential buffering effects of biodiversity (Hisano et al., 2018), which would have confounded our analysis on the relationship between stress intensity and ΔNBE. However, in the appendix, we also quantified the responses of mixtures to global change drivers, in order to examine the overall effects of environmental changes.

Statistical analyses

To derive pooled effect sizes for biodiversity effects (NBE, ΔNBE, BE_{Slope}, and ΔBE_{Slope}) and their 95% confidence intervals (CIs), we used three-level, hierarchical mixed-effects models to account for the non-independence between biodiversity effect sizes (Nakagawa & Santos, 2012; see Appendix A for details). In these models, samples were weighted by the inverse of their variance (see Appendix A for derivation). Fixed-effects terms are type of global change drivers (α), ambient or manipulated environmental conditions (τ), taxonomic group (β) and category of ecosystem functions (γ). Random-effects terms are study (θ) and the combination of species richness (η), level of environmental manipulation (λ), specific ecosystem function (ψ) and experimental time (φ) nested within study (i.e. as a sub-study ID). The models thus read:

$$\text{NBE} \sim (\alpha\tau\beta\gamma)_{ijkl} + (\theta/\eta\lambda\psi\varphi)_{mnrst} + \in_{ijklmnrst} \quad (8)$$

$$\Delta\text{NBE} \sim (\alpha\beta\gamma)_{ijk} + (\theta/\eta\lambda\psi\varphi)_{mnrst} + \in_{ijkmnrst} \quad (9)$$

$$\text{BE}_{Slope} \sim (\alpha\tau\beta\gamma)_{ijkl} + (\theta/\lambda\psi\varphi)_{mnrst} + \in_{ijklmnrst} \quad (10)$$

$$\Delta\text{BE}_{Slope} \sim (\alpha\beta\gamma)_{ijk} + (\theta/\lambda\psi\varphi)_{mnrst} + \in_{ijkmnrst} \quad (11)$$

Similarly, we estimated the average and 95% CIs of CE and SE and the differences between ambient and manipulated environment (i.e. ΔCE and ΔSE) using the following models:

$$\text{CE or SE} \sim (\alpha\beta\tau)_{ijk} + (\theta/\eta\lambda\varphi)_{mnrs} + \in_{ijkmnrs} \quad (12)$$

$$\Delta\text{CE or } \Delta\text{SE} \sim (\alpha\beta)_{ij} + (\theta/\eta\lambda\varphi)_{mnrs} + \in_{ijmnrs} \quad (13)$$

We used the function "rma.mv()" of the *metafor* package in R to estimate these effect sizes (Viechtbauer, 2010).

Between-study heterogeneity of effect sizes was evaluated using the extended I^2 and Cochran's Q statistic (Nakagawa & Santos, 2012; see Appendix A for details). The extended I^2 quantified the fraction of variation in effect size attributed to between-study variance in multi-level models, and the Cochran's Q statistic evaluated the significance of between-study variance (Appendix A). Our analyses found high between-study heterogeneity of effect sizes ($I^2 > 60\%$ and $p < 0.01$ for NBE, ΔNBE, BE_{Slope} and ΔBE_{Slope}; see Appendix B: Table B3). We thus conducted multi-level meta-analyses for both NBE and BE_{Slope} to explore how between-study heterogeneity may be explained by potential moderators. Our analyses showed significant differences in NBE and BE_{Slope} across different combinations of taxonomic groups, type of global change drivers and category of ecosystem functions (Appendix B: Table B4 and B5). Therefore, we did not estimate overall effect sizes across all 46 studies. We also tested the effects of other potential moderators (type of nutrient addition, vegetation type, and experimental unit), which were found to have non-significant effects on NBE or BE_{Slope} and thus omitted in the main text (see Appendix A).

Using five long-term studies in our dataset (one on microbes and four on grasslands; see Appendix B: Table B7), we tested whether the effects of global change drivers on NBE and BE_{Slope} for biomass production varied through time. For each study, we used mixed-effects models with experiment duration as a fixed effect, and the combination of species richness level and level of environmental manipulation as the random effect. Similarly, we further tested the relationship between ΔNBE/ΔBE_{Slope} and experimental duration. We fitted each model using linear, quadratic and logarithmic forms of environment duration and calculated the Akaike information criterion (AIC) to determine the best model. We used the function "lmer()" of the *nlme* package in R to fit these models.

