

# Accepted Article

## Changes in plant diversity and its relationship with productivity in response to nitrogen addition, warming, and increased rainfall

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**Abstract**

Human-induced global changes such as nitrogen (N) deposition, climatic warming, and rainfall changes have been determined to be common drivers of current plant community dynamics. However, it is unclear if and how the individual and combined effects of these drivers differently influence plant diversity and its relationship with productivity at the global scale. Here, we performed meta-analyses with data compiled from 133 articles, comprising >2000 effect sizes, to assess the individual and combined effects of N addition, warming, and increased rainfall on plant diversity and its relationship with productivity (using aboveground biomass as a proxy). We found that N addition decreased species richness, Shannon–Wiener index ( $H'$ ), and evenness, while it increased aboveground biomass. In contrast, warming and increased rainfall had no effect on diversity although both also increased aboveground biomass. The combined effects of N addition + warming and N addition + increased rainfall showed significant negative effects on plant diversity, with additive and synergistic interactions, respectively. Warming + increased rainfall did not influence plant diversity. Both the individual and combined effects on plant diversity were influenced by several moderator variables, with negative impacts of the magnitude and experimental duration on N addition effects and of latitude on N addition + warming effects. Importantly, our results showed that the greater the increase in plant productivity with long-term N addition, the greater the decline in plant diversity, and vice versa, indicating that the commonly observed positive diversity-productivity relationship would be reduced under long-term N addition. Our study provides new insights for the development of predictive models of plant diversity dynamics in response to multiple concurrent global change drivers, while also highlighting a consistent, strong negative effect of N addition, pointing to a clear need for reducing N deposition.

**Keywords:** individual effect, combined effect, species richness, Shannon–Wiener index, evenness, Bayesian meta-analysis

## Introduction

Anthropogenic activities are changing the global environment at unprecedented rates, leading to a worldwide decline in biodiversity (Ceballos et al. 2015, Pimm et al. 2014). Species losses are important in their own right, but also alters key processes important to the productivity and sustainability of Earth's ecosystems (Hooper et al. 2005, Wardle et al. 2011), and may ultimately diminish the biodiversity-enhanced benefits that people derive from nature (e.g., climate regulation and wood production) (Isbell et al. 2017). A wave of research has been triggered to study how multiple global change drivers can affect biodiversity and related ecosystem functions (e.g., primary productivity). Among the global change drivers studied, reactive nitrogen (N) deposition from intensive agricultural and industrial activity, climatic warming as a result of anthropogenic emissions of greenhouse gases, and associated rainfall regime changes have been commonly identified threats to global terrestrial biodiversity (Bellard et al. 2012, Payne et al. 2017). While a number of empirical studies and reviews have demonstrated the individual effects of these global change drivers on biodiversity (Bellard et al. 2012, Humbert et al. 2016), our understanding of their combined effects at regional and global scales remains limited. More importantly, despite the well-documented positive general relationship between plant diversity and productivity (Liang et al. 2016, Tilman et al. 2014), we know little about how global change drivers may alter the biodiversity-productivity relationship, despite its importance for the global extinction crisis and ecosystem functioning (Liang et al. 2016).

Reactive N addition to terrestrial ecosystems has increased substantially in recent decades. N addition is one of the most widespread drivers of global change (Galloway et al. 2008), and a substantial threat to biodiversity in ecosystems of high conservation value (Steffen et al. 2015). A recent meta-analysis showed that, on average, N addition in mountain grasslands causes increases in plant productivity, and reductions in species

richness and, to a lesser extent, Shannon-Wiener index ( $H'$ ) (Humbert et al. 2016).

Because terrestrial ecosystems have mainly evolved under N-limiting conditions (Elser et al. 2007), the observed results may be attributed to the fact that N addition increases productivity and compositional turnover by favoring a small number of opportunistic species (Harpole et al. 2016). However, we need to understand how general such dynamics are. Additionally, because N addition supposedly has opposing effects on plant diversity and productivity, any established relationship between the two may be altered by N addition. Existing syntheses, however, have only addressed the effects of N addition on either plant diversity or productivity (Humbert et al. 2016, Tang et al. 2017, Yue et al. 2016). Given that N deposition is predicted to increase further on a global scale (Fowler et al. 2013), assessing its general effects on biodiversity and the biodiversity-productivity relationship is important for adequately forecasting biodiversity change.

Climatic warming is emerging as another major driver of changes in terrestrial ecosystems worldwide. Warming-induced shifts in plant species phenology, ranges, and abundance are predicted to alter local biodiversity within and across ecosystems (Dawson et al. 2011). The effects of warming on plant biodiversity can be difficult to predict owing to species-specific effects on vital rates (Elmendorf et al. 2012). Long-term observational studies have connected global climatic changes to geographical range shifts (CaraDonna et al. 2014, Wischnewski et al. 2011). Recent meta-analyses have shown that warming may increase plant productivity, but reduce plant species richness in terrestrial ecosystems at the global scale (Gruner et al. 2017, Yue et al. 2017). However, as concurrent N deposition and warming in natural ecosystems are common, these two factors may interact to jointly affect plant diversity and its relationship with productivity. For example, warming effects on plant productivity might depend on soil N availability (Lu et al. 2013), indicating that a larger increase in

plant biomass may only occur when soil N is simultaneously added. Thus, the combined effects of N addition and warming may be higher than the sum of their individual effects. On the other hand, although warming tends to increase plant productivity, it also induces warming-associated drought that is likely to decrease productivity (Craven et al. 2016). As plant productivity may not only be directly affected by N addition or warming, but also indirectly through changes in diversity (Isbell et al. 2013), predicting the effects of warming and its combination with N addition on plant diversity, productivity, and their relationship becomes much more complex.

In addition, rainfall is one of the dominant factors controlling plant community structure and composition (Weltzin et al. 2003) and is likely to change in many areas as a consequence of global warming (IPCC 2014). While increasing drought is a primary focus as a risk to biodiversity and productivity (Fahey et al. 2018, Prieto et al. 2009), increased rainfall is also likely to affect plant biodiversity and its relationship with productivity. Further, increasing atmospheric CO<sub>2</sub> concentrations increase plant water use efficiency, providing an effect on plant water economy potentially analogous to increased rainfall (Keenan et al. 2013). Previous studies reporting the response of plant diversity to increased rainfall are inconsistent, with negative (Suttle et al. 2007), positive (Stevens et al. 2006), and neutral (Harpole et al. 2007) effects all being found. More importantly, because both the effects of N addition and warming on plant productivity and diversity may depend on water availability, increasing rainfall combined with N addition and/or warming could lead to synergistic effects. However, the combined effects of these global change drivers on plant biodiversity and its relationship with productivity remain unclear, despite their importance for predicting plant diversity dynamics in a changing world.

