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LETTER

Species loss due to nutrient addition increases with spatial scale in global grasslands

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Abstract

The effects of altered nutrient supplies and herbivore density on species diversity vary with spatial scale, because coexistence mechanisms are scale dependent. This scale dependence may alter the shape of the species–area relationship (SAR), which can be described by changes in species richness (S) as a power function of the sample area (A): $S = cA^z$, where c and z are constants. We analysed the effects of experimental manipulations of nutrient supply and herbivore density on species richness across a range of scales (0.01–75 m^2) at 30 grasslands in 10 countries. We found that nutrient addition reduced the number of species that could co-occur locally, indicated by the SAR intercepts (log c), but did not affect the SAR slopes (z). As a result, proportional species loss due to nutrient enrichment was largely unchanged across sampling scales, whereas total species loss increased over threefold across our range of sampling scales.

KEYWORDS
biodiversity, community ecology, grasslands, herbivores, nutrients

INTRODUCTION

What determines the number of species at a location? This question lies at the core of community ecology. The answer is inherently scale dependent (Arrhenius, 1921; Chase et al., 2018; Gleason, 1926; Godwin, 1923; Grace et al., 2011; MacArthur & Wilson, 1967) because different mechanisms influence diversity at different spatial scales (Chesson, 2000; Hart et al., 2017; Leibold & Chase, 2017; Leibold et al., 2004; Thompson et al., 2020). For example, non-spatial coexistence mechanisms that depend on trade-offs (e.g. in resource use efficiency or susceptibility to consumers) or temporal variability (e.g. temporal storage effects) can lead to coexistence at very small spatial scales (Chesson, 2000; Holt et al., 1994; Hutchinson, 1961; Tilman, 1982). In contrast, coexistence mechanisms that depend on spatial variability, such as dispersal limitation or competition-colonisation trade-offs, influence diversity at larger spatial scales (Chesson, 2000; Gleason, 1926; Godwin, 1923; Hastings, 1980; Leibold et al., 2004; MacArthur & Wilson, 1967; Vellend, 2010). Furthermore, the size of individuals and the spatial heterogeneity of the environment will determine the scales at which species interact and the minimum possible scale of coexistence (Goldberg & Miller, 1990; Oksanen, 1996; Seabloom et al., 2005). For these reasons, differences in diversity observed in field studies, across space or in response to environmental changes induced by ecological and anthropogenic drivers, will reflect both sampling scale and the scale dependence of coexistence mechanisms. Nevertheless, most empirical studies sample and compare diversity at a single scale, leading to an incomplete understanding of diversity responses to ecological drivers (Chalcraft et al., 2008; Chase et al., 2018; Lan et al., 2015).

A variety of approaches have been used to incorporate scale explicitly into measures of diversity, the most canonical of which is the species–area relationship (SAR) (Arrhenius, 1921; Chase et al., 2018; Flather, 1996; MacArthur & Wilson, 1967). Although a wide variety of SAR models exist (Dengler et al., 2020; Flather, 1996), a simple model that has been found to be applicable in many systems is

$$S = cA^z, \tag{1a}$$

or equivalently

$$\log(S) = \log(c) + z\log(A), \tag{1b}$$

where S is the number of species and A is the area sampled (Arrhenius, 1921; Dengler et al., 2020; Drakare et al., 2006; Flather, 1996; Fridley et al., 2005).

In this formulation, the y-intercept, log (c), reflects a measure of local diversity (proportional to α diversity when $A = 1$), and the slope (z) is a measure of spatial heterogeneity in community composition (proportional to some measures of β diversity) (Crist & Veech, 2006; Grace et al., 2011; Scheiner et al., 2011). Although the SAR only attains a true asymptote at a global scale (Williamson et al. 2001), saturation within sampling confines can be taken as a measure of the available species pool (γ diversity) (Chao et al., 2014; Grace et al., 2011). The x-intercept indicates the minimal insular area ($A_{\min}$) (sensu, Heatwole, 1975), the area at which only a single species is found ($S = 1$ or $\log(S) = 0$) and is a non-linear function of c and z:

$$A_{min} = c^{\frac{-1}{z}}. \tag{2}$$

A_{min} can be thought of as the minimal area of co-existence, the area above which more than one species can co-occur (Connor & McCoy, 1979; Heatwole, 1975; Seabloom et al., 2005).