We also used mixed-effects models to test the relationships between ΔNBE, ΔBE_{Slope}, ΔCE or ΔSE and stress intensity (SI):

$$\Delta\text{NBE}, \Delta\text{BE}_{Slope}, \Delta\text{CE or } \Delta\text{SE} \sim \text{ SI} + (\alpha\beta\gamma/\theta/\eta\lambda\psi)_{ijkmnrs} + \in_{ijkmnrs} \quad (14)$$

where SI was the fixed effect, and other variables (α, β, γ, θ, η, λ, ψ) were random effects. We also tested the two-way interactions of stress intensity with taxonomic group, type of global change drivers, and category of ecosystem function (Appendix B: Table B6). Again we used the function "lmer()"to fit this model.

Publication bias was analysed using the function "funnel()" from the *metafor* package in R (Viechtbauer, 2010) and Egger's test was conducted to test the asymmetry of the funnel plot of our model (with only random effect) in NBE, ΔNBE, CE, ΔCE, SE and ΔSE, as well as BE_{Slope} and ΔBE_{Slope} (Nakagawa et al., 2017). We found overall low publication biases in our dataset; a significant bias occurred only for ΔSE (Egger's $p = 0.0110$, Appendix B:

Fig. B2). But our further sensitivity analysis showed that the publication bias in ΔSE did not influence the robustness of our results (see Appendix A).

RESULTS

Biodiversity had generally positive effects (NBE and BE_{Slope}) on biomass production in both ambient and manipulated environments, regardless of the type of global change drivers and taxonomic group ($p < 0.05$; Figure 2 and Appendix B: Fig. B3). Biodiversity also tended to enhance biogeochemical processes, but these effects were weaker and non-significant for certain combinations of global change drivers and taxonomic groups ($p > 0.05$; Figure 2 and Appendix B: Fig. B3). NBEs under ambient and manipulated environmental conditions were positively correlated in each of the six combinations of global change drivers and taxonomic groups ($r = 0.42$–0.82; Appendix B: Fig. B4).

Although warming did not change the sign of NBEs, it modulated their magnitude (as measured by ΔNBE) in microbes and phytoplankton (Figure 2; $Q_M = 24.76$, $p < 0.0001$, Appendix B: Table B4). In microbial communities, warming decreased NBEs on biomass production on average by 20% ($e^{-0.222}$, number of effect sizes (N) = 506, number of studies (n) = 3, $p = 0.0726$). In phytoplankton communities, however, warming increased NBEs on biomass production on average by 61% ($e^{0.360}$, $N = 64$, $n = 3$, $p = 0.002$; Figure 2), and this increase was stronger as the degree of warming increased (Appendix B: Fig. B5). For biodiversity effects measured by BE_{Slope}, warming also increased BE_{Slope} on biomass production in phytoplankton ($\Delta BE_{Slope} = 0.109$, $N = 12$, $n = 3$, $p = 0.019$; Appendix B: Fig. B3), but it had a non-significant effect in microbes ($p > 0.05$; Appendix B: Fig. B3).

In plants, global change drivers had overall non-significant effects on NBE, regardless of the type of global change drivers and ecosystem functions measured ($p > 0.05$; Figure 2). Global change drivers also did not influence BE_{Slope} for biogeochemical processes, but BE_{Slope} for biomass production responded significantly to global change drivers, except for CO_2 enrichment. Specifically, BE_{Slope} was decreased by warming ($\Delta BE_{Slope} = -0.103$, $N = 28$, $n = 4$, $p = 0.034$; Appendix B: Fig. B3) and nutrient addition ($\Delta BE_{Slope} = -0.085$, $N = 49$, $n = 7$, $p = 0.011$; Appendix B: Fig. B3), whereas it was increased by drought ($\Delta BE_{Slope} = 0.099$, $N = 21$, $n = 10$, $p = 0.026$; Appendix B: Fig. B3).

Based on the 12 studies with monocultures where raw data were available, we found that complementarity effects (CE) were generally positive ($p < 0.05$) and selection effects (SE) were generally not different from 0 in both ambient and manipulated environments, regardless of the type of global change drivers or taxonomic group (Figure 3). Warming decreased CE for microbial biomass production by 24.3% ($N = 470$, $n = 2$, $p < 0.0001$) and

increased CE for phytoplankton production by 82.6% ($N = 10$, $n = 1$, $p = 0.008$) (Figure 3a). But warming did not alter SE in either microbes or phytoplankton communities (Figure 3b). In plant communities, global change drivers had no significant effects on either CE or SE on biomass production ($p > 0.05$; Figure 3).