To address this knowledge gap, here we report the results from meta-analyses using more than 2000 observations (i.e., pairwise-comparisons) from 133 published

articles and academic dissertations reporting manipulative experiments in natural ecosystems. We explicitly evaluated the individual and combined effects of N addition, warming, and increased rainfall on plant diversity and its relationship with productivity. The effects of decreased rainfall (i.e., drought) were not included in this study because the available data meeting our extracting criteria were not enough to conduct a meta-analysis. The main objectives were to assess: (1) what are the global patterns of the response of plant diversity (species richness,  $H'$ , and evenness) to the individual and combined effects of N addition, warming, and increased rainfall; (2) are these effects influenced by moderator variables such as climate, geography, experimental duration, and treatment magnitude; and (3) how do the individual and combined effects of these global change drivers influence the plant diversity-productivity relationships.

## **Materials and methods**

### **Data collection and compiling**

To locate relevant studies for our meta-analyses, we searched for peer-reviewed journal articles and academic dissertations published before 30 August 2018 that evaluated the individual and/or combined effects of N addition, warming, and increased rainfall on plant species richness,  $H'$ , and/or evenness using *ISI Web of Knowledge*, *Google Scholar*, *China Knowledge Resource Integrated Database*, and the reference lists in primary studies and in review papers. The search terms were “(nitrogen addition OR nitrogen enrichment OR nitrogen deposition OR nitrogen loading OR nitrogen fertilization OR nitrogen input OR nitrogen application OR warming OR increase temperature OR temperature rising OR precipitation OR rainfall OR water) AND (species richness OR biodiversity OR diversity)”. To be included in our meta-analysis, studies had to satisfy the following criteria: (1) experiments were conducted in field and at least one of the considered global change drivers was assessed; (2) the treatment and

control plots were conducted within the same ecosystem; (3) measurements of the variables in the treatment and control plots were carried out at the same spatiotemporal scales and both magnitude of the considered global change driver and experimental duration were clearly reported; (4) the experimental duration was no less than one growing season; (5) the means, standard deviations and sample sizes of the tested variables were directly reported or could be calculated from the related publications; (6) studies were conducted in terrestrial ecosystems; and (7) studies using different treatment magnitude in different experimental periods were excluded. After extraction, a total of 133 articles, representing 2450 observations, satisfied the above criteria and were included in our analyses (Fig. 1, Table S1).

Many studies reported more than one treatment (e.g., different global change drivers and different magnitudes or types of a specific driver) and some studies reported the results of the same experiment conducted in different ecosystem types or experimental conditions. In such cases, all comparisons were treated as separate effect sizes because they represented different measurements of global change effects on plant diversity. Original data regarding to species richness,  $H'$ , and/or evenness were extracted directly from the main text, tables, and appendices of the publications. When data were graphically presented in figures, we used the Engauge Digitizer version 10.11 (<http://markummitchell.github.io/engauge-digitizer/>) to obtain numeric data. To assess the influence of moderator variables on the response of plant diversity to global change drivers, we recorded latitude, altitude, mean annual temperature (MAT), mean annual precipitation (MAP), treatment magnitude, experimental duration (yr), and ecosystem type. We extracted the data directly from the articles, except for MAT and MAP, which were obtained from the *WorldClim* database (<http://www.worldclim.org>) for the study sites when not provided in the studies. In addition, to evaluate the effects of global change drivers on plant diversity-productivity relationship, we also recorded

aboveground and belowground biomass where available, but only when the corresponding biodiversity values were also reported. We used aboveground biomass as a proxy of productivity because most of the studies only reported this productivity-related measure. This method is appropriate because the majority of our data were from grasslands where total aboveground biomass is approximately equal to the productivity, and strong positive relationships between biomass and productivity in other ecosystems such as forests were observed in the regions where our study sites were from (Keeling and Phillips 2007, O'Neill and De Angelis 1981).

### Statistical analysis

We used the natural log-response ratio (lnRR) as the effect size metric for both the individual and combined effects of global change drivers on plant biodiversity and biomass. The lnRR for each observation was calculated by Eqn (i):

$$\ln RR = \ln \left( \frac{X_t}{X_c} \right) \quad (i)$$

where  $X_t$  and  $X_c$  are the means of the treated and control groups. We used lnRR because it is a robust effect size metric commonly used in ecological meta-analysis, it is easily interpretable, and its sampling distribution approximates normality (Hedges et al. 1999).

The variance ( $v$ ) associated with each lnRR was calculated by Eqn (ii),

$$v = \frac{s_t^2}{n_t X_t^2} + \frac{s_c^2}{n_c X_c^2} \quad (ii)$$

where  $X_t$  and  $X_c$  are means of a response variable,  $n_t$  and  $n_c$  are the sample size, and  $s_t$  and  $s_c$  are the standard deviations in the treatment (t) and control (c) groups, respectively.

To conduct our meta-analyses, we calculated all possible pairwise effect sizes within an experiment; for example, if a N addition study contained five addition amounts and sampled once each year during a four-year experimental duration, there are



twenty possible comparisons and we thus calculated twenty effect sizes. However, because such effect sizes are based on the same treatment data, this method leads to covariance (Olkin and Gleser 2009). To address such issues of non-independence, we used the Bayesian method of multilevel meta-analyses (MLMAs) with random factors (Nakagawa and Poulin 2012). We implemented MLMAs as linear mixed models using the *MCMCglmm* function in the R package *MCMCglmm* (Hadfield 2010). For each global change driver and each tested response variable (i.e., species richness,  $H'$ , evenness, and biomass), we initially ran intercept-only models to calculate the overall effect sizes ( $\ln RR_{++}$ ). These intercept-only models fitted  $\ln RR$  as the response variable and included a random factor for study ID, a random slope for sampling time within study, and a variance-covariance matrix where the diagonal elements contain sampling variances and the off-diagonal elements contain any covariance arising due to effect sizes being contrasted with the same treatment groups (Lajeunesse 2011). Multi-level meta-regression models (MLMRs), which included fixed effects, were then run to explore the effects of treatment magnitude, ecosystem type (i.e., grassland, forest, tundra, wetland, desert, and shrubland), N addition form (i.e., N, N with phosphorus, N with potassium, and N with both phosphorus and potassium), and warming facility (i.e., heater and open top chamber) on  $\ln RR_{++}$  by fitting these variables as continuous or categorical fixed factors. MLMRs were also fitted without intercept to yield overall effects within each subgroup. All models were run for 5 million iterations, with a thinning interval of 1000, which resulted in 1000 samples from the posterior distributions for each model parameter estimated. An inverse Wishart prior was specified for all random effects and residuals in our analysis, which was specified in *MCMCglmm* function as  $V = 1$ ,  $nu = 1$ , where  $V$  is an estimate of variance and  $nu$  is a parameter for the degree of belief in  $V$  in an inverse Wishart distribution (Hadfield 2010). To assess the convergence of all MLMAs and meta-regressions, we visually

checked trace plots of MCMC chains. We also carried out Gelman-Rubin diagnostic tests based on four independent runs in the R package *coda* (Plummer et al. 2006), and confirmed that all models had potential scale reduction factor (PSRF) < 1.1, indicating convergence (Gelman and Rubin 1992). The overall effect sizes were back-transformed using the equation  $(e^{\ln RR_{++}} - 1) \times 100\%$  to aid interpretation.