Understanding the patterns and determinants of diversity across scales has gained increased relevance as human domination of the biosphere has altered many of the controls on species diversity, leading to scale-dependent changes in diversity (Chase et al., 2019). For example, humans have increased the supply of biologically limiting nutrients and have changed the density of herbivores in many ecosystems (Foley et al., 2005; Ripple et al., 2015; Steffen et al., 2015), both of which can alter plant diversity at a range of spatial scales (Bakker et al., 2006; Chalcraft et al., 2008; Chaneton & Facelli, 1991; Crawley et al., 2005; Hillebrand et al., 2007; Lan et al., 2015; Leps, 2014; Olff & Ritchie, 1998).

The effects of environmental change on diversity may shift with spatial scale, and this scale dependence may be reflected in diversity–scaling relationships such as the parameters of the SAR (Bakker et al., 2006; Chalcraft et al., 2008; Chaneton & Facelli, 1991; Chase et al., 2018; Lan et al., 2015; Olff & Ritchie, 1998). For example, in grassland ecosystems, increasing the supply rates of biologically limiting nutrients like nitrogen (N) and phosphorus (P) often leads to reduced plant diversity at local scales. This leads to lower log c and higher A_{min} (Figure 1) by reducing the opportunity for coexistence through trade-offs in soil-resource-use efficiency and increasing competition for light (Borer et al., 2014b; Dybzinski & Tilman, 2007; Goldberg & Miller, 1990; Harpole et al., 2016; Harpole & Tilman, 2007; Hautier et al., 2009; Midolo et al., 2019). Although the effects of nutrient addition and herbivory on local

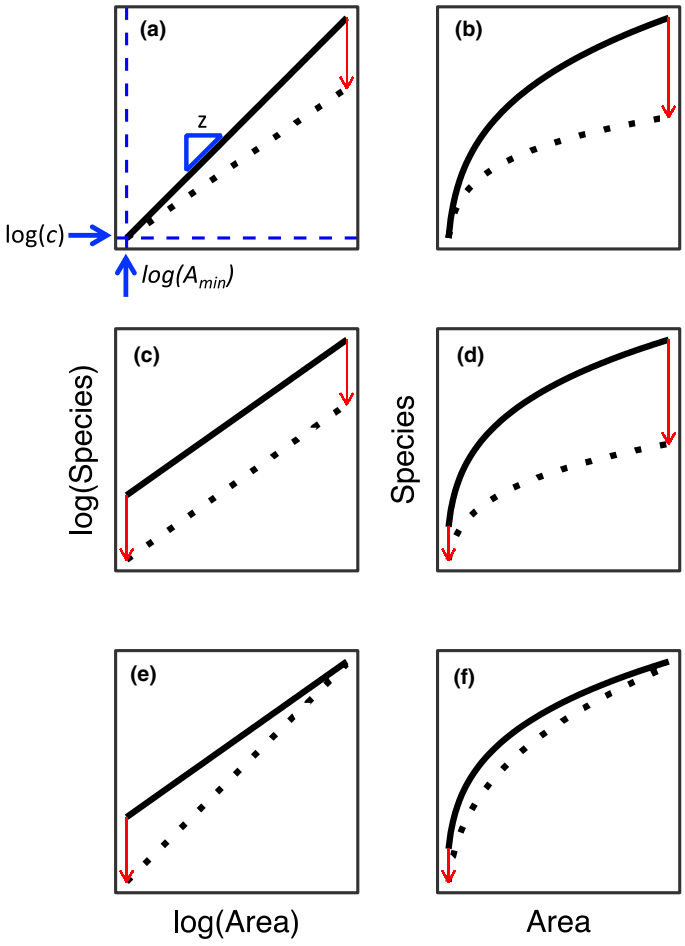

FIGURE 1 Hypothetical effects of experimental treatments (e.g. nutrient addition or herbivore exclusion) on species richness across spatial scales. The solid black line is constant in all panels and shows the species–area relationship (SAR) in control plots plotted in logged and untransformed units. Panel A shows the slope (z), y-intercept (log c) and x-intercept (A_{min}), which are the focus of the analyses in this paper. The black dotted line shows the SAR in the treated plots, and the red arrows show the change in richness at small or large scales. The blue dashed lines show the x and y intercepts in log space ($\log(A) = 0$ and $\log(S) = 0$). Left panels show log(Area), and right panels show the same relationship with area untransformed. The dotted lines in panels A and B show the effects of a reduced species pool, which reduces the slope but leaves the y-intercept unchanged. In this case, species loss increases with increasing spatial scale. Panels C and D show the effects of a constant proportional loss of species with increasing area (C), which leads to increasing total species loss with area (D). In this case, the y-intercept is reduced, whereas the slope is held constant. Panels E and F show the effects of reduced local richness without a reduction in the total species pool. In this case, the y-intercept is decreased, but the slope is increased, such that species loss declines with area

coexistence in grasslands have been examined experimentally, it remains unclear how these effects will change with spatial scale. Importantly, if environmental changes alter the shape of the SAR, diversity change measured at a single scale may overestimate or underestimate diversity change at larger spatial scales (Figure 1) (Lan et al., 2015).