Using the five long-term studies in our dataset, we found that biodiversity effects (i.e. NBE and BE_{Slope}) generally increased with experimental duration in both ambient and manipulated environments (Figure 4; Appendix B: Fig. B6). The difference in biodiversity effects between ambient and manipulated environments, measured by either ΔNBE or ΔBE_{Slope}, decreased with experimental duration in microbial experiments ($p < 0.05$; Appendix B: Fig. B7 and B8). Yet, such differences did not vary with experimental duration in the four grassland studies ($p > 0.1$; Figure 4; Appendix B: Fig. B7 and B8).

Warming in phytoplankton communities and drought in plant communities on average decreased monoculture functions (positive value of stress intensity), and nutrient addition in plant communities on average increased monoculture functions (negative value of stress intensity) ($p < 0.05$; Figure 5a). However, the effects of drought and nutrient addition on ecosystem functions became non-significant in more diverse plant communities ($p > 0.10$; Appendix B: Fig. B9). We found that both ΔNBE and ΔBE_{Slope} increased as stress intensity increased ($p < 0.001$ for both; Figure 5b,c), indicating stronger biodiversity effects in more stressful environments. These results were robust whether we used biodiversity effects (i.e. ΔNBE and ΔBE_{Slope}) averaged across time or at the end of the experiment (Appendix B: Fig. B10). Moreover, the positive relationship between stress intensity and ΔNBE or ΔBE_{Slope} also held in models that incorporated the effects of taxonomic groups, type of global change drivers, category of ecosystem function, and their interaction with stress intensity (Appendix B: Table B6).