To further examine whether the combined effects are additive or not, we performed paired meta-analyses following previous studies (Dieleman et al. 2012, Yuan and Chen 2015) by comparing the effect size (lnRR) of the combined effects with the sum of those of the corresponding individual effects using linear regression analysis. Individual observations situated above and below the 1:1 line were interpreted as synergistic and antagonistic, respectively, and as additive when on the 1:1 line (Dieleman et al. 2012). Owing to the limited data for three treatment combinations, only two-way interactions were considered in this study. To assess the effects of continuous moderator variables across all individual lnRRs, we used structural equation modeling (SEM) (Grace 2006). Based on ecological knowledge, we hypothesized a set of relationships in a path diagram (Fig. 2a), which simultaneously account for the effects of latitude, altitude, MAT, MAP, treatment magnitude, and experimental duration. The proposed *a priori* model predicted a direct effect of MAT, MAP, experimental duration, and treatment magnitude on the effect size of global change (i.e., lnRR), and both direct and indirect effects of latitude and altitude on lnRR. To assess the relationship between plant diversity and biomass under N addition, linear regression analyses were used. However, as the regression analysis did not suggest any causal relationship between diversity and biomass under N addition treatment, we thus conducted SEMs (Fig. 2b) to quantify the magnitude of direct and indirect effects of N addition on plant biomass or diversity under different experimental durations, in line with previous studies (Adler et al. 2011, Isbell et al. 2013). Global change drivers were coded as a binary variable to indicate the

control (0) and treatment (1) level, while diversity and biomass were represented by the raw data extracted from publications, but ln-transformed to meet linear model assumptions. However, because of limited data for warming, increased rainfall, and the interactions of all three drivers, we only assessed the diversity-productivity relationship under N addition treatment. We examined the distributions of the endogenous variables and tested their normality. The results of the SEM analysis were retained only when a good model fit was obtained. The overall goodness-of-fit of each model was tested against the dataset and checked following a previous study (Schermerle-Engel et al. 2003). Because the traditional  $\chi^2$  goodness-of-fit test is sensitive to sample size, we also used the root mean square error of approximation (RMSEA) index (Grace 2006). The SEM analyses were performed with AMOS software version 24.0 (IBM SPSS Amos, SPSS Inc., Chicago, IL, USA). We used a bootstrapping method for resampling based on 5000 iterations when the number of observations was  $< 100$  (Grace 2006). For moderator variables, where the number of observations was not enough to get a good model fit for a SEM analysis (generally  $< 30$ ), we used Pearson correlation analysis to assess the relationship between lnRR and each moderator variable, which allowed us to interpret whether the assessed moderator variables are linked with the effect sizes of global change drivers on plant diversity.

### **Publication bias**

Publication bias can arise when studies in the published literature are a non-random subset of the total number of studies performed (e.g., studies of large effect are more likely to be published). We searched for publication bias in our meta-analyses using Egger's regression tests along with funnel plots (Egger et al. 1997) and trim-and-fill tests (Duval and Tweedie 2000). However, as our multilevel data may not be amenable to these methods in their original forms, we applied both Egger's regression and trim-and-

fill tests using the meta-analytic residuals (Nakagawa and Santos 2012). The meta-analytic residuals consist of sampling errors as well as the effect-size-level effects that are equivalent to normal residuals. The trim-and-fill tests were conducted using the  $R_0$  estimator implemented with the trimfill function in the R package *metafor* (Viechtbauer 2010).

## Results

### Individual and combined effects

Across all observations, N addition significantly reduced species richness,  $H'$ , and evenness by an average of 11.5%, 8.4%, and 4.4%, respectively (Fig. 3a), with an average estimate of 0.1%, 0.1%, and < 0.1% decrease in response to an addition of 1 kg N/yr/ha (Fig. S1), respectively. At the same time, N addition significantly increased plant aboveground biomass by 31.8%, but had no significant effect on belowground biomass. Warming was estimated to reduce measures of plant diversity (by around 5%), although its effects were non-significant. Both warming and increased rainfall significantly increased the aboveground biomass of plants by 12.0% and 19.5%, respectively (Fig. 3a). Similar to the individual effects of N addition, the combined effects of N addition + warming and N addition + increased rainfall both significantly reduced species richness,  $H'$ , and evenness, while warming + increased rainfall had no significant effects on either plant diversity or aboveground biomass (Fig. 3b). The interaction of N addition  $\times$  warming and N addition  $\times$  increased rainfall were found to be additive and synergistic, respectively, but warming  $\times$  increased rainfall was more likely to be additive (Fig. 4). Even though, there was likely a tendency towards synergistic interactions at low levels of effects (i.e., low lnRR value) but additive or even antagonistic interactions at high levels (Fig.4).

### **Influences of moderator variables on effect sizes**

The effects of N addition were more generally affected by moderator variables than those of warming and increased rainfall, although all were subject to influences by moderator variables (Fig. 5). Among the various positive and negative moderator effects, increasing MAT generally reduced effects of N addition, but increased effects of warming. In contrast, MAP showed significantly positive impact on the effect size of N addition, but negative influences on the effects of warming and increased rainfall. Experimental duration significantly reduced the effect of N addition, but increased that of increased rainfall. When considering the effect by ecosystem type, significant effect sizes of N addition on species richness were restricted to grassland, while those for aboveground biomass were significant in grassland and tundra (Fig. S3). The forms of added N may also alter the effects, with N + phosphorous and N + phosphorous + potassium having negative effects on species richness, and positive effects on above ground biomass. N alone had significant effects on  $H'$  and aboveground biomass (Fig. S4a). We did not observe any statistical differences among warming facilities on plant diversity (Fig. S4b).

Similarly, the combined effects were also associated with moderator variables. The effect size of N addition + warming on species richness was negatively correlated with latitude and experimental duration, but was positively correlated with MAT (Table 1). The effect sizes of N addition + warming on  $H'$  and evenness were both positively correlated with altitude. The effect size of N addition + increased rainfall on species richness was negatively associated with MAP, while the effect size of which on evenness was positively correlated with MAT and MAP, but negatively correlated with experimental duration (Table 1). Furthermore, increases in MAT and MAP were associated with decreases in effect size of warming + increased rainfall on species

richness. Effect sizes for warming + increased rainfall on  $H'$  and evenness were not correlated with moderator variables (Table 1).

### **Biodiversity-biomass relationship as affected by global change drivers**

The positive effects of N addition on plant aboveground biomass increased as experimental duration increased (Fig. 6a). Likewise, the negative effects of N addition on species richness or  $H'$  also became more profound with longer experimental duration (Fig. 6b). Fitting the effect size for plant diversity (i.e., species richness or  $H'$ ) as a predictor of aboveground biomass in response to N addition (i.e., aboveground biomass ratio of the treated and control group), we found a significant negative relationship (Fig. 6c). These results indicated that as aboveground biomass increases in response to long-term N addition, there is a simultaneous decline in plant diversity. This inference was further supported by the results from our SEM analysis (Fig. 7), suggesting that the indirect effects of N on plant diversity through biomass increased with a longer duration of experiment and biomass showed higher negative effects on plant diversity in the later stages. When assessing the effects of plant diversity on aboveground biomass under N addition, a similar trend was found. However, such relationships were not detected between lnRR for biomass and plant diversity in response to warming (Fig. S5), increased rainfall (Fig. S6), and the combined effects (Fig. S7-S9), except for  $H'$  in response to N addition + increased rainfall (Fig. S8d).

