Scaling up biodiversity–ecosystem function relationships across space and over time

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Abstract. Understanding how to scale up effects of biological diversity on ecosystem functioning and services remains challenging. There is a general consensus that biodiversity loss alters ecosystem processes underpinning the goods and services upon which humanity depends. Yet most of that consensus stems from experiments performed at small spatial scales for short time frames, which limits transferability of conclusions to longer-term, landscape-scale conservation policies and management. Here we develop quantitative scaling relationships linking 374 experiments that tested plant diversity effects on biomass production across a range of scales. We show that biodiversity effects increase by factors of 1.68 and 1.10 for each 10-fold increase in experiment temporal and spatial scales, respectively. Contrary to prior studies, our analyses suggest that the time scale of experiments, rather than their spatial scale, is the primary source of variation in biodiversity effects. But consistent with earlier research, our analyses reveal that complementarity effects, rather than selection effects, drive the positive space–time interactions for plant diversity effects. Importantly, we also demonstrate complex space–time interactions and nonlinear responses that emphasize how simple extrapolations from small-scale experiments are likely to underestimate biodiversity effects in real-world ecosystems. Quantitative scaling relationships from this research are a crucial step towards bridging controlled experiments that identify biological mechanisms across a range of scales. Predictions from scaling relationships like these could then be compared with observations for fine-tuning the relationships and ultimately improving their capacities to predict consequences of biodiversity loss for ecosystem functioning and services over longer time frames across real-world landscapes.

Key words: BEF; ecosystem production; ecosystem service; landscape management; plant diversity; productivity; scaling function; spatial scale; temporal scale.

INTRODUCTION

We are living in an era that many are calling the "Anthropocene"—a period in which humans and their activities dominate almost all ecosystems on the planet (Crutzen 2002, Ellis et al. 2010). One of the most prominent consequences of anthropogenic environmental change in the Anthropocene is changing biodiversity both on land and in water (Barnosky et al. 2011, Pimm et al. 2014, Ceballos et al. 2015, Elahi et al. 2015). There is a growing recognition that local biodiversity is increasing in some locations because of, for example, human-driven disturbance or exotic species (Sax et al. 2002, Devictor and Robert 2009, Vellend et al. 2013). However, recent studies suggest that declines in local biodiversity are common, averaging up to 14% of species lost

at terrestrial sites, with losses >75% in the worst-affected habitats (Newbold et al. 2015). Declines in local biodiversity have raised substantial concerns about consequences for ecosystem functioning and services such as food, clean water, disease control, and climate regulation, all of which underpin human well-being (Balvanera et al. 2006, Cardinale et al. 2012, Bennett et al. 2015). Yet accurately predicting effects of biodiversity change remains challenging, because there is a mismatch between large scales at which species are lost and ecosystem services are provided, and small scales where most knowledge on the functional consequences of species loss is derived (Isbell et al. 2018). Such understanding is, nonetheless, crucial for the ongoing management and policy initiatives, including the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) for assessing regional and global changes in biodiversity and ecosystem services (Larigauderie and Mooney 2010), and the United Nations Sustainable Development Goals for halting biodiversity loss (Griggs et al. 2013).

Over the past two decades, remarkable theoretical and empirical advances have been made towards understanding ecological and societal consequences of biodiversity change (Loreau et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Tilman et al. 2014, Isbell et al. 2017). Ecological theories and mathematical models predict that biodiversity should increase the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose, and recycle nutrients (Tilman et al. 1997, Loreau 2010). Possible mechanisms include (1) *niche complementarity*—coexisting species differ in their use of biologically limiting resources in space and/or time, thus reducing interspecific competition relative to intraspecific competition and leading to greater total exploitation of resources (Tilman 1999); (2) *facilitation*—positive species interactions increase efficiency by which communities utilize resources and/or the total magnitude of resource use (Mulder et al. 2001, Bruno et al. 2003); (3) *sampling* or *selection effects*—more diverse communities have a higher probability that species with particularly effective functional traits will be present and, through competition, dominate the community, thus enhancing ecosystem functions (Huston 1997, Hector et al. 2002); and (4) *intraguild predation*—killing/eating of species occupying the same functional group and sharing similar limiting resources can mediate cascading effects of predator diversity on plant biomass, thus altering resources consumption of primary producers (Finke and Denno 2005).

A proliferation of >600 experiments, along with quantitative syntheses, have collectively confirmed the predictions that biodiversity enhances resource-use efficiency and biomass production of ecological communities; although tests of how biodiversity influences the rate of decomposition and nutrient recycling have been less conclusive (Balvanera et al. 2006, Worm et al. 2006, Srivastava et al. 2009, Quijas et al. 2010, Cardinale et al. 2011, Handa et al. 2014, Boyero et al. 2016). Nevertheless, most of this body of work stems from experiments performed at small spatial scales for short time frames. There has been debate over whether small-scale experiments represent biodiversity–ecosystem function (i.e., BEF) relationships in real-world ecosystems (Srivastava and Vellend 2005, Wardle 2016). As such, numerous empirical studies and syntheses have recently begun to explore how biodiversity affects ecosystem functioning, such as the production of biomass, in larger and more natural systems (Grace et al. 2007, Mora et al. 2011, Paquette and Messier 2011, Gamfeldt et al. 2013, Liang et al. 2016, Duffy et al. 2017, Felipe-Lucia et al. 2018). Of those that statistically controlled for abiotic covariates that can affect biomass production, most have demonstrated that biodiversity effects are common in nature, and qualitatively consistent with findings in small-scale experiments. Nonetheless, these studies have also indicated that, if anything, small experiments have probably underestimated the effects of biodiversity on productivity in natural ecosystems (Duffy et al. 2017).

Hence, although small-scale experiments have been instrumental for identifying biodiversity effects on ecosystem functioning and for confirming mechanisms, results of these experiments have yet been fully used to improve inferences and predictions on the consequences of biodiversity change at landscape scales that are more relevant for policy, conservation, and management.

There are several nonexclusive reasons why biodiversity effects tend to be stronger in nature than in small-scale experiments. In natural systems characterized by larger spatial scales and greater temporal fluctuations, more environmental heterogeneity may increase opportunities for species to exploit a greater variety of niches (Cardinale et al. 2004, Tscharntke et al. 2005, Reich et al. 2012). For example, a recent study by Isbell et al. (2018) showed that net diversity effects were mostly explained by complementarity that tended to increase with spatial scales. Regional processes such as dispersal or disturbance, which control species abundances in nature but are absent from most experiments, can interact with local processes to amplify biodiversity effects (Tscharntke et al. 2005). Whether or not these or other hypotheses explain the disparity between experimental results and observations in real ecosystems, the key to reconciling such disparities is to develop quantitative scaling relationships based on BEF experiments first. Indeed, prior studies (e.g., Reich et al. 2012, Isbell et al. 2017, O'Connor et al. 2017) have explored the magnitude of diversity effects as a function of the scale of experiments, and also provided several theoretical expectations on the scale dependence of diversity effects (e.g., Thompson et al. 2018). These empirical studies have generally found that diversity effects did, in fact, increase with the scales at which experiments were conducted.