DISCUSSION

The past decades have seen major progress in understanding the responses of ecosystems to environmental and biodiversity changes. Recent meta-analyses have documented the individual effects of global environmental change (Song et al., 2019; Yuan et al., 2017) or biodiversity (Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2012) on ecosystem functioning. Our synthesis of 46 factorial experiments advances current understanding by demonstrating the interactive effects between biodiversity and environmental changes on ecosystem functions. We found that biodiversity consistently enhanced ecosystem functioning in both ambient and manipulated environments, but global change drivers could modulate the strength of biodiversity effects. Specifically, the effects of biodiversity on ecosystem functioning were stronger in stressful environments than
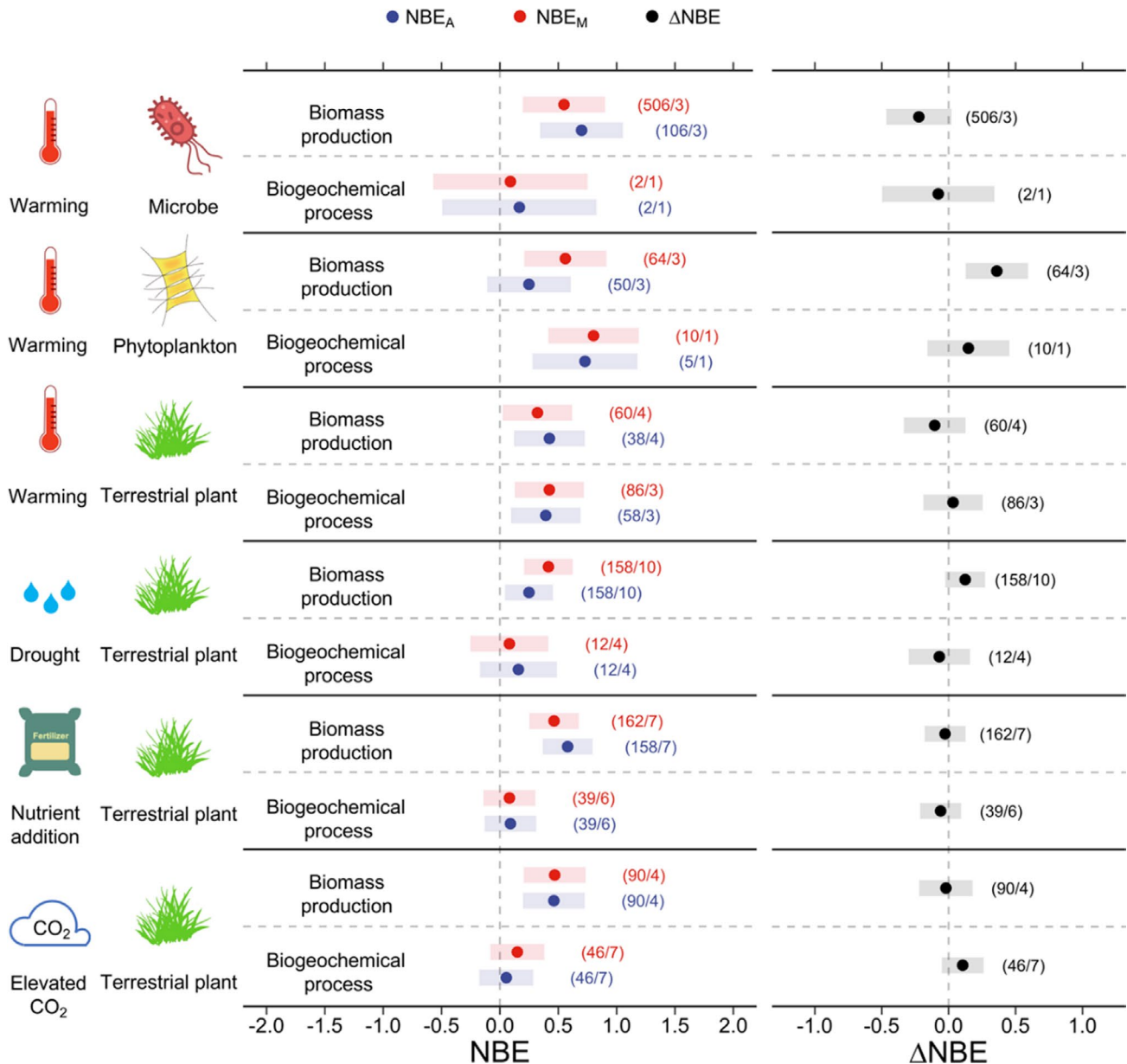
FIGURE 2 Net biodiversity effects (NBE) on ecosystem functioning under ambient (NBE$_A$, blue) and manipulated environmental conditions (NBE$_M$, red), and the difference between them (ΔNBE = NBE$_M$ − NBE$_A$, black) across different combinations of types of global change drivers (warming, drought, nutrient addition or elevated CO_2), taxonomic groups (microbes, phytoplankton or plants) and ecosystem functions (biomass production or biogeochemical process). The numbers in brackets show the number of effect sizes and studies. The points and shades represent the estimated mean and confidence interval, respectively, from linear mixed-effects models (see Methods). Confidence intervals (95%) not overlapping with the dashed line (i.e. 0) indicate statistical significance ($p < 0.05$)