Changes in the scaling relationship will depend on the specific coexistence mechanisms (e.g. spatial vs. non-spatial mechanisms) affected by nutrient enrichment or herbivore exclusion. Furthermore, different mechanisms will be associated with the total biomass, light availability and size of the species pool (Bakker et al., 2006; Borer et al., 2014b; Chalcraft et al., 2008; Harpole et al., 2016; Lan et al., 2015). For example, nutrient enrichment or herbivore exclusion may increase biomass, which can lead to thinning due to light competition and, in turn, reduce the SAR slope and intercept because there are fewer larger individuals in each sample (Lan et al., 2015). These treatments also may increase the dominance of a few species, which would reduce evenness and decrease the SAR intercept but increase its slope (Lan et al., 2015) (Figure 1E). Treatments also may cause the extinction of specific species, leading to a smaller species pool and lower SAR slope (Figure 1A) (Lan et al., 2015).

We have more specific expectations for cross-scale effects of nutrient addition than for herbivore exclusion, because nutrient addition has more consistent effects on grassland plant diversity across scales (Borer et al., 2014b; Chalcraft et al., 2008; Lan et al., 2015). For example, if nutrient-induced light limitation reduces coexistence opportunities for a consistent set of species through non-spatial processes such as reduced niche dimensionality (Harpole et al., 2016; Harpole & Tilman, 2007), then the local diversity loss (log c ↓) will be accompanied by a reduced total species pool (γ diversity ↓) (Chalcraft et al., 2008; Harpole & Tilman, 2007; Lan et al., 2015) (Figure 1C,D). These effects also would be associated with increased biomass and reduced light availability. In this case, the effects on the SAR slope depend on the relative rate of species loss across scales (Lan et al., 2015). If there is a constant proportional loss of species with increasing area, then the slope of the SAR would remain constant (Figure 1C,D). In contrast, the slope would decline if there is greater proportional loss at larger spatial scales (z↓) (Figure 1A,B), resulting in a more spatially homogeneous community. In a less extreme case, nutrient addition could increase the dominance of species that favours high-nutrient conditions without causing species extinction. In this case, nutrient addition would increase the SAR slope (z ↑) due to local diversity loss (log c ↓), but the total species pool would remain unchanged (Figure 1A,B). This effect also would be reflected in reduced species evenness (Lan et al., 2015).

Nutrient addition could also influence spatial coexistence mechanisms, such as competition–colonisation trade-offs or mass effects, by reducing dispersal and local recruitment (Hastings, 1980; Leibold et al., 2004; Tilman et al., 1994; Vellend, 2010). Reduced dispersal and colonisation would lower local diversity (log c ↓) but leave the total species pool unchanged, resulting in an increased SAR slope (z↓) in communities with low to moderate dispersal (Lan et al., 2015; Mouquet & Loreau, 2003)(Figure 1A,B), although very high rates of dispersal may reduce both the local richness and the total species pool (Mouquet & Loreau, 2003). Finally, nutrient addition could increase individual plant size (Goldberg, 1987; Oksanen, 1996), thereby reducing local diversity (log c ↓). As with reduced dispersal, increased plant size would not affect the total species pool but would increase the SAR slope (z↓) (Lan et al., 2015) (Figure 1E,F).

In any of these cases, a constant SAR slope indicates constant proportional change in species with increasing spatial scale, whereas a change in the SAR slope indicates an increasing or decreasing proportional change in the numbers of species with increasing spatial scale (Lan et al., 2015). Importantly, if there is a constant proportional loss (or gain) of species, there will be an increase in the total number of species lost (or gained) at larger spatial scales (Lan et al., 2015) (Figure 1C,D).