### **Publication bias**

We found little evidence for publication bias in our meta-analyses. The Egger's regression tests on the meta-analytic residuals suggested no evidence for funnel asymmetry for all the response variables (Table S3). However, the trim-and-fill tests indicated that some data points were potentially missing for all response variables

except  $H'$  (Fig. S10). Nevertheless, the meta-analytic means incorporating the missing data that were added by the trim-and-fill tests indicated that the overestimated amount of the meta-analytic means is negligible (Table S3). Taken together, we conclude that our results are robust against publication bias.

## **Discussion**

### **Individual and combined effects differently affect plant diversity**

Here, we present an assessment of the effects of three common global change drivers on plant diversity and its relationship with biomass. When evaluating the individual effect of N addition on plant diversity, our study indicated that N addition generally reduced plant diversity across terrestrial ecosystem types, which is in line with previous meta-analyses (Hillebrand et al. 2007, Humbert et al. 2016). Previous studies have shown that N addition is an important driver of changes in species composition across a broad range of ecosystem types by altering the competitive interactions that affect composition and/or making conditions unfavorable for some species (Bobbink et al. 2010, de Schrijver et al. 2011). This mechanism is supported by a recent study that showed N addition reduces niche dimensionality and diversity while increasing productivity and compositional turnover (Harpole et al. 2016). Compared with previous meta-analyses, our results demonstrate a negative pattern of N addition on plant diversity for a broader geographic extent by using a dataset that represents geographical regions including Europe, North America, and Asia (Fig. 1), further indicating the general nature of this effect.

We did not detect significant effects of either warming or increased rainfall on plant diversity, although both significantly stimulated plant aboveground biomass (Fig. 3a). For warming we estimated a non-significant tendency for negative effect of around 5%, in somewhat contrasts to another recent meta-analysis, which found warming to

decrease terrestrial species richness by an average of 12% (Gruner et al. 2017). This inconsistency may be attributed to the different methods that were used to estimate warming effect on plant diversity. Among other things, in the previous study, the authors used unweighted meta-analysis and included both artificial microcosm studies and field studies (Gruner *et al.* 2017). Although the use of an unweighted meta-analysis will not necessarily bias estimates (Nakagawa and Lagisz 2016), artificial microcosm experiments included in their analyses may detect larger effects of warming than field studies. The positive effect of warming on plant biomass accumulation is also in agreement with findings from previous meta-analyses (Lin et al. 2010, Lu et al. 2013). This positive effect has mainly been attributed to changes in soil N availability and plant phenology in response to warming that stimulates plant net primary productivity (Luo et al. 2009, Vitousek and Howarth 1991).

Changes in the amount of precipitation associated with other global change drivers have been found to have particularly large impacts on the structure and function of ecosystems (Huxman et al. 2004, Suttle et al. 2007). In these cases, the effects of increased rainfall on plants were mainly mediated through soil moisture. However, our results suggest no effect of increased rainfall on plant diversity, but only on aboveground biomass. The non-significant effect of increased rainfall on plant diversity may be attributed to the fact that different species have differential responses to increased rainfall (Zavaleta et al. 2003), resulting in an overall non-significant response within or across ecosystems. In addition, shifts in natural precipitation that often increased drought could also influence the effects of increased rainfall treatment, resulting in a non-significant effect. However, we cannot address any such drought effect in our study because of the lack of enough data to conduct a meta-analysis. Even though, for most of the individual studies included in our database, the within study temporal shifts were generally much smaller than the experimental treatments because



of the short experimental duration, indicating that this issue may not be a problem for our study.

Despite the non-significant effects of warming and increased rainfall, when combined with N addition, N addition + warming and N addition + increased rainfall both showed strong negative effects on plant diversity (Fig. 3b), albeit these interactions were different in being additive and synergistic, respectively (Fig. 4). The negative effects of N addition + increased rainfall on plant diversity may be mainly attributed to the reduced niche dimensionality by stimulating dominance of small sets of competitive species (Harpole et al. 2007). Likewise, the negative effects of N addition in combination with warming is supported by previous work (Zavaleta et al. 2003), also supporting that the combined effects of N addition and warming on plant diversity are generally additive. In contrast, the interaction of N addition  $\times$  increased rainfall on plant diversity was synergistic, i.e., with a larger combined effect than the sum of the individual effects (Fig. 4). This may reflect that the positive effects of N addition on plant biomass productivity increases the demand of water (Yan et al. 2014), so that additional water input would allow the full positive effects of N addition to be expressed. The warming + increased rainfall treatment did not have a significant effect on plant diversity and the interaction was additive, as has a previous studies (Zavaleta et al. 2003). Nevertheless, we note that small sample size may have limited the statistical power to detect a significant effect (Loladze 2014), and more factorial designed field experiments are needed to better evaluate the combined effects of multiple global change drivers on plant diversity at the global scale.

### **Influences of moderator variables on individual and combined effects**

Both the individual and combined effects of the considered global change drivers on plant diversity were strongly influenced by several moderator variables. For species

richness or  $H'$ , the effect of N addition was generally negatively correlated with MAT (Fig. 4a). This association indicates that N addition has weaker effects on species diversity in colder regions than in warmer regions, pointing to temperature constraints on biomass production (Cross et al. 2015). In contrast, the individual effect of warming and the combined effect of N addition + warming on plant diversity generally showed an opposite trend, with positive correlations with MAT, suggesting a stronger effect of warming on plant diversity in warmer regions. N addition had more pronounced effects on plant diversity in wetter than in drier regions, as MAP generally showed positive effects on the effect sizes of N addition on plant diversity (Fig. 4a). This may be attributed to the fact that sufficient water supply would help the effects of N addition to be well expressed (Yue et al. 2017). However, MAP was negatively correlated with the effect sizes of warming, increased rainfall, N addition + increased rainfall, and warming + increased rainfall on plant diversity, indicating stronger effects of these drivers on plant diversity in drier conditions.