However, studies to date that have examined how diversity effects change with spatial and temporal scale have not gone beyond correlations to generate quantitative scaling relationships, nor have they separated the effects of space from time, or explicitly addressed their interactions. These more detailed scaling relationships are an important step towards quantifying biodiversity effects across space and over time, and linking mechanisms supported in small experiments with large-scale patterns observed across landscapes. Specifically, the scaling relationships developed from experiments can first be used to provide an initial predicted biodiversity effect for a given spatial or temporal scale; the prediction can then be compared against observations of real ecosystems at equivalent scales to inform parameter adjustments and further hone the predictions of scaling relationships. Through such an iterative process, the predictive capacities of scaling relationships can thus be improved. Developing these scaling relationships is critical, especially given the well-recognized logistic challenges and/or ethical concerns that are likely to prevent us from doing controlled, manipulative biodiversity experiments at the scale of whole ecosystems (e.g., an entire island, lake, or forest). Scaling relationships are

also fundamental to developing mechanistic models to predict real-world consequences of biodiversity loss for ecosystem functioning and services across dynamic landscapes (Brose and Hillebrand 2016, Isbell et al. 2017).

Here we attempted to develop improved BEF scaling relationships. We focused on experiments that have examined plant diversity effects on biomass production, because (1) this subset offers the largest number of studies ($N = 374$); (2) the range of spatial/temporal scales represented in these experiments spans many orders of magnitude; and (3) the production of ecosystems is a fundamental function underpinning many ecosystem goods and services (O'Connor et al. 2017). We used species richness as the measure for biodiversity, as this measure is most widely adopted in the literature. Aside from the null hypothesis that biodiversity effects on biomass production are scale invariant, two hypotheses have been proposed (Appendix S1: Fig. S1): Plant diversity effects on biomass production: (1) increase with spatial/temporal scales, which might occur if, for example, greater environmental variations allow for more niche partitioning (Tscharntke et al. 2005, Tylianakis et al. 2008, Duffy 2009), or (2) decline with spatial/temporal scales if, for example, abiotic factors overwhelm biodiversity effects (Srivastava and Vellend 2005, Wardle and Zackrisson 2005, Grace et al. 2007, Wardle 2016). As we show, plant diversity effects increase with spatial and temporal scales, and the time scale of experiment is the main source of variation in diversity effects. Our results also reveal the positive space–time interactions for plant diversity effects, likely driven by complementarity effects.

Materials and Methods

Selection of case studies

We used the database by Cardinale et al. (2009), which summarized results of BEF relationships from 164 experiments (reported in 84 publications) through 2006. As part of a National Center for Ecological Analysis and Synthesis Working Group, this data was updated with additional peer-reviewed papers published through September 2009. Although additional experiments have been published over the past decade, updating this data set with more recent literature can be an enormous undertaking (e.g., collation of the original data set has taken almost a decade). We thus chose to use this data set, which is still by far one of the largest existing data sets of BEF studies, and selected a subset (see Selection criteria below) for our analyses.

All studies included in this database experimentally manipulated species richness of a given tropic group, and measured effects of species richness on (1) standing stock abundance or biomass of all species within a focal tropic group t; (2) standing stock of resources used by t; and (3) total resources depleted by t. Details on the methods of data collection were summarized in Cardinale et al. (2009). For the purposes of this paper, we extracted records that describe how species richness of terrestrial plants impacts biomass or density of plants. Our selection criteria resulted in a total of 374 independent experiments (from 54 published studies) that vary in diversity effect sizes by >threefold (Appendix S1: Fig. S2A) and differ in spatial and temporal scales by 6.5 and 2.4 orders of magnitude, respectively (Appendix S1; Fig. 2B). This subset included experiments conducted in wetland (13 total), temperate grassland (331), forest (20), bryophyte (2), agriculture (2), and tundra (6). The fundamental response for all experiments was total plant biomass (mass per area) or abundance (density) summed across all species, reported across a set of species richness treatments with all other factors controlled.

Analysis of diversity effect sizes

We used two complementary analyses to quantify diversity effect sizes in each experiment. First, we used log response ratios to quantify the proportional change in plant biomass/density between the highest vs. lowest levels of species richness used in each experiment. The log response ratio is a widely used metric for measuring effect sizes in meta-analysis (Hedges et al. 1999, Koricheva et al. 2013), because (1) it is dimensionless, and thus allows for comparing effect sizes among studies where independent and dependent variables differ in scale, and (2) its sampling properties are known to be approximately normal and relatively robust to bias from small sample sizes (Hedges et al. 1999). Specifically, for our purposes, the log ratio, LR_{net}, was calculated as proportional difference between the average productivity/density of all replicates from most species-rich polyculture (y_p), and the average of these same species grown in monoculture (y_m), using the equation $\ln(y_p/y_m)$.

Although log response ratios can be calculated for nearly every experiment in the data set, one limitation is that these ratios only compare the most diverse polyculture to the monocultures. In other words, they provide no further information about the functional form of diversity effect in between these two extremes. Hence, we complemented our analyses of log response ratios with a second analysis that fits data to the power function for experiments that manipulated three or more levels of plant species richness. Prior research (e.g., Reich et al. 2012) has demonstrated that power function is a good descriptor of BEF relationships from experiments, and ranks among the highest statistical models in terms of explanatory power. In addition, the coefficient b from power function is easy to interpret and compare among studies. Specifically, in our analyses, the power function was mathematically expressed as follows:

$$\ln\left(\frac{Y_s}{Y_m}\right) = a + b \times \ln(Sp),$$

where Y_s is the biomass/density at species richness Sp, Y_m is the mean biomass/density of monoculture of all

species, a is the constant, and b is the power exponent. Thus, when $b = 0$ there is no diversity effect, when $b = 1$ the proportional increase in biomass/density across levels of species richness is linear, and for all $0 < b < 1$, the proportional increase in biomass/density across levels of species richness is nonlinear and decelerating.