In summary, as we expect nutrient addition to decrease local diversity in grasslands (log c↓) (Borer et al., 2014b; Midolo et al., 2019), the SAR slope will either increase (z↑) or decrease (z↓) depending on the change in diversity at larger scales (Chalcraft et al., 2008; Lan et al., 2015) (Figure 1). Although there are few specific predictions for the minimal area of coexistence (A_{min}), we expect this to be negatively correlated with local diversity (log c) via the relationship in Equation 2, such that the expected nutrient-induced reduction in c should lead to an increase in A_{min} depending on the change in z.

Although the predictions for herbivore effects on diversity scaling are less developed, the effects should be mediated through changes in the same core processes governing nutrient effects. For example, herbivores may reduce diversity if the community becomes dominated by a few unpalatable species that are resistant to grazing (log c↓), or they may increase diversity if they reduce the abundance of dominant, competitive or fast-growing species (log c↑) (Koerner et al., 2018; Lind et al., 2013; Olff & Ritchie, 1998; Viola et al., 2010). Herbivores also may increase diversity by increasing the availability of a limiting resource (e.g. light) or increasing the seed dispersal and colonisation rates (Borer et al., 2014b; Olff & Ritchie, 1998). The presence of herbivores also may change environmental variation, for example through localised deposition of faeces or urine (Olff & Ritchie, 1998), which may increase the SAR slope (z↑). As is the case with nutrient effects, we expect herbivore effects on plant diversity to be related to evenness, light availability and plant biomass, such that herbivores will likely have positive effects on diversity at light-limited, productive sites that are dominated by a few plant species (Bakker et al., 2006; Borer et al., 2014b; Koerner et al., 2018).

Here, we analyse species richness data from 30 grasslands or low-stature shrublands (hereafter grasslands) spanning spatial scales of three orders of magnitude (0.01–75 m^2; Figure S1) in the context of the Nutrient Network Distributed Experiment (NutNet, www.nutnet.org), a globally replicated experiment manipulating nutrient supply and herbivore density (Borer et al., 2017; Borer et al., 2014a). The sites for this study are located in 10 countries on five continents and represent a wide range of environmental conditions and ecosystem types including annual grasslands, deserts, tundra, montane meadows, semi-arid and mesic grasslands and old fields. We use these data to address the long-standing gap in our understanding of how environmental drivers affect diversity across spatial scales (Chalcraft et al., 2008; Chase et al., 2018). Specifically, we quantify variability among sites in the slope and intercept of the SAR and test the effects of nutrient addition and herbivore exclusion on the SAR. In addition, we test whether among-site differences in the SAR are correlated with evenness, light availability, plant biomass, the size of the total species pool and whether these covariates affect the strength of the nutrient or consumer reduction treatments (Chalcraft et al., 2008; Lan et al., 2015).

MATERIALS AND METHODS

Experimental design and data collection

We include data from 30 sites in 10 countries, which are part of the Nutrient Network (NutNet) distributed experiment (Borer et al., 2017; Borer et al., 2014a) (Table S1). Sites were dominated by herbaceous or low-statured vegetation and spanned wide gradients in elevation (6 to 3500 m), latitude (52° S to 69° N), mean annual precipitation (249 to 1877 mm yr^{-1}), mean annual temperature (−3 to 23 °C) and mean aboveground live biomass (34 to 900 g m^{-2}). Local richness (4 to 43 species m^{-2}) and total site richness (18 to 142 species $site^{-1}$) were highly variable among sites. We used data from control plots at 30 sites and from two experiments at subsets of the sites: the multiple-nutrient experiment (21 sites) and the consumer–nutrient experiment (16 sites). Experimental duration at the time of sampling varied from 3–11 years (Table S1); inclusion of duration in statistical models did not qualitatively change the results.

Multiple-Nutrient experiment

This experiment factorially combined three nutrient-addition treatments each at two levels (control or fertilised): Nitrogen addition (10 g N m^{-2} yr^{-1} as timed-release urea), phosphorus addition (10 g P m^{-2} yr^{-1} as triple-super phosphate) and potassium and micronutrient addition (10 g K m^{-2} yr^{-1} as potassium sulphate and 100 g m^{-2} yr^{-1} of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo and 1% Zn). N, P and K were applied annually, and the micronutrient mix was applied once at the start of the study.