Our results also showed that increased magnitude of added N and longer experimental duration were both associated to a stronger negative effect of N addition on species richness,  $H'$ , and evenness. Therefore, low doses of N added for long periods may lead to similar diversity loss as high doses of N applied for short periods. Previous studies have recurrently presumed cumulative effects of N addition on plant diversity, but was seldom tested in experimental studies (Bobbink et al. 2010, Clark and Tilman 2008). A previous meta-analysis found that declines in species richness with cumulative N addition follow a negative exponential pathway, with species loss occurring faster at low levels of cumulative N addition or at the beginning of the addition, which was followed by an increasingly slower species loss at higher cumulative N addition (de Schrijver et al. 2011). As plant species compete for the same set of limiting resources, addition of a limiting resource can eliminate potential trade-offs, reducing the number

of species that can coexist (Tilman 1982). Therefore, because N limitation is common and thus the addition of extra N may immediately reduce plant diversity by reducing the dimensionality of the belowground limiting factors (Harpole et al. 2016). Such a trend was also observed in a recent meta-analysis for the effects of N addition on plant species richness (Humbert et al. 2016). Concordantly, in our study, using a much larger dataset than the abovementioned studies, our results showed that N addition has similar cumulative effect on  $H'$  and evenness in addition to species richness, indicating a general pattern of N addition effect on plant diversity. In contrast, we saw that as duration of increased rainfall experiments increased, species richness increased. The potential mechanism may be that water availability is not a limiting resource in the observed systems, thus increased rainfall does not reduce the number of limiting resources (DeMalach and Kadmon 2017). It could also be that water is so limiting that additional water input can increase habitat heterogeneity, thereby increasing species richness.

Furthermore, when assessing the individual effects on plant diversity in different ecosystem types, only the effect sizes of N addition on species richness in grassland and on aboveground biomass in grassland and tundra were significant, indicating that ecosystem type may be an important moderator of global change effects on plant diversity. We note that non-significant effects in ecosystem types may also be attributed to relatively small sample sizes. More studies are required in these other ecosystem types before robust conclusions can be drawn. Likewise, N addition form can have significant impact on plant diversity to N addition (Fig. 6). As discussed above, N addition can negatively affect species richness by reducing the number of available limiting resources, diminishing trade-off opportunities that allow species coexistence (Harpole et al. 2011). Thus, the non-significant effect of N addition alone became significant when phosphorus or phosphorus and potassium were jointly added, which is

in line with the concept of nutrient co-limitation (Harpole et al. 2016, Ren et al. 2010). However,  $H'$  showed an opposite to N addition form, with the effects of N addition alone having a significant negative effect on  $H'$ .

### **Changes in biodiversity-biomass relationship as affected by global change drivers**

Our results suggested that both the negative effects of N addition on species richness and  $H'$  were negatively correlated with N-induced increase in plant aboveground biomass (Fig. 5), indicating that the greater the increase in biomass as stimulated by N addition, the greater the decline in plant diversity, and *vice versa* (Fig. 7). A previous study found that changes in plant productivity play a crucial role in regulating the response of plant diversity to N addition (Clark et al. 2007). It is generally acknowledged that a positive biodiversity-productivity relationship is common across ecosystems (Duffy et al. 2017, Liang et al. 2016). A recent meta-analysis suggested that the positive effects of plant diversity on grassland productivity are robust to nutrient enrichment (Craven et al. 2016). However, it did not address the effects of variation in treatment duration. If there is a divergent response of plant diversity and biomass to short- or long-term N addition, any positive relationship between plant diversity and biomass in early N addition period could be tempered, or even be reversed, with a longer term of N addition. This mechanism was supported by our results, as we found that the responses of plant biomass and diversity to N addition change with increased experimental duration, with species richness and  $H'$  having increasingly negative effects on biomass with longer duration of the N addition treatment, and *vice versa* (Fig. 7). Even though, it is noteworthy that because our data were not from a full factorial design with all treatments, we cannot clearly disentangle the effects of N addition on productivity from the effects of diversity on productivity.

On the other hand, the changed biodiversity-productivity relationship under N addition treatment may also be a kind of disequilibrium response, as time lags and transient effects have been found to be evident in the responses of plant communities and ecosystems to global change (Svenning and Sandel 2013). As discussed above, N addition can lead to increase in dominance and biomass of a few species, but reduces niche dimensionality and diversity at the same time. However, the positive relationship between diversity and productivity could potentially reestablish after a longer term (e.g., >10 yr) if other species adapted to high N concentrations immigrate to the community (Svenning and Sandel 2013). Nevertheless, we lack such data from long-term studies to assess the potential of such disequilibrium response. Furthermore, although the positive relationship between plant diversity and productivity can be reduced under N addition, it does not necessarily mean that diversity would no longer be important given that the reduced plant diversity might result in a decreased stability (McCann 2000). Thus, more studies are needed to better understand how the reduced plant diversity under N addition can affect ecosystem stability. In contrast to N addition, similar changes in the biodiversity-biomass relationship were not observed under warming, increased rainfall, and their combined effects, although again the limited sample sizes of these analyses limit the strength of conclusions drawn (Loladze 2014). In addition, although the sample sizes for our analyses were much larger compared with previous meta-analyses, our analyses generally failed to cover regions other than North America, Europe, and Asia, particularly for pairs addressing combined effects. Hence, further well-designed full-factorial experiments assessing the individual and combined effects of global change drivers on plant diversity and the diversity-productivity relationship are needed at the global scale, especially in Africa, Oceania, and South America, to generate a better global-scale perspective.

### **Summary and concluding remarks**

The key findings from our meta-analyses are as follows: (1) N addition increases aboveground biomass, but decreases plant diversity; in contrast, warming and increased rainfall also increased aboveground biomass, but had no effect on diversity; (2) the combined effects of N addition + warming and N addition + increased rainfall also had negative effects on plant diversity, with additive and synergistic interactions, respectively, while warming + increased rainfall did not influence plant diversity; (3) the effects of the three drivers on plant diversity are modulated by moderator variables such as climate, latitude, experimental duration, and treatment magnitude; and (4) the greater the increase in plant biomass with N addition, the greater the decline in plant diversity, and *vice versa*. Overall, these results highlight the importance of assessing the combined effects of concurrent global change drivers rather than studying them separately, as they interact in varying ways. Our results indicate that while it is common to observe positive relationships between plant diversity and productivity under natural conditions, these associations may be reduced and even reversed under long-term N deposition, as N deposition consistently increased biomass, while decreasing diversity. We expect that these results will help the development of improved predictive models of plant diversity dynamics in response to multi-factorial global change.

### **Conflict of Interest**

The authors declared no conflict of interest.

### **Data accessibility**

All the raw data used in the meta-analysis are included in the Supporting Information, and will also be deposited in figshare (<https://figshare.com>) should the manuscript be accepted.

## Authorship

K.Y. and J.-C.S. conceived the study. K.Y. and Y.P. collected data from the literature. K.Y., S.J., K.V.M. and A.M.S. performed the statistical analyses. K.Y. wrote the first draft of the paper and all authors contributed to revisions.