in more favourable environments. Therefore, biodiversity contributes to buffering ecosystem functions across a range of stressful conditions associated with current and future global change scenarios.

Biodiversity effects in ambient and manipulated environments

Biodiversity generally promoted ecosystem functioning in both ambient and changing environments (Figure 2; Appendix B: Fig. B3), although its positive effects on biogeochemical processes were relatively weak and often non-significant, possibly due to small sample sizes. Based on a subset of our dataset (12 studies where the necessary data were available), we found that these positive biodiversity effects were mainly due to complementarity effects (Figure 3), which was consistent with earlier findings from plant diversity experiments under ambient environmental conditions (Huang et al., 2018; Loreau & Hector, 2001; Tilman et al., 2014) as well as under altered conditions (Craven et al., 2016).

While global change drivers did not change the directions of biodiversity effects (both NBE and BE$_{Slope}$), they
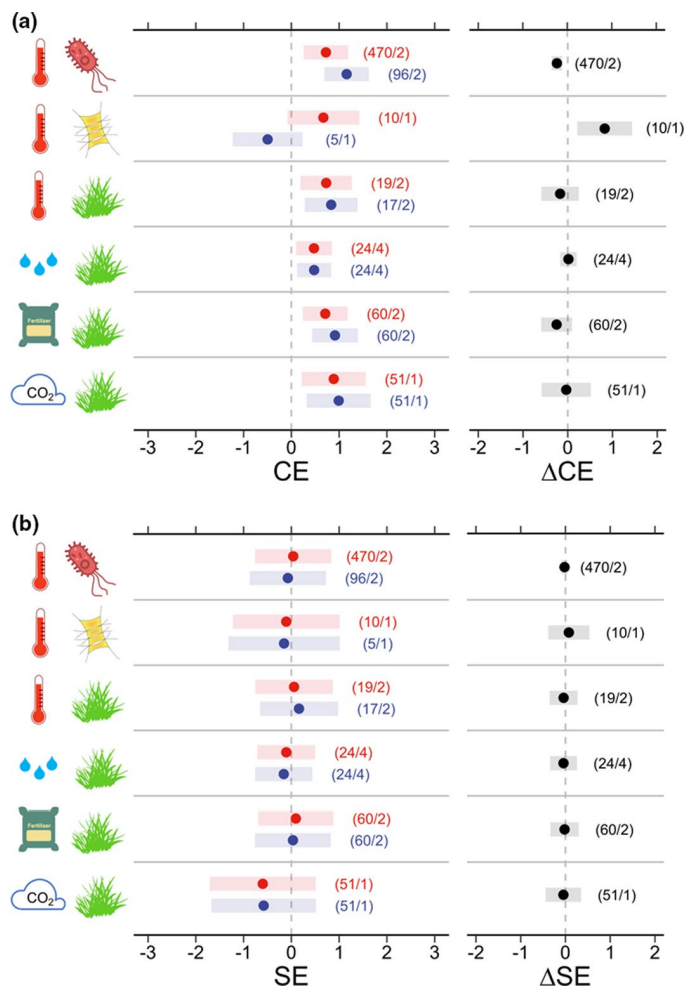
FIGURE 3 Complementarity (CE) (a) and selection (SE) (b) effects on biomass production under ambient (CE_A and SE_A, respectively, blue) and manipulated environmental conditions (CE_M and SE_M, respectively, red) and the difference between them ($\Delta CE = CE_M - CE_A$, $\Delta SE = SE_M - SE_A$, black), across different combinations of types of global change drivers (warming, drought, nutrient addition or elevated CO_2) and taxonomic groups (microbes, phytoplankton and plants). The numbers in brackets show the number of effect sizes and studies. Analyses were based on 12 experiments with raw data of monocultures, and CE and SE were square-root transformed (restoring the sign after transformation; see Methods). The points and shades represent the estimated means and confidence intervals, respectively, from linear mixed-effects models (see Methods). Confidence intervals (95%) not overlapping with the dashed line (i.e. 0) indicate statistical significance ($p < 0.05$)

mediated the magnitude of biodiversity effects (Figure 2, Appendix B: Fig. B3). Warming increased biodiversity effects on biomass production in phytoplankton but decreased it in microbes. The contrasting responses of biodiversity effects to warming in microbes versus phytoplankton may be explained by differential effects of warming on interspecific interactions. In microbial communities, warming has been shown to enhance interspecific competition between culturable microbial species, even leading to competitive exclusion (Jiang & Morin, 2004). Such intensified competition by warming should lead to a reduction in CE in microbes (Figure 3; Parain et al., 2019). In phytoplankton communities, however, warming might promote interspecific facilitation, for instance by stimulating certain groups or species such as N_2-fixing cyanobacteria (Brauer et al., 2015; Striebel et al., 2016), which would lead to an increased CE (Figure 3).

In plant communities, warming and nutrient addition decreased, and drought increased biodiversity effects quantified by the regression slope (BE_{slope}) between species richness and biomass production (Appendix B: Fig. B3). These global change drivers also similarly influenced NBEs (as well as CE), but the effects were weak and often non-significant (Figures 2 and 3). These apparently inconsistent results for ΔNBE and ΔBE_{slope} may be due to the fact that BE_{slope} usually have smaller variances compared with NBE, which makes it easier to detect statistically significant effects for ΔBE_{slope} (see Appendix A). Furthermore, the responses of NBE and BE_{slope} to global change drivers are reconciled from the perspective of stress intensity (see below).