Consumer–nutrient experiment

This experiment factorially combined nutrient addition (control or fertilised) and vertebrate consumer presence (control or fenced). To do this, we combine the unfenced control and unfenced plots with all nutrients added from the multiple-nutrient experiment with two additional treatments using herbivore fencing: Fenced with no nutrients added and fenced with all nutrients added. Fences were 2.1 m tall and excluded aboveground, non-climbing, vertebrate herbivores. The lower 0.9 m was composed of 1-cm woven wire mesh with a 0.3 m outward-facing flange stapled to the ground to exclude digging animals. The top 1.2 m was composed of five rows of wire. Minor variations in fence design are described by Borer et al. (2014a).

Data collection

We estimated SARs using data collected at five spatial scales: 0.01, 1, 6.25, 25 and 75 m^2 (sampling scheme illustrated in Figure S1). We recorded the presence of all species in each 5 × 5 m plot (25 m^2), a 2.5 × 2.5 m subplot nested within each 5 × 5 m plot (6.25 m^2), a 1 × 1 m subplot nested within each 2.5 × 2.5 m plot (1 m^2) and four 0.1 × 0.1 m subplots placed at the corners of the 1 m^2 subplot (4 by 0.01 m^2). We aggregated species lists across the three replicate 5 × 5 m plots to estimate species richness at the 75 m^2 scale. We also sampled plant species abundances in the 1 × 1 m subplot by visually estimating the areal cover of each species, allowing us to calculate Simpson's evenness at the 1 m^2 scale (Smith & Wilson, 1996).

We used the mean richness of the four 0.01 m^2 subplots in our analyses, and we excluded a small number of 0.01 m^2 subplots with a mean species richness of zero as log richness was undefined (0.1% of samples). We note here that the 75 m^2 richness estimate is based on non-nested data and includes among-block variability, as it is composed of three spatially separate 25 m^2 plots. Nested and non-nested SARs typically have similar slopes in non-forested terrestrial habitats (Drakare et al., 2006). Furthermore, when we only used the fully nested samples with a maximum area of 25 m^2, our results were qualitatively similar. One site did not collect species richness data at the 75 m^2 scale (chilcas.ar) and had a maximum area of 18.75 m^2 (area of three 6.25 m^2 plots). Inclusion or exclusion of this site did not qualitatively change results. We calculated site richness (i.e., site species pool) as the

total number of species found across all sampled plots and years at the site (Table S1).

We sampled aboveground plant biomass by clipping all aboveground biomass (live and dead) in two 0.1 m × 1 m strips, sorting current year's biomass (live biomass) from previous years' biomass (dead biomass), drying the biomass to a constant mass at 60 °C and weighing it to the nearest 0.01 g. Within each 1 m^2 quadrat, we measured the proportion of photosynthetically active radiation reaching the ground level and above the canopy.

Statistical analyses

All analyses were conducted using R version 4.0.2 (R Development Core Team, 2010). We fit a SAR for each treatment at each site using Equation 1b (Figures S2–S5) with the lmList function in the lme4 R library (version 1.1–23), which fits linear models to subgroups of data (e.g., different sites). We used the site-level estimates of z, c and A_{min} in subsequent analyses. A_{min} was natural log transformed due to a highly skewed distribution. We tested whether among-site differences in the SAR parameters were correlated with evenness, light availability, plant biomass and the size of the total species pool. Although we focus on the SAR model in Equation 1, there are a wide range of potential models for SARs (e.g., Flather, 1996). We found that a general three-parameter model (Equation S1) did not provide a better fit to the data than the two-parameter model (Appendix S1) (Flather, 1996).

For the multiple-nutrient or consumer–nutrient experiments, we tested whether experimental treatments altered the SAR parameters with mixed-effects models using the lmer function in the lme4 R library with p-values generated using Satterthwaite's degrees of freedom method using the lmerTest R library (version 3.1–2). We included site as a random effect in these models, and model specifications are included in Tables S2–S4. Inclusion of experimental duration as a random effect in these models did not qualitatively change any results and occasionally prevented the models from fitting due to singularities. We tested for effects of differential errors associated with the estimates of c and z at each site using weighted regression in which weights were the inverse of the standard error of site-level parameter estimates. Weighted regressions were nearly identical to unweighted regressions and did not change interpretation of any results presented here. Here, we present the results of unweighted regressions for simplicity.

In testing for interactions between treatment effects and covariates (evenness, light availability, plant biomass and the size of the total species pool), we used site-level treatment mean of evenness, light availability and plant biomass, whereas the total species pool has only a single measurement per site. Evenness (1 m^2), light (1 m^2) and plant biomass (0.2 m^2) were measured at different scales, and the total species pool is the summed number of species across 30 1 m^2 plots. We used a multi-model approach to model selection using the dredge and model.avg functions in the MuMIn library (version 1.43.17) (Grueber et al., 2011). We standardised the input variables using the arm library (version 1.11–1) and included all models within 4 AIC_c units of the best model.