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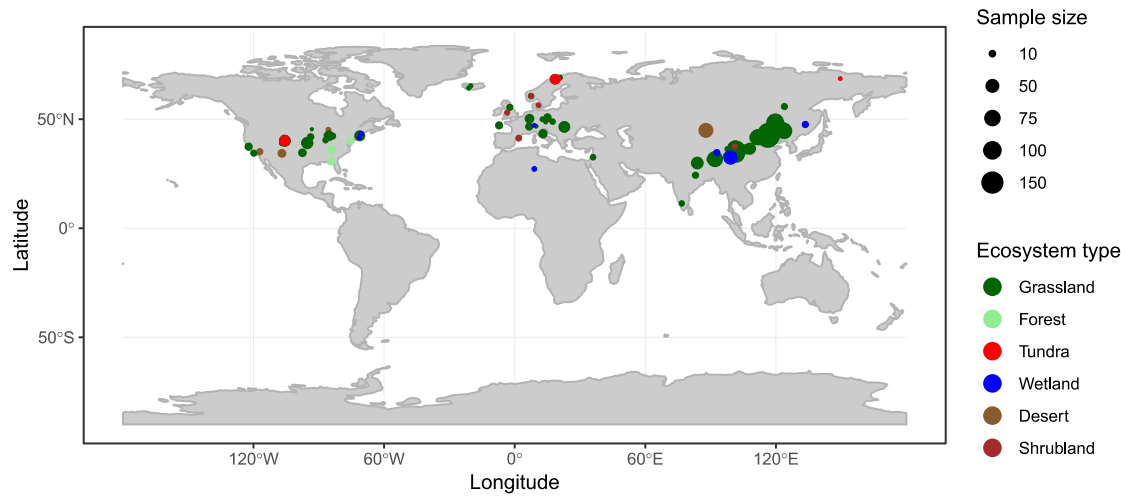
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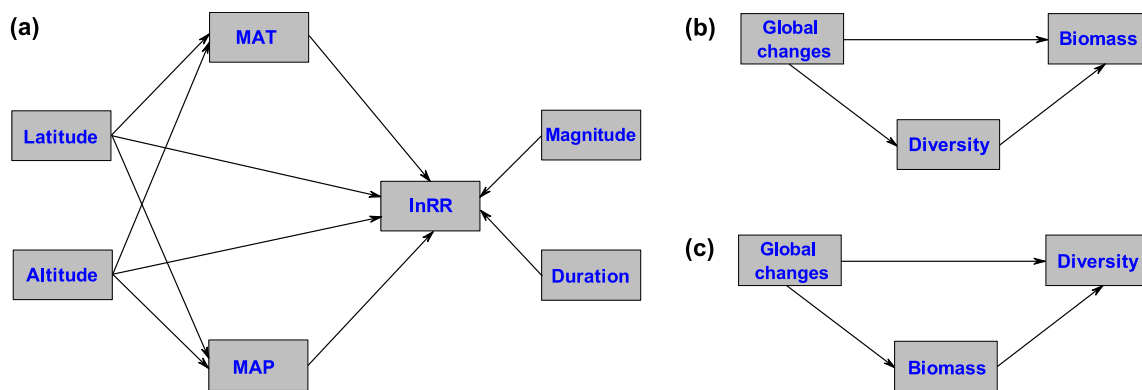
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## Figures Legends

**Fig. 1** Map showing the location of the study sites from the 133 articles reporting field manipulative studies used in the meta-analysis. The number of observations (i.e., pairwise-comparisons) from each site is represented by symbol size, and ecosystem type is indicated by color. Grassland includes all types of grasslands such as temperate grasslands, alpine meadow, and prairies; forest represents forests in temperate regions; and wetland includes fens, marshes, and peatlands; shrubland includes shrublands and heathlands.

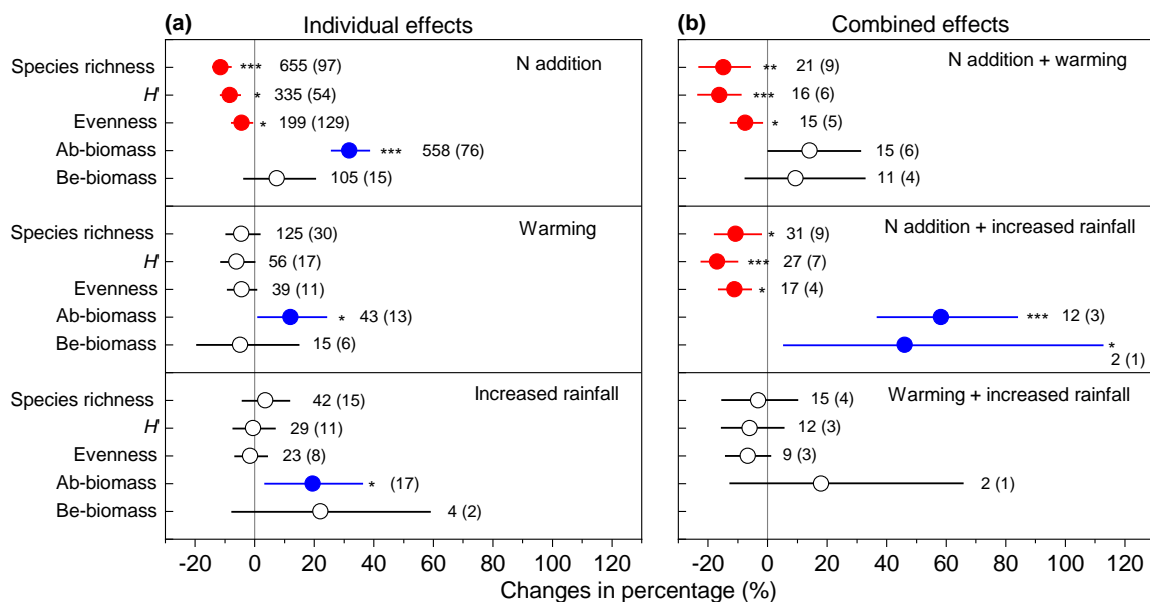


**Fig. 2** Structure of the generalized *a priori* conceptual structural equation models (SEM) depicting (a) the influence of moderator variables (i.e., latitude, altitude, mean annual temperature (MAT), mean annual precipitation (MAP), global change magnitude, and experimental duration) upon the effect sizes of natural log-response ratios (LnRR) of global change drivers (i.e., nitrogen (N) addition, warming, and increased rainfall) on plant species richness, Shannon-Wiener index, and evenness, and (b and c) the impact of nitrogen (N) addition on plant diversity and aboveground biomass. The single-headed arrows represent a hypothesized directional impact of one variable on another.