Loreau and Hector (2001) developed a technique to partition the net effects of diversity into two components statistically: *sampling/selection effects* (SE) and *niche complementarity effects* (CE). SE represents the proportion of diversity effects on polyculture biomass that can be attributable to the productivity of individual species, such as those that occur when the most productive species dominate the biomass of diverse polyculture. In contrast, CE represents the portion of diversity effects that cannot be attributed to any single species, and thus denotes the balance of all forms of niche partitioning that might influence biomass and all forms of indirect and nonadditive species interactions. The Cardinale et al. (2009) data set used for our analyses included estimates of SE and CE that were calculated from published studies, or provided by the study authors. This allows us to examine how CE and SE change with spatial and temporal scales of the experiments. Although CE and SE do not, by themselves, provide unambiguous evidence of biological mechanisms, they do tell us how the relative importance of single-species (i.e., SE) vs. multispecies (i.e., CE) processes changes with scales.

Spatial and temporal scales

To allow comparison of studies performed at very different spatial scales using organisms of vastly different sizes, we standardized spatial scales (S) by calculating the log ratio of the area or volume of the experimental unit divided by mean body mass of the focal taxa, i.e., $S = \ln (S_{experiment}/S_{organism})$. To allow comparison of studies that varied in their time scales using organisms with vastly different generation times, we standardized temporal scales (T) as the log ratio of the duration of studies divided by mean generation time of the organism, that is, $T = \ln(D_{study}/G_{organism})$, which represents the number of generations an experiment was run. Log ratios were used because the untransformed ratios varied 2.4–6.5 orders of magnitude across all experiments. Details on how the information regarding spatial and temporal scales was collected from experiments were described in Cardinale et al. (2009).

Statistical analyses

General linear mixed-effects models were used to quantify how effects of plant species richness on biomass production vary across spatial and temporal scales. Analyses were done separately for diversity effects quantified by log response ratio, and for parameter estimates from the fitting of power function. The general statistical model was $y_i = \mu + S_i + T_i + S_i \times T_i + e_i + \epsilon_i$, where y_i is either LR_{net} or scaling exponent b from curve fitting, S_i, T_i and $S_i \times T_i$ are fixed effects of spatial scale, temporal scale, and their interactions, e_i is the random effect with which each experiment was associated with independent errors following normal distribution, $N[0, \sigma_b^2]$, and ϵ_i is the residual error. Random effects were included in the model to account for potential systematic variations among experiments resulting from factors such as climatic differences among sites, site-specific environmental parameters (e.g., soil), ecosystem types, taxonomic groups, species or functional trait composition within those groups, or other ecological and scientific particularities that varied among different experiments (O'Connor et al. 2017). General linear mixed-effects models were used for three reasons: (1) multicollinearity between spatial and temporal scales was reasonable in all models (with all variation inflation factors, VIFs < 3.0); (2) random effects can be included; and (3) interaction term between spatial and temporal scales can be readily included in the model. We included the interaction term because the models with the interaction had lower Akaike information criterion (AIC) values compared to their counterparts without the interaction term. Heterogeneity of residuals and normality of errors were assessed for the full models, and no violations were detected. We also explored heterogeneity of effect sizes across ecosystems, and examined nonindependence of effect sizes and publication bias (i.e., selective publication of significant over nonsignificant findings; see Appendix S2), and found no systematic bias.

We performed additional analyses using the same linear mixed-effects models with absolute (raw, or nonstandardized) spatial and temporal scales from each experiment (i.e., experimental unit size or study duration) to assess whether our results were driven by spatial and temporal scale per se, or were driven by organismal traits like generation time and body size (see Appendix S3). Our first analyses were suggested by a referee to analyze how diversity effects across all studies in the data set varied as a function of the raw (nonstandardized) spatial and temporal scales of the experiment, and the generation time and body size. Although this approach maximizes the use of data, it potentially suffers from confounding factors that could hinder the interpretation. This is because, for example, studies of microalgae growing on a time scale of days in milliliter-scale laboratory flasks differ from those of large plants grown for a decade in 100-m^2 field plots in a multitude of ways beyond just biological traits (e.g., experimental units and conditions, methods, measurements, etc.), and thus may not be directly comparable without standardization. Because these confounding factors cannot be directly controlled with the existing data, we performed second analyses that were focused on all grassland studies. Not only are these grassland studies more comparable to one another, they also dominate the data set.

To explore how single- vs. multispecies processes contribute to changes in BEF relationships across scales, we

first assessed how CE and SE metrics varied with standardized spatial and temporal scales. Based on the distribution of scales in the original data set, we further categorized the experiments into three subgroups: (1) *large* temporal and spatial scales (i.e., both >90th percentile); (2) *large* temporal (i.e., >90th percentile) but *small* spatial scales (i.e., <60th percentile); and (3) *large* spatial (i.e., >90th percentile) but *small* temporal scales (i.e., <60th percentile). We then performed the same linear mixed-effects models to test for differences in CE and SE values between these deliberately grouped experiments. Such subgrouping allows us to attribute explicitly the extent to which CE or SE contributes to enhanced diversity effects from increasing spatial scales while the temporal scales of experiments are large (i.e., comparing subgroup 1 and 2), or vice versa (comparing subgroup 1 and 3). In other words, such analyses could shed light onto whether CE or SE drives the interactions between spatial and temporal scales on diversity effects. All statistical analyses were performed in the R statistical software 3.3 (R Development Core Team 2016). We used 'lmer' function in '*lme4*' package (Bates et al. 2015) for general linear mixed-effects models, and significance of fixed effects was evaluated using the Satterthwaite approximation for degrees of freedom in the '*lmerTest*' package (Kuznetsova et al. 2015). We used 'vif.mer' function for calculating VIF in the linear mixed-effects models.

RESULTS

Scaling up net plant diversity effects

Among 374 experiments, the net plant diversity effects on biomass production, LR_{net}, ranged from -0.73 to 1.51, with 89% showing positive effects (Appendix S1: Fig. S2). Individually, LR_{net} showed positive relationships with standardized temporal (Fig. 1A) and spatial scales (Fig. 1B; both $P < 0.001$). A general linear mixed-effects model revealed that spatial and temporal scales also interacted to affect LR_{net} ($\beta_{int} = 0.015$, $P = 0.014$; Table 1). In other words, the influences of spatial scale on plant diversity effects were contingent upon temporal scale, and vice versa. Additional analyses using nonstandardized temporal and spatial scales (with the full data set, as well as a subset of grassland studies) showed qualitatively similar results, with significant positive pairwise correlations with LR_{net} (both $P < 0.001$; Appendix S3: Figs. S1, S2), as well as positive space–time interactions ($P = 0.013$; Appendix S3: Table S1). We further found no significant correlations between LR_{net}, and body size and generation time of focal organisms (Appendix S3: Figs. S1, S2), suggesting that it is the scale of experiments per se (rather than the functional traits of organisms) that drives the scaling relationships of plant diversity effects.