RESULTS

Across all sites, there was more variability in the SAR intercept (c) than in the SAR slope (z) (Figure S2). The coefficient of variation (CV = standard deviation/mean) for z (0.19) was about three times lower than for c (0.58). Across all sites (N = 30) under ambient conditions (control plots), SAR slopes ranged from 0.12 to 0.33 (mean = 0.23 log(species)/log(m^2)), and the intercept ranged from 2.6 to 33.0 species m^{-2} (mean = 10.7). The x-intercept (A_{min}) had a mean of 1.2×10^{-3} m^2 (12 cm^2) and was highly variable ranging from near 0 to 0.02 m^2 (200 cm^2) with a CV of 2.5. We used natural log-transformed values of A_{min} in our analyses, which ranged from −14.5 to −4.6 log(m^2) (Figures 2 and 3).

In the control plots, the SAR slope (z) and (log c) were uncorrelated ($r = 0.11$, $p = 0.548$); slope (z) and x-intercept (log(A_{min})) were positively correlated ($r = 0.51$, $p = 0.004$) and (log c) and x-intercept (log(A_{min})) were negatively correlated ($r = -0.73$, $p < 0.001$). As would be expected, the SAR intercept was highly correlated with species richness at 1 m^2 when log(A) = 0 ($r = 0.97$, $p < 0.001$).

Among sites, the SAR slope increased with site richness but was unrelated to any other of our covariates in the observational data (evenness, live biomass or proportion of light at ground level) (Table S2; Figure 4). As predicted, local richness (log c) increased with light availability and total site richness (Table S2; Figure 4), and the minimal area of coexistence (A_{min}) declined with light availability (Table S2; Figure 4). There were no significant correlations among the site means of the covariates ($p > 0.05$).

Nutrient addition reduced local diversity (log c) and increased the minimal coexistence area (A_{min}) but did not affect the slope of the SAR (Figures 2 and 3; Tables S3 and S4). The lack of a treatment effect on the SAR slope may reflect either a lack of change in the slope or high variability in the estimates. As noted above, slopes did not vary widely among sites or within treatments (Figures 3 and 4). For example, in our analyses of the experimental data, the standard error in the slope estimates and treatment effects were close to 0.01 (Tables S3 and S4), suggesting that we could detect small differences in slopes among sites and treatments.

Because slopes remained constant and species loss was proportional across scales, addition of all nutrients in combination caused more absolute species loss at the largest scale (mean of 3.2 species lost at 75 m^2) than at