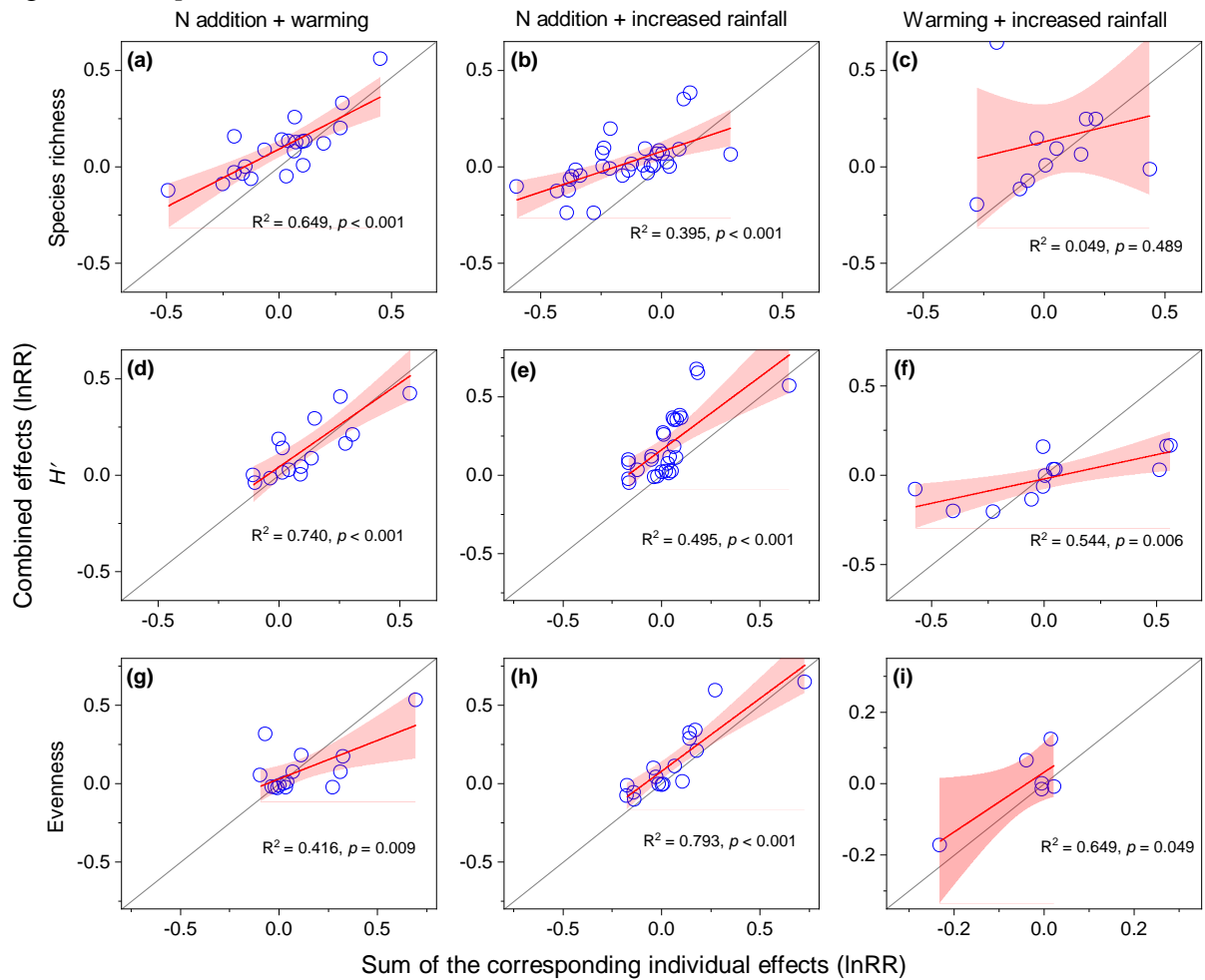




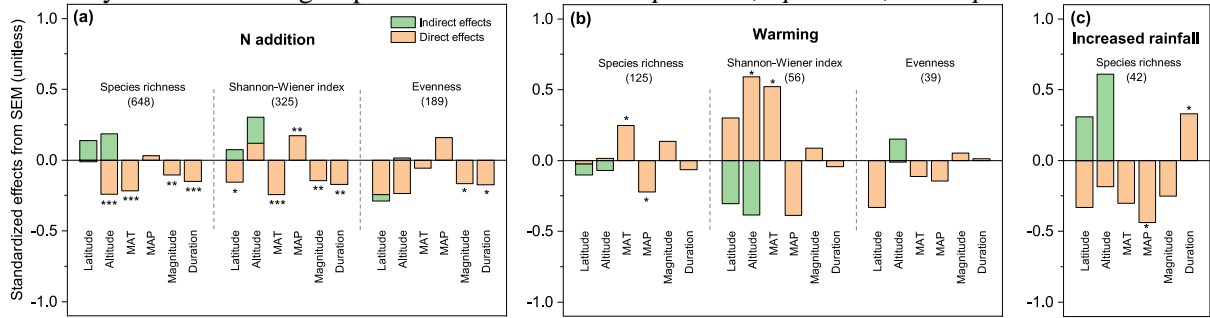
**Fig. 3** The individual (a) and combined (b) effects of nitrogen (N) addition, warming, and increased rainfall on plant species richness, Shannon-Wiener index ( $H'$ ), evenness, aboveground biomass (ab-biomass), and belowground biomass (be-biomass). Results are expressed as the percentage changes in treatment groups relative to the control groups (%), and estimates indicate the means with 95% credible intervals (CIs). The numbers of effect sizes and the articles that each estimate is based on are shown beside and in brackets, respectively. Estimates with a 95% CI that does include zero are statistically significant, with positive and negative effects shown in blue and red, respectively. \* $p_{\text{MCMC}} < 0.05$ , \*\* $p_{\text{MCMC}} < 0.01$ , and \*\*\* $p_{\text{MCMC}} < 0.001$ .



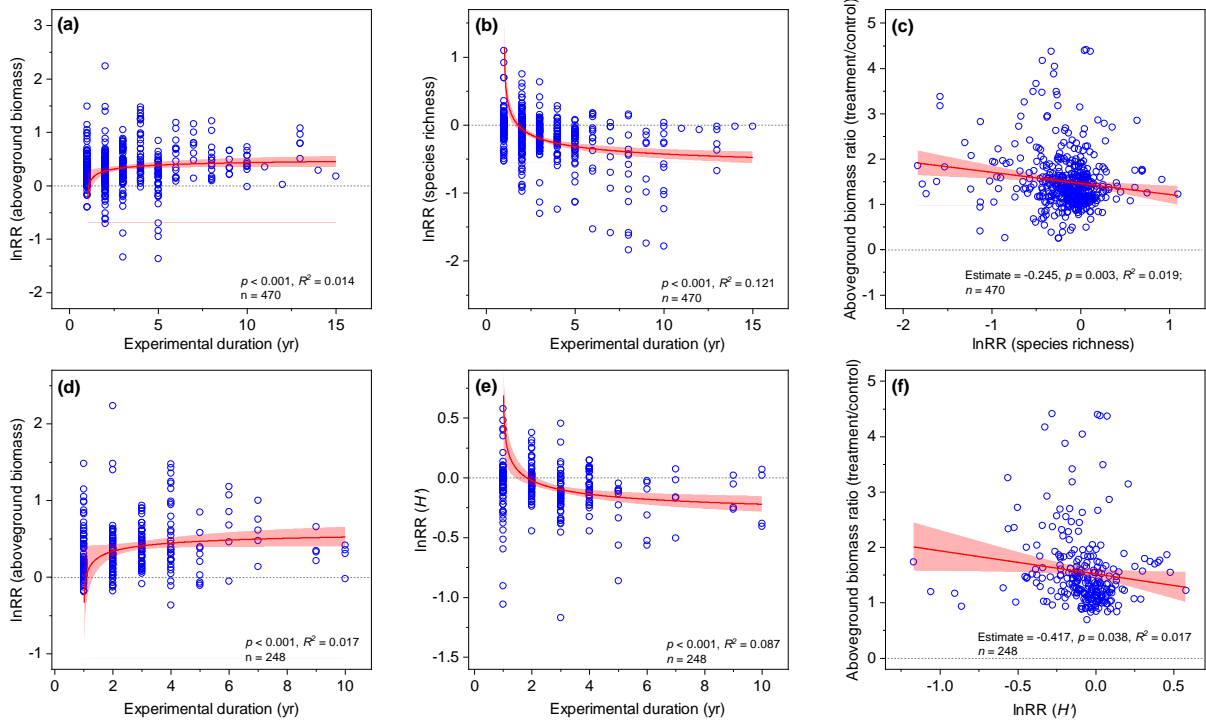
**Fig. 4** Paired meta-analyses assessing the relations of combined effects against the sum of corresponding individual effects of nitrogen (N) addition, warming, and increased rainfall. Data are reported as natural log-response ratio (lnRR), and only studies reporting individual and combined effects simultaneously are included in a given regression. Linear regression lines are shown in red, 95% confidence intervals are shown within the shaded red section, and the  $p$ -values and  $R^2$  for linear regressions are given. The 1:1 lines are shown in gray, and regression are considered to be statistically significant at  $p < 0.05$ .