To examine the interaction between spatial and temporal scale, we estimated how plant diversity effects changed with temporal scale while holding spatial scales constant at the minimum and maximum values in the data set. Specifically, at the minimum spatial scale in the data set, LR_{net} remained positive irrespective of temporal scale (red line in Fig. 2A). However, at the maximum spatial scale, the effects of temporal scale increased LR_{net} from $e^{-0.34}$ (i.e., the most diverse polycultures achieved $0.71 \times$ the biomass of average monoculture) to $e^{0.90}$ (i.e., the most diverse polycultures achieved $2.46 \times$ the biomass of average monoculture; blue line in Fig. 2A). Thus, effects of plant species richness on biomass production changed both qualitatively (from negative to positive) and quantitatively ($e^{-0.34}$ to $e^{0.90}$) through time, and this variation required at least four generations of population growth, if not more, to be realized (x-axis in Fig. 2A).
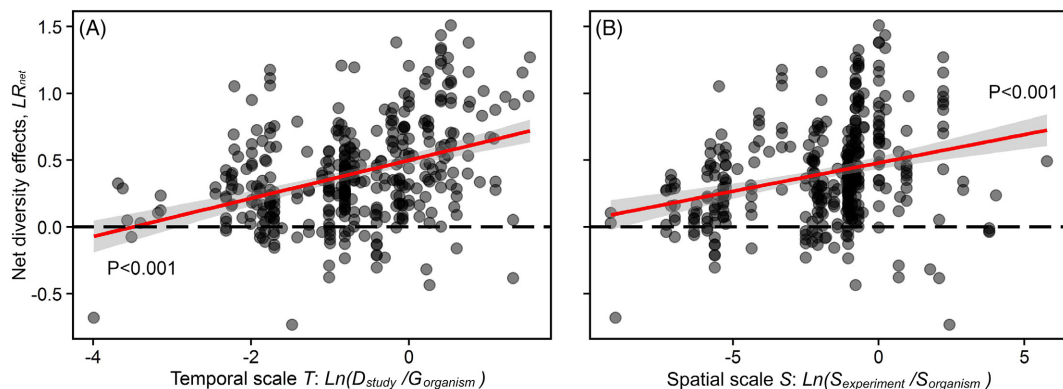

FIG. 1. Pairwise correlations between net effects of plant diversity on biomass production and standardized (A) temporal scale (i.e., natural log of $D_{study}/G_{organism}$, where D_{study} represents study duration and $G_{organism}$ as the organism generation time), and (B) spatial scale (i.e., natural log of $S_{experiment}/S_{organism}$, where $S_{experiment}$ represents experimental unit size, and $S_{organism}$ as organism body mass). Red solid lines are derived from linear regressions fitted to the data, with the 95% confidence intervals shown in grey band.

TABLE 1. General linear mixed-effects model results showing how standardized spatial (S) and temporal scales (T) influence plant diversity effects, LR_{net}, and parameters a and b derived from curve fitting of the power function.

	Estimated β	SE	t-value	Prob. ($>|t|$)
LR_{net}				
Intercept	0.448	0.031	14.44	<0.001
S	0.019	0.011	1.69	0.091
T	0.141	0.027	5.21	<0.001
$S{:}T$	0.015	0.006	2.48	0.014
Parameter a				
Intercept	0.02	0.012	1.60	0.11
S	-0.005	0.004	-1.24	0.22
T	0.003	0.012	0.30	0.77
$S{:}T$	-0.001	0.002	-0.46	0.65
Parameter b				
Intercept	0.19	0.026	7.54	<0.001
S	0.006	0.007	0.86	0.39
T	0.07	0.017	4.15	<0.001
$S{:}T$	0.008	0.003	2.35	0.02

Notes: Power function is mathematically expressed as: $\ln\left(\frac{Y_s}{Y_m}\right) = a + b \times \ln(S)$, where Y_s is the biomass/density at species richness S, Y_m is the mean biomass/density of monoculture of all species, a is the constant, and b is the exponent. Spatial and temporal scales were log-transformed prior to analysis. Model was fitted by restricted maximum likelihood (REML), and significant test was performed with the Satterthwaite approximations. All predictors had variance inflation factors (VIF) < 2.8, and all model assumptions were met.

We similarly examined how plant diversity effects changed with spatial scale while holding temporal scales constant at the minimum and maximum values in the data set. At the minimum temporal scale in the data set, LR_{net} declined from $e^{0.24}$ to $e^{-0.35}$ as spatial scale increased (red line in Fig. 2B). At the maximum temporal scale in the data set, the effects of spatial scale increased LR_{net} from $e^{0.29}$ to $e^{0.91}$ (blue line in Fig. 2B). Again, these results demonstrated that effects of plant species richness on biomass production changed both qualitatively (from negative to positive) and quantitatively ($e^{-0.35}$ to $e^{0.91}$) across several orders of magnitude of spatial scales as represented in the experiments (x-axis in Fig. 2B).

The complex space–time interactions can also be portrayed in a different manner. In Fig. 2C, effects of temporal scale on plant diversity effects, LR_{net} (shown on y-axis) rose quickly as the spatial scale of experiments (i.e., x-axis) increased. However, beyond a spatial scale of ~12, effects of temporal scale on LR_{net} decelerated towards a maximum of $e^{0.27}$. In contrast, in Fig. 2D, effects of spatial scale on LR_{net} (shown on y-axis) were much smaller, and also decelerated towards a maximum of $e^{0.044}$ when the experiments were run for ~4 generations.

Scaling up the functional form of plant diversity effects

Our complementary analysis detailing the functional form of plant diversity effects on biomass production

was constrained to experiments that manipulated three or more levels of plant species richness ($N = 227$) (Appendix S1: Fig. S3). Among this subset, the fitted power exponent b ranged from −0.70 to 0.63 (mean = 0.19 ± 0.17), with 92% showing positive b values. Pairwise correlations suggested that, individually, the power exponent b tended to increase as spatial and/or temporal scales of experiments increased (both $P < 0.001$).

Consistent with results from analyses of LR_{net}, we found significant interactive effects between spatial scale and temporal scale of experiments on the power exponent b ($\beta_{int} = 0.008$, $P = 0.02$; Table 1). Increasing spatial and temporal scales interacted to make the form of plant diversity–productivity relationships more linear and less saturating as b approached its maximum of ~0.40 (Fig. 3). Specifically, at the minimum spatial scale in the data set, the exponent b was uniformly positive but independent of temporal scale; in contrast, at the maximal spatial scale in the data set, b was negative at small temporal scales but increased to positive as temporal scale of experiments increased (Fig. 3A). On the other hand, at the minimum temporal scale, b decreased from 0.13 to −0.24 as spatial scale increased (Fig. 3B); in contrast, at the maximal temporal scale, b increased nonlinearly towards its saturation point. In other words, effects of temporal scale on exponent b increased from negative to positive in a nonlinear and concave-down manner at large spatial scales (Fig. 3C). Likewise, effects of spatial scale on b also increased from negative to positive as temporal scale increased (Fig. 3D), though the magnitude of effects of spatial scale tended to be smaller than those of temporal scales.