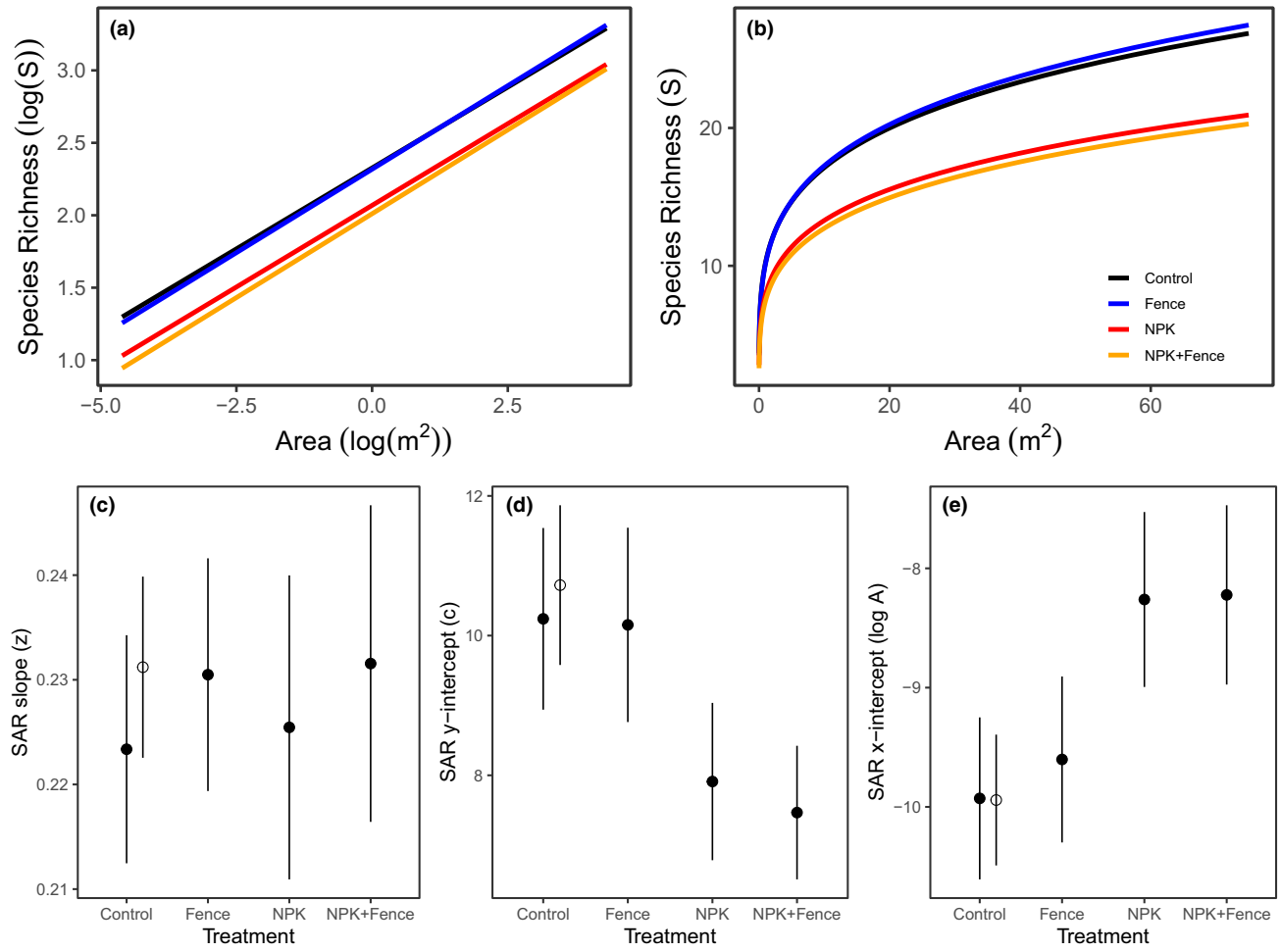

FIGURE 2 Effects of consumers and nutrient addition on slope (z), (log c), and x-intercept (a) of the species–area relationships (SARs) in grasslands (16 sites). SAR plots (Panels A & B) use the mean parameter value for each treatment (Panels C–E). Open circle shows the values in control plots at the larger set of 30 observational sites, which includes the 16 experimental sites (solid circles). Error bars represent 1 standard error of the mean (SEM). Full analysis is shown in Table S3, which includes estimates of treatment effect sizes and significance

the smallest scale (mean of 0.9 species lost at 0.01 m^2). The nutrient effect on species loss was driven by the effects of N addition (Figure 3; Table S4). Fencing did not have a consistent effect on any of the SAR parameters (Figure 2; Table S3).

There were significant interactions between experimental treatments and the environmental covariates. For example, the interaction between site richness and the effects of nutrient enrichment on local richness (log c) was such that sites with more species had higher rates of species loss in the experimental plots (Figure 4, Table S5). Fencing effects on local richness were strongly affected by light transmission, with higher species loss at sites in which fencing reduced light availability (Figure 4, Table S5).

Live biomass and light transmission were affected by experiment treatments. Nutrient addition, primarily N and P addition, reduced light transmission and increased live biomass (Figure 4; Tables S6 and S7). Evenness was unaffected by the experimental treatments (Figure 4; Tables S6 and S7). Site richness, the covariate, is measured at the site scale, so it does not vary among plots or treatments within a site.

DISCUSSION

We found that experimental addition of nutrients, and nitrogen in particular, reduced the SAR intercept (log c) but did not have a consistent effect on the SAR slopes (z) across sites. As a result, proportional species loss was unchanged across spatial scales, whereas total species loss increased more than 3.6-fold with spatial scale within individual sites (Figures 1C,D, 3 and 4). Furthermore, we found that nutrient-induced loss of species was highest at sites with larger species pools (i.e., site-level species richness) (Harpole et al., 2016) and that the effects of fencing were mediated by light availability (Borer et al., 2014b) (Figure 4; Table S5). Although our maximum sample area was rather small relative to other studies, the SAR slopes in our data (mean = 0.23) were similar to those spanning much larger spatial scales in other terrestrial,