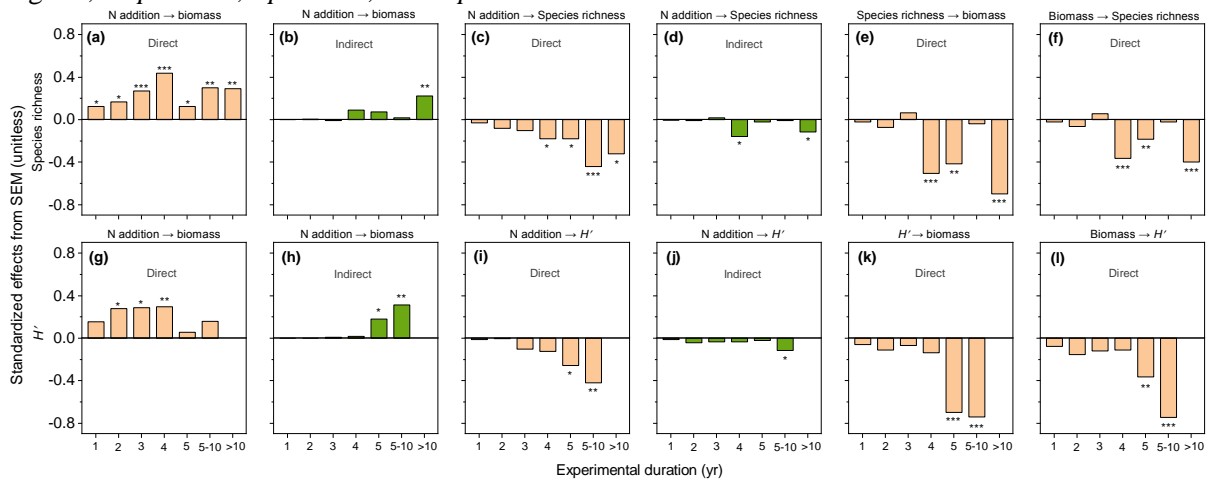
**Fig. 5** The standardized direct and indirect effects derived from the structural equation models (SEMs) for N addition (a), warming (b), and increased rainfall (c) on the effect size (lnRR) of plant species richness, Shannon-Wiener index ( $H'$ ), and evenness. These effects describe the influence of the variables depicted in the x axis on lnRR of each global change driver on species richness, diversity, and evenness. Due to the lack of sufficient data of  $H'$  and evenness for increased rainfall to conduct SEM, only results of species richness for increased rainfall are shown. See Table S2 in *Supporting Information* for results of the goodness-of-fit test for each SEM. Asterisks indicate statistically significant direct effects, and number of data points used in the analysis within each group are shown in brackets. \*  $p < 0.05$ , \*\*  $p < 0.01$ , and \*\*\*  $p < 0.001$ .



**Fig. 6** The natural log response ratio (lnRR) of N addition on aboveground biomass, species richness and Shannon-Wiener index ( $H'$ ) as a function of experimental duration and the relationships between aboveground biomass ratio (i.e., treatment/control) and lnRR of N addition on species richness and  $H'$  across all data points. Fitted regressions (red line), the corresponding 95% credible intervals (shaded), slope estimates, and number of data points ( $n$ ) are shown. Observations were included only when data for both diversity and biomass were provided in each sampling event.



**Fig. 7** The standardized direct effects of N addition on plant aboveground biomass, species richness, and Shannon-Wiener index ( $H'$ ), indirect effects of N addition on aboveground biomass through diversity (i.e., species richness or  $H'$ ) or on diversity through aboveground biomass, direct effects of diversity on aboveground biomass, and direct effects of aboveground biomass on diversity that were generated from the structural equation models as described in Fig. 2b, c. \*  $p < 0.05$ , \*\*  $p < 0.01$ , and \*\*\*  $p < 0.001$ .



## Table Legend

**Table 1** Pearson correlation coefficients ( $r$ ) between the effect sizes of natural log-response ratios (lnRR) of global changes on plant diversity index and moderator variables.

Global change driver	Diversity index	$n$	Latitude	Altitude	MAT	MAP	Magnitude	Duration
Increased rainfall	$H'$	29	<b>-0.607**</b>	<b>0.407*</b>	<b>-0.384*</b>	-0.225	0.027	0.061
	Evenness	23	-0.093	-0.044	0.197	-0.049	-0.128	0.046
N addition + warming	Species richness	21	<b>-0.538*</b>	-0.102	<b>0.589**</b>	0.060	-	<b>-0.461*</b>
	$H'$	16	-0.457	<b>0.606*</b>	0.216	-0.446	-	-0.115
N addition + increased rainfall	Evenness	15	-0.051	<b>0.727**</b>	-0.213	-0.274	-	0.316
	Species richness	31	0.159	-0.046	-0.118	<b>-0.468**</b>	-	0.149
	$H'$	27	-0.337	0.288	0.078	0.017	-	-0.365
Warming + increased rainfall	Evenness	17	-0.329	0.089	<b>0.495*</b>	<b>0.642***</b>	-	<b>-0.501*</b>
	Species richness	15	-0.098	0.290	<b>-0.592*</b>	<b>-0.636*</b>	-	0.270
	$H'$	9	0.090	-0.058	0.203	-0.447	-	-0.327
	Evenness	12	0.144	-0.114	0.076	-0.018	-	-0.340

Correlation analysis was conducted only when the number of data points were not enough to generate a good model fit for structural equation

model analyses, but were also  $> 8$ . Data in bold and asterisks indicate significant correlations (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). Magnitude

was only assessed for individual effects.  $n$ : number of data points; MAT: mean annual temperature; MAP: mean annual precipitation;

Magnitude: treatment magnitude; Duration: experimental duration;  $H'$ : Shannon-Wiener index.