Factors driving plant diversity effects across scales

In determining factors that drive plant diversity effects across scales, we found that CE positively correlated with temporal scale ($P < 0.001$), whereas SE negatively correlated ($P = 0.02$) (Fig. 4A,C). Spatial scale, however, shows nonsignificant correlations with either SE or CE (Fig. 4B,D). These results indicated that changes in the magnitude of CE were most likely the reason why plant diversity effects increased across scales. We further examined whether CE or SE were the primary factor underlying positive space–time interactions for plant diversity effects. We found that, in experiments characterized as large temporal scales, CE were substantially greater with increasing spatial scales (Fig. 5A), whereas SE showed the opposite pattern (Fig. 5B). Similarly, in experiments of large spatial scales, CE increased as the temporal scales increased (Fig. 5C), but no significant difference was found for SE (Fig. 5D).

DISCUSSION

On the basis of >370 experiments spanning 2.4–6.5 orders of magnitude in scales and across a range of terrestrial ecosystems, we have developed a set of scaling
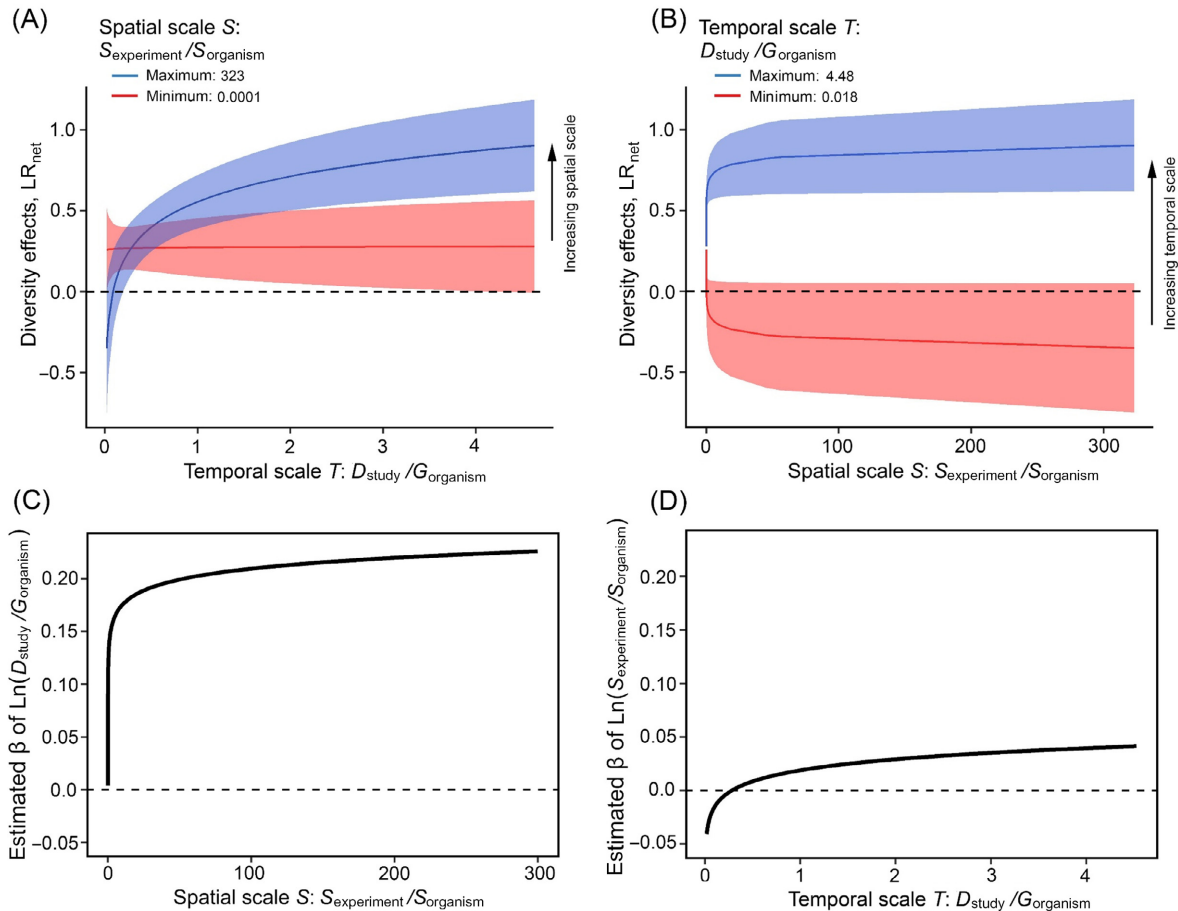
Fig. 2. Interactive effects of scales on altering plant diversity effects on biomass production: (A) how plant diversity effects, LR_{net}, vary in response to temporal scale (x-axis), whereas spatial scales are held constant at two extremes (i.e., minimum and maximum, in red and blue color, respectively); (B) how plant diversity effects, LR_{net}, vary in response to spatial scale (y-axis), whereas temporal scales are held constant at two extremes (i.e., minimum and maximum, in red and blue, respectively); (C) estimated slope β of temporal scales (i.e., effects of temporal scales on LR_{net}) in responses to spatial scales; (D) estimated slope β of spatial scales (i.e., effects of spatial scales on LR_{net}) in responses to temporal scales.

relationships that relate plant diversity effects on biomass productivity across space and over time (Table 1). By explicitly accounting for space–time interactions, our analyses showed that (1) the spatial and temporal scales of experiments interacted to control the qualitative form of how plant species richness affects biomass production, as well as the magnitude of effects; (2) within the range of the data set, LR_{net} and the power exponent b increased by factors of 1.68 and 0.27, respectively, for each 10-fold increase in the number of generations run in experiments (while statistically holding spatial scale as constant), and by factors of 1.10 and 0.04, respectively, for each 10-fold increase in the spatial scale of experiment (while statistically holding temporal scale as constant); (3) plant diversity effects on biomass production changed with both spatial and temporal scale of experiments in a nonlinear manner, precluding simple linear interpolation or extrapolation from one scale to another; and lastly (4) the temporal scale of experiments

appeared to have a substantially greater influence on biodiversity effects than did the spatial scale. Predictions from these scaling relationships can be compared with the ever-increasing observations to further fine-tune the relationships and advance their predictive capacities on the consequences of biodiversity loss for ecosystem functioning and services across real-world landscapes.