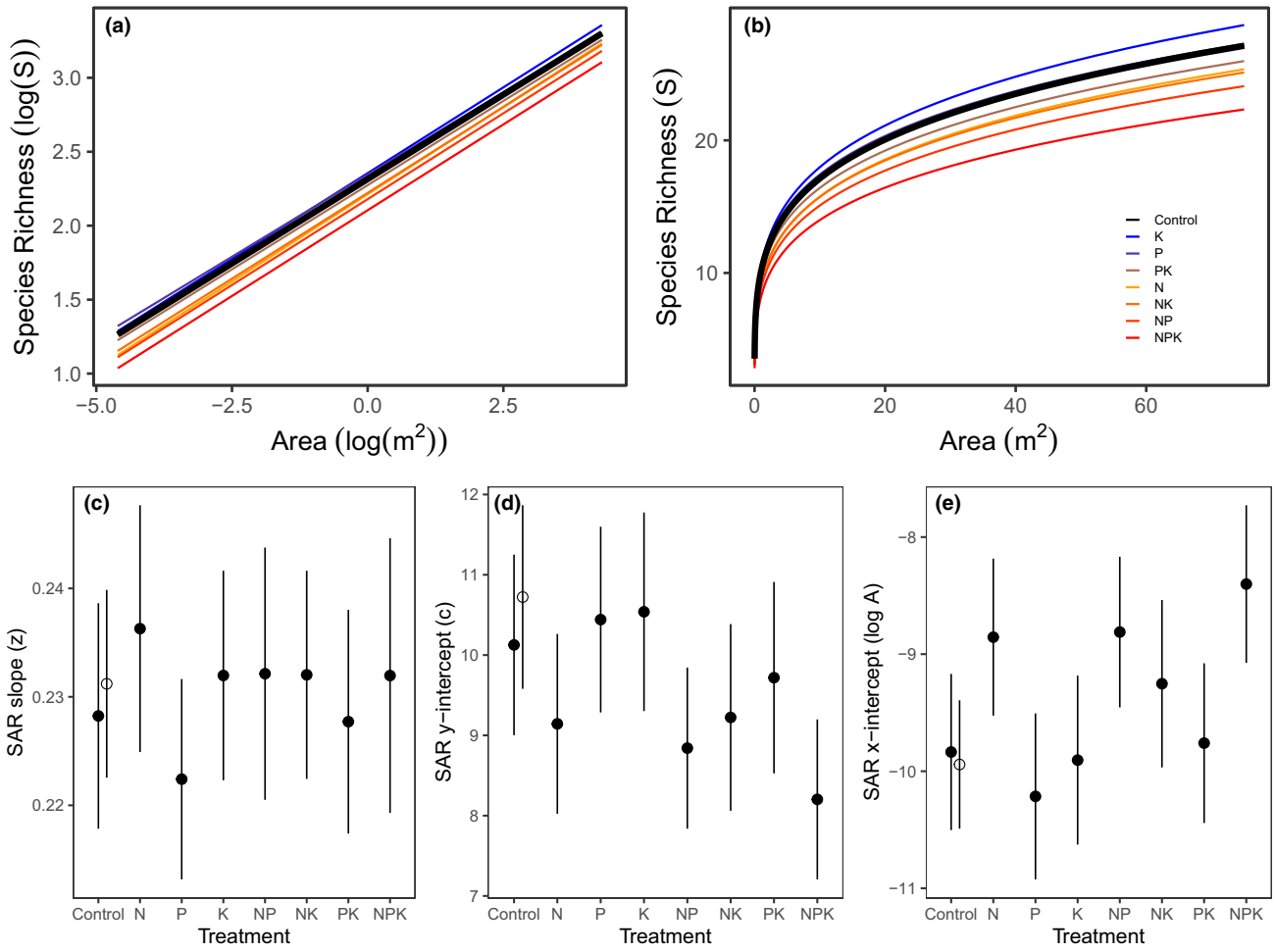

FIGURE 3 Effects of nutrient addition on slope (z), (log c) and x-intercept (a) of the species–area relationships (SARs) in grasslands (21 sites). SAR plots (Panels A & B) use the mean parameter value for each treatment (Panels C–E). Open circles show the values in control plots at the larger set of 30 observational sites, which includes the 21 experimental sites (solid circles). Error bars represent 1 standard error of the mean (SEM). Full analysis is shown in Table S4