Several recent studies showed that biodiversity effects increased with time (Guerrero-Ramírez et al., 2017; Huang et al., 2018; Reich et al., 2012). In line with this finding, our analysis based on five long-term studies
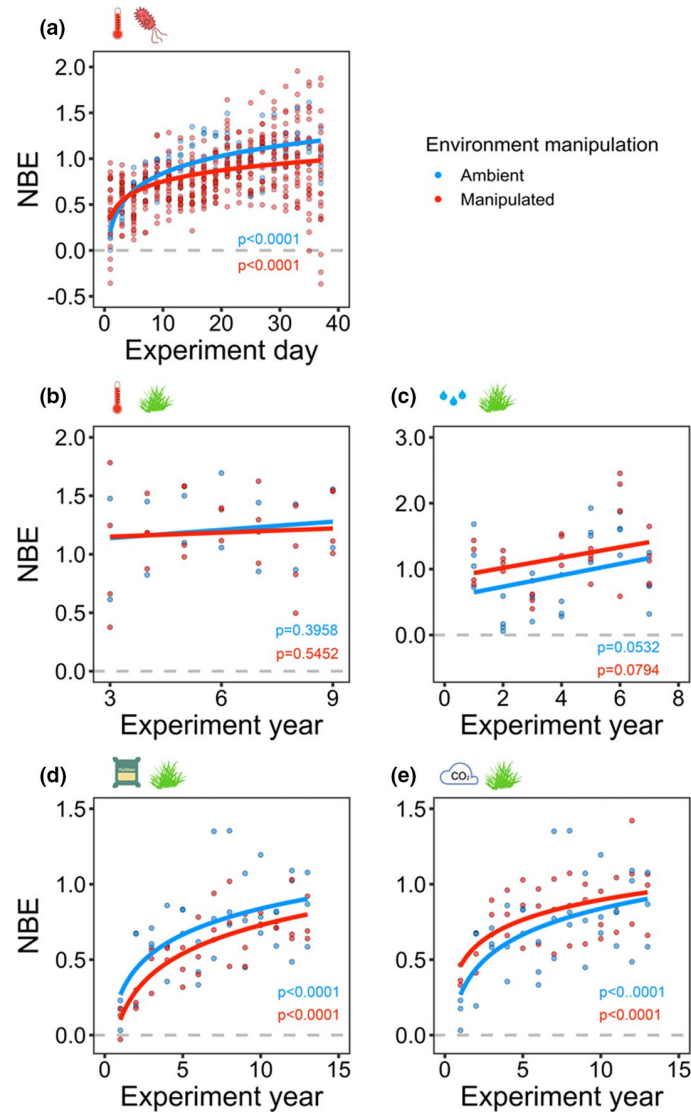
FIGURE 4 Net biodiversity effect (NBE) as a function of experimental duration across different types of environmental manipulations and taxonomic groups: (a) warming on microbes (Pennekamp et al., 2018); (b) warming on plants (Cowles et al., 2016); (c) drought on plants (Wagg et al., 2017); (d) nutrient addition on plants (Reich et al., 2001); (e) CO_2 enrichment on plants (Reich et al., 2001)

(one on microbes and four on plants) showed that biodiversity effects generally increased with time under both ambient and altered environmental conditions (Figure 4, Appendix B: Fig. B6). Moreover, we found a negative interaction between warming and experimental duration on biodiversity effects in the microbial experiment (Appendix B: Fig. B7 and B8), suggesting that the negative effect of warming on biodiversity effects increased over time. In the four plant experiments, interactions between global change drivers and time were all nonsignificant, possibly explained by their longer generation times and less intense manipulations of global change drivers compared with microbes. In particular, the longest plant experiment in our data lasted 15 years, which may not be sufficient for the plants to acclimate to environmental changes and for novel interspecific interactions to manifest or evolve (Jessup et al., 2004; but see Zuppinger-Dingley et al., 2014).