Across the data set, the power exponent b increased by 0.27 for each 10-fold increase in the number of generations run in an experiment (note: this is similar to the range reported in Reich et al. 2012), and increased by 0.04 for each 10-fold increase in the spatial scale of an experiment. These results reinforce the caution by prior authors who have suggested that the results of small-scale, short-time-frame experiments are likely to be overly conservative, and probably underestimate the influences of biodiversity on ecosystem functioning and services in real-world landscapes. Our results corroborate other studies (Dimitrakopoulos and Schmid 2004,
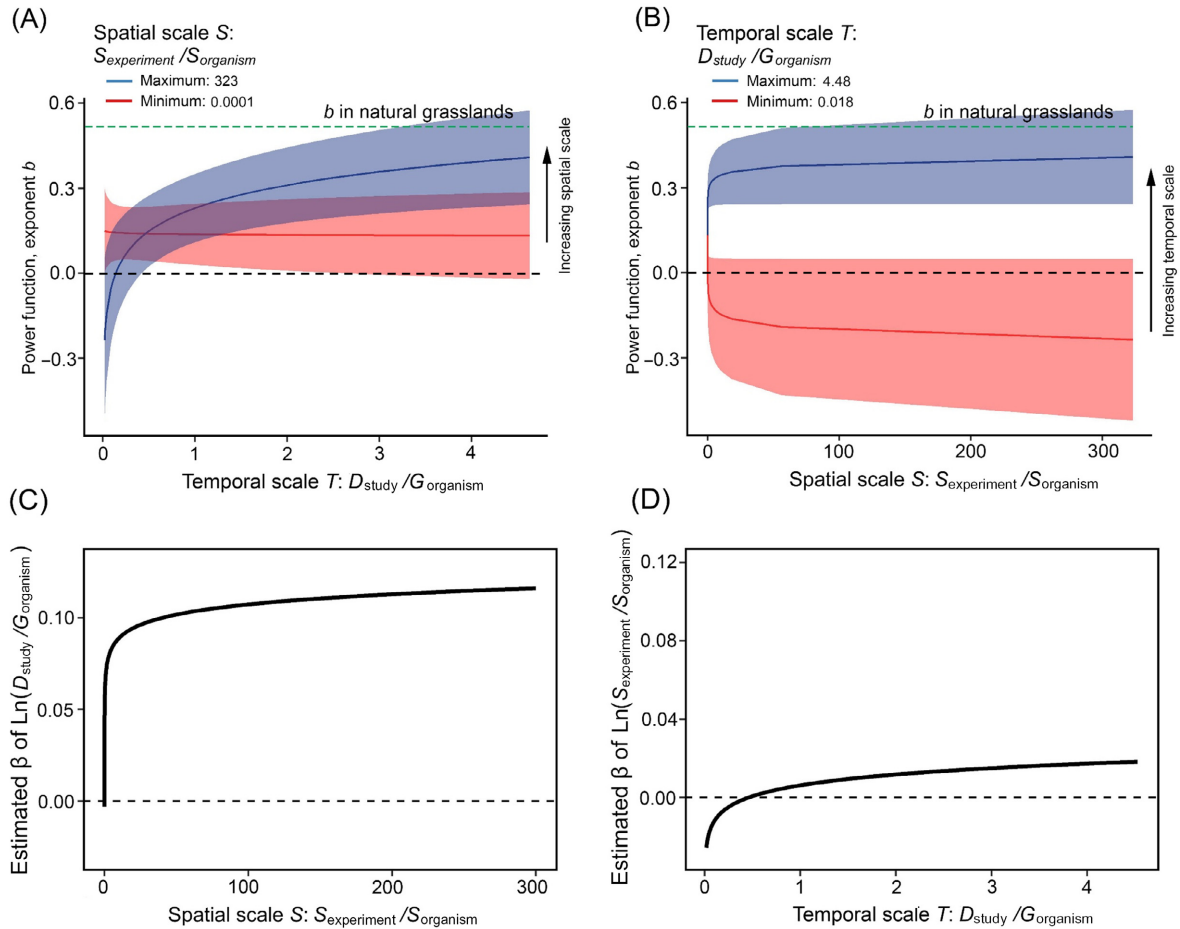
FIG. 3. Interactive effects of scales on the form of plant diversity–biomass relationships, quantified by exponent b from power function fit: (A) how exponent b varies with temporal scale whereas spatial scales are held constant at two extremes (i.e., minimum and maximum, in red and blue, respectively); (B) how exponent b varies with spatial scale while temporal scales are held constant at two extremes; (C) estimated slope β of temporal scales (i.e., effects of temporal scales on exponent b) in responses to spatial scales; (D) estimated slope β of spatial scales (i.e., effects of spatial scales on exponent b) in responses to temporal scales. In (A) and (B), horizontal dashed green lines represent mean exponent b estimated in natural grassland ecosystems from Duffy et al. (2017).

Griffin et al. 2013) that have separately assessed the role of spatial scales and time scales in affecting BEF relationships. We found that the power exponent b reached its saturation point of ~0.40 at the extremes of spatial and temporal scales captured in experiments (Fig. 3). Although the estimate of 0.40 from our study is close to the value of b reported in natural grasslands (i.e., $b = 0.53$ in Duffy et al. 2017), there is still a good amount of disparity between experiments and natural systems ($b = 0.40$ vs. $b = 0.53$). Because our data set was dominated by grassland experiments, we suspect that this gap in exponent b is due to differences in ecosystems, but may be influenced by some mechanism(s) that control the BEF relationships in natural systems, which have yet to be fully incorporated into experiments. Understanding how this gap of biodiversity effects can be bridged (empirically or theoretically) and integrated

into scaling relationships is an area that requires more work, and will be instrumental in linking biological and ecological mechanisms of biodiversity effects with broad-scale patterns.

Our study further explored how single- vs. multi-species contributions to the BEF relationship change with scale, and why space and time interacted to affect the effects of plant diversity on biomass production. We found that, consistent with other studies (e.g., Cardinale et al. 2007, Isbell et al. 2018), the net diversity effects increased through time as a consequence of complementarity becoming stronger as experiments are run longer (Fig. 4). Selection effects, on the other hand, declined with the duration of experiments, indicating that selection effects are unlikely to be the mechanism driving the positive effects of temporal scale on BEF relationships. Similar findings were also reported in Reich et al. (2012),
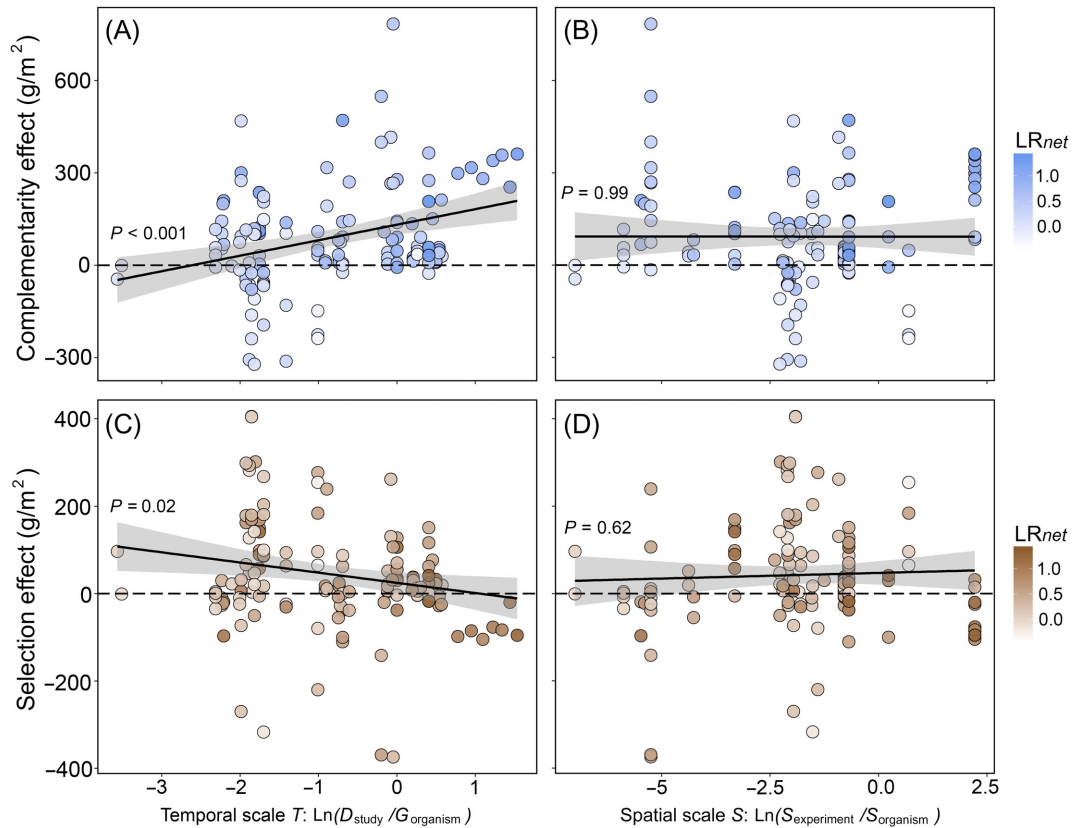
Fig. 4. Pairwise correlations between partitioned complementarity effects (CE) vs. standardized temporal (A) and spatial (B) scales, as well as partitioned selection effects vs. standardized temporal (C) and spatial (D) scales. Color gradient represents the magnitude of net plant diversity effects. Black solid lines are derived from linear regressions fitted to the data, with the 95% confidence interval shown in the gray band.

who suggested that complementarity effects accumulated over time, causing species-rich polycultures that are functionally redundant earlier to become more functionally unique through successional time. As for the spatial scale, our results revealed that neither complementarity nor selection effects change significantly with spatial scale—results that contrast with those of other studies (e.g., Dimitrakopoulos and Schmid 2004) showing that complementarity effects can be amplified when more space is provided. We suspect that this discrepancy results from the interactions between spatial and temporal scales that were not explicitly addressed in prior studies, which could mask the individual effects of spatial scales.

One thing that is unique about our study relative to others that have considered scaling relationships is that we explicitly analyzed the effects of both spatial and temporal scale simultaneously (as opposed to examining the influence of one scale at a time) and found significant interactions (Table 1). Our analyses suggest that increasing spatial and temporal scales can have facilitative effects on one another to alter plant diversity effects, and sometimes simply changing one scale might have limited influences on plant diversity effects. In extreme

cases, for example, plant diversity effects can be independent of time when spatial scale is very small, or even decline with spatial scales when a study fails to allow reproduction to occur (<1 generation; Figs. 2 and 3). We further explored possible factors responsible for synergistic space–time interactions, and found that CE was likely the main factor driving positive interactions between spatial and temporal scales for plant diversity effects (Fig. 5). Specifically, temporal complementarity effects could be more enhanced when experiments are conducted across a sufficiently large, heterogeneous environment that allows species specialization to be expressed (as compared to experiments at small spatial scales; Fig. 5A,B), as also shown in Stachowicz et al. (2008). Similarly, spatial complementarity and resource partitioning could be more fully utilized when experiments are run over a large number of generations that allows for sufficient species interactions and exploration of all potential niches (Fig. 5C,D). In tandem, our results provide evidence that increasing spatial and temporal scales and associated heterogeneity could regulate the performance of species and offer more niche opportunities for species to exploit in ways that are complementary in time and space (Loreau et al. 2003).
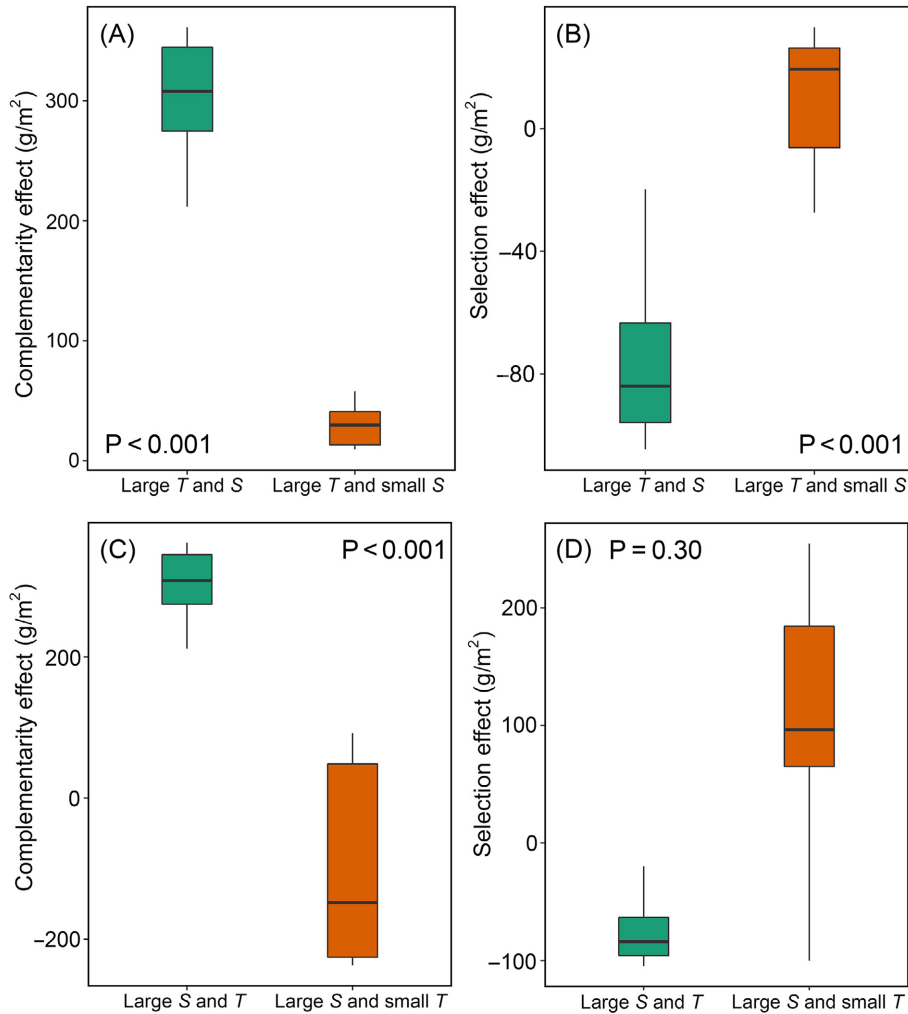
FIG. 5. Boxplots showing the complementarity effects (A) and selection effects (B) between experiments categorized into *large* temporal and spatial scales (i.e., both >90th percentile) vs. *large* temporal (>90th percentile) but *small* spatial scales (<60th percentile). Additional two boxplots showing the complementarity effects (C) and selection effects (D) between experiments categorized into *large* spatial and temporal scales (i.e., both >90th percentile) vs. *large* spatial (>90th percentile) but *small* temporal scales (<60th percentile). Please note that (1) *y*-axes for panels A vs. C, and B vs. D are in different scales; (2) *P*-values denote the significant differences between groups of experiments estimated from the linear mixed-effects models; (3) the purpose of our deliberate comparisons is to highlight the contributions of complementarity effects vs. selection effects at high spatial scales while increasing temporal scales, or vice versa.