Biodiversity buffers environmental stress

By quantifying the responses of monocultures in each study, we found that the stress induced by the altered environment differed markedly among studies, even for the same global change driver and taxonomic group (Figure 5). In other words, the same environmental manipulation can be perceived as either more or less stressful by different experimental communities (e.g. different plant species pools used in different experiments). Interestingly, we found that stress intensity was positively related to both ∆NBE and ∆BE$_{Slope}$. Thus, stress intensity provides a useful indicator to predict how global change drivers alter biodiversity effects. The positive relationship between ∆NBE or ∆BE$_{Slope}$ and stress intensity could be due to higher resistance to environmental stress of diverse mixtures compared with monocultures (H1 in Figure 1; Appendix B: Fig. B9). When global change
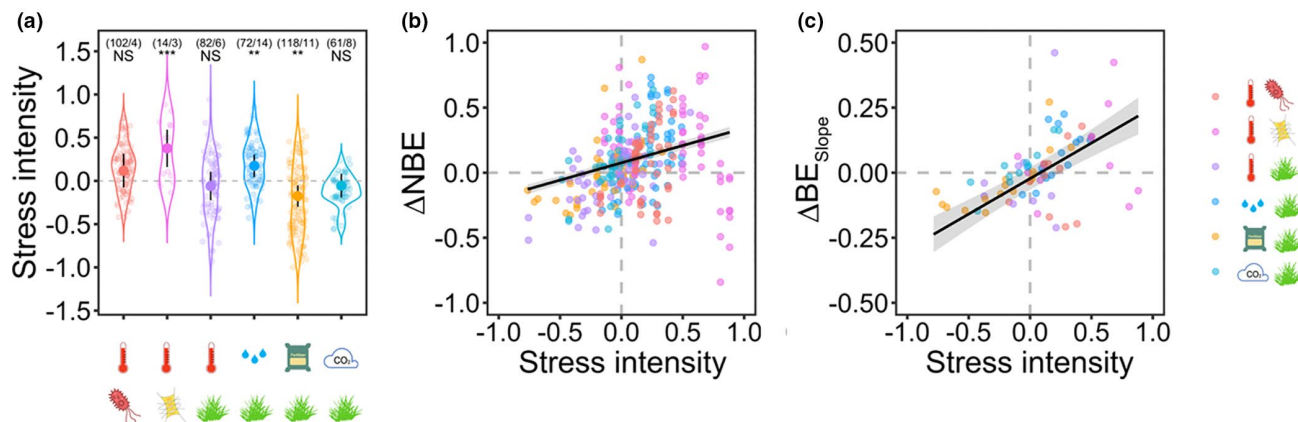
FIGURE 5 Distribution of environmental stress intensity for each combination of types of global change drivers and taxonomic group (a), and relationship between changes in biodiversity effects (ΔNBE, ΔBE$_{Slope}$) and stress intensity (b, c). In (a), light-coloured points represent the distribution of stress intensity, which was calculated as the relative difference under ambient vs. manipulated environmental conditions in each study. Positive (negative) values mean lower (higher) monoculture functions in manipulated environments. Coloured points represent their averages with 95% confidence intervals (black bars). The numbers in brackets show the number of effect sizes and studies. In (b) and (c), changes in biodiversity effects between manipulated and ambient environmental conditions were calculated in two ways: the difference in net biodiversity effect (ΔNBE; $N = 327$, $n = 46$, $p < 0.0001$) (b) and the difference in the log-log slope between ecosystem functioning and species richness (ΔBE$_{Slope}$; $N = 76$, $n = 46$, $p = 0.0003$) (c). Trendlines and 95% confidence intervals are given. NS, not significant ($p > 0.1$); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

drivers induced high-stress intensity (e.g. warming in phytoplankton communities or drought in plant communities), diverse mixtures exhibited higher resistance to environmental stress and better maintained their functions (in line with Isbell et al., 2015), resulting in an enhanced biodiversity effect. Conversely, when global change drivers reduced environmental stress compared with ambient conditions (e.g. nutrient addition on plants), diverse mixtures benefitted less than monocultures, resulting in a weakened biodiversity effect. Overall, communities with higher species diversity were less influenced by environmental changes, because biodiversity could buffer the negative or positive effects of global change drivers on ecosystem functioning (Figure 5, Appendix B: Fig. B9). This can occur directly through niche complementarity, via buffering of microenvironmental stress (Wright et al., 2014), or both. Such buffering effects can increase not only ecosystem resistance to directional changes in the environment but also the temporal and spatial stability of ecosystems in fluctuating environments (Wang et al., 2019; Yachi & Loreau, 1999).

Our results are consistent with recent findings that biodiversity can increase the resistance and resilience of ecosystems (Mori et al., 2013; Isbell et al., 2015; Hisano et al., 2018; but see Baert et al., 2016; De Boeck et al., 2018; Pennekamp et al., 2018). The results are also in line with the stress gradient hypothesis (Bertness & Callaway, 1994), which predicts increased biodiversity effects (particularly CE) with increasing stress intensity due to reduced interspecific competition or enhanced facilitation (He et al., 2013; Wright et al., 2017). That said, our analyses based on a small sample size showed that neither CE nor SE exhibited a significant relationship with stress intensity, although both showed positive trends (Appendix B: Fig. B11).

Recent studies hypothesised that biodiversity effects could first increase but then decrease with stress intensity, because high-stress intensity may restrict population growth to such a level that ecosystem functions are extremely low regardless of the level of biodiversity (Baert et al., 2018). Our results did not support this hypothesis. This could be due to the fact that our data included few experiments with extreme environmental conditions, hence most values of stress intensity in our data fell into a relatively narrow interval (e.g. the 5% and 95% quantiles of stress intensity were [−0.54, 0.60], see Figure 5). Alternatively, it may be intrinsically difficult to detect the threshold level of environmental conditions based on empirical data, even if such a threshold exists (Hillebrand et al., 2020). Disentangling these possibilities will require future experiments that cover more extreme values of stress intensity (De Boeck et al., 2018).

Future directions

Several future directions emerge from our study. On the experimental side, more efforts are needed to better understand the interactions between biodiversity and the environment. First, most studies in our datasets (34 out of 46) are from grasslands; so, research efforts should be extended to other ecosystems (e.g. forests) and taxonomic groups (e.g. microbes and phytoplankton). In particular, we did not find any study that tested the interaction between biodiversity and eutrophication in microbes or phytoplankton. Recent studies showed that nutrient addition in microbial communities could shift species interactions from facilitation to competition (Hoek et al., 2016; Piccardi et al., 2019), whereas nutrient addition in

phytoplankton communities shifted competition from nutrients to light and thus altered species interactions (Burson et al., 2018). Thus, biodiversity effects might be altered by eutrophication in microbes and phytoplankton. Second, all studies in our dataset manipulated species richness as the main facet of biodiversity. However, recent studies highlighted effects of other facets of biodiversity (e.g. functional or phylogenetic diversity) on ecosystem functioning (Craven et al., 2018; Huang et al., 2018; Steudel et al., 2016). Whether environmental change alters the effects of different facets of biodiversity in different ways remains unclear and should be explored further. Third, very few experiments (one in our dataset) tested the interaction between biodiversity and multiple environmental change drivers (Reich et al., 2001). Although a recent meta-analysis suggested that different global change drivers might have weak interactive effects (Song et al., 2019), there are case studies showing significant interactions (Reich et al., 2020; Rillig et al., 2019), and whether they exhibit higher-order interactions with biodiversity remains unknown. Future experiments should address the interactions between different global change drivers, including additional ones to those considered here (e.g. climatic variability). On the other hand, new theory is required for clarifying the ecological mechanisms underlying interactions between biodiversity and the environment. Classic theories on biodiversity-ecosystem functioning were built upon competition models that assumed constant environmental conditions (Loreau, 1998; Tilman et al., 1997). A constant environment can be readily achieved in experimental settings but rarely in natural ecosystems. New theoretical studies should allow for different environmental conditions under which biodiversity-ecosystem functioning relationships are predicted, to explore possible mechanisms by which the physical and biological environments might modify biodiversity effects (e.g. De Laender, 2018).

Lastly, experimental and theoretical findings need to be reconciled with the increasing number of observational studies along natural gradients of biodiversity and environmental conditions, for both terrestrial (Fei et al., 2018; Guo et al., 2019) and marine (Benkwitt et al., 2020) ecosystems. Recent observational studies revealed either enhanced (Fei et al., 2018; Hisano & Chen, 2020), similar (Liang et al., 2016) or weakened (Mori, 2018) effects of tree diversity on ecosystem productivity in warmer regions. In comparison, our meta-analysis revealed an overall weak, negative effect of warming on plant biodiversity effects. Moreover, several continental-scale studies showed that plant diversity increased ecosystem productivity or biomass in dry regions, but such effects were weakened or even reversed in moist regions (Fei et al., 2018; Guo et al., 2019; Ratcliffe et al., 2017). These results are consistent with the overall positive effects of drought on plant biodiversity effects in our analyses (Figure 2 and Appendix B: B3). Syntheses across different approaches (e.g. experimental, theoretical, and observational) will help clarify which patterns and mechanisms are general and which are context dependent.

CONCLUSIONS

By synthesising experiments across various taxonomic groups and types of global change drivers, our study demonstrates the persistent positive effects of biodiversity on ecosystem functions across taxa despite environmental change. The positive effects of biodiversity increased over time under both ambient and manipulated environmental conditions and were stronger when environmental change increased stress intensity. Independent of the level of environmental stress, biodiversity helps to maintain ecosystem functioning at relatively stable levels, whereas stability is lowered in species-poor communities or monocultures. Moreover, our synthesis contributes to exposing knowledge gaps and informing future research to advance our understanding of the interaction between biodiversity and environment. Recent studies showed that the magnitude of biodiversity effects on ecosystem functioning was comparable to that of effects of environmental changes in both experimental and natural communities (Duffy et al., 2017; Hooper et al., 2012; Tilman et al., 2012). Thus, biodiversity provides an important biological buffer to maintain ecosystem functioning in the face of environmental changes.

AUTHOR CONTRIBUTIONS

S.W. conceived the idea; P.H. performed the study; P.H. assembled the data, with help from all coauthors; P.H. did the statistical analyses, with inputs from B.S, F.D.L, S.W.; P.H. and S.W. wrote the first draft of the manuscript, and all authors contributed substantially to the interpretation of the results and revision of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data supporting the results has been deposited to Figshare (https://doi.org/10.6084/m9.figshare.16947451.v1).

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