Space–time interactions also underline the importance of adopting a dynamic and landscape lens in understanding biodiversity effects on ecosystem functioning and services, and informing conservation and management (Tscharntke et al. 2005, Brose and Hillebrand 2016).

For our primary analyses, we used spatial scales that were standardized to the mean body mass of the focal organisms, and temporal scales that were standardized to their mean generation time. Scale standardization is vital in order to synthesize diversity effects across studies that used organisms of different sizes and life spans (e.g., grass vs. tree vs. fish vs. bird), and in different systems. However, it may also face potential challenges, such as (1) making direct inferences in regards to effects of altering raw scales (e.g., area or duration) for conservation and management, and (2) obtaining accurate estimates of mean body mass or generation time for species that may have limited information or are heterogeneous with high levels of intra- or interspecific variations. Nonetheless, our conclusions were robust regardless of standardization, as additional analyses using raw or nonstandardized scales for grassland studies revealed qualitatively similar results. Our study did also demonstrate that it is possible to perform analyses using raw scales in order to draw direct inferences, but perhaps only for the same functional group of species at a time.

Our research points to several avenues for future research. First, our analysis is based on experiments that used species richness as the measure of biodiversity. A growing number of studies have focused on other dimensions of biodiversity, such as phylogenetic or functional diversity, and some have argued that alternative metrics of biodiversity might be better predictors of ecosystem functioning or services (Purvis and Hector 2000, Isbell et al. 2017). Thus, scaling relationships may be improved and more universal (e.g., across trophic groups) if other dimensions of biodiversity are considered. Second, our study is focused on experiments of plant diversity effects on biomass production, in which grasslands dominate the data set. Hence, there is a need to determine (1) whether scaling relationships revealed here are broadly applicable to other ecosystem functions or services that are more relevant for human well-being (e.g., water quality, pest control, pollination; Lefcheck et al. 2015); and (2) whether scaling relationships are consistent across ecosystems, especially in nonterrestrial ecosystems (e.g., freshwater and marine). Moreover, it is important to note that the maximum temporal and spatial scales in the data set that we analyzed are 4.63 generations and 20,000 m^2, respectively (Appendix S1: Fig. S2), which may be relevant to many policy and conservation needs. Yet the extent to which our scaling relationships can be extrapolated beyond these scales warrants future work and validation when there are sufficient large-scale observational and remote-sensed studies. Such validations are also helpful to fine-tune the scaling relationships and ultimately improve their predictions in real-world landscapes. One roadmap for doing so is to first use scaling relationships to predict diversity effects at larger spatial and temporal scales, and then the predictions can be confirmed or refined (e.g., via parameter adjustments) by comparing with BEF relationships derived from equivalent observational scales. Finally, our analysis demonstrates strong space–time interactions on plant diversity–ecosystem function relationships, and also explores possible driving factors of such interactions. Future research is needed, designed to measure and quantify the relative importance of different mechanisms, and conditions under which they operate, explicitly and accurately. Such mechanistic understanding is crucial for developing landscape models that more accurately predict changes in multiple ecosystem services and their trade-offs due to biodiversity losses (Qiu and Turner 2013, O'Connor et al. 2017, Qiu et al. 2018a).

The rapid pace of species extinction amid the Anthropocene has prompted substantial concerns and efforts to determine their ecological, social, and economic consequences (Naeem et al. 2016, Hungate et al. 2017, Qiu et al. 2018b). Of particular interest is the extent to which species losses undermine continued functioning of ecosystems and their long-term resilience to deliver ecosystem services (Oliver et al. 2015). There is still a good window of opportunity to safeguard biodiversity and sustain goods and services essential for human society. However, accomplishing these goals requires sound knowledge to forecast real-world consequences of biodiversity change in landscapes where concerted societal actions can be motivated. Our research develops useful scaling relationships that quantify and scale up biodiversity effects on productivity across space and over time. Results of nonlinear responses of biodiversity effects, along with complex space–time interactions, suggest that simple linear extrapolation of results from small-scale, controlled experiments to large-scale landscapes without proper scaling functions will likely underestimate biodiversity effects. Our study moves us one step closer to use results of small-scale experiments to help predict the consequences of biodiversity change in more natural ecosystems. Findings from this study will be relevant for designing conservation strategies, and can be integrated into predictive models to examine consequences of realistic extinction scenarios in a changing and uncertain future more accurately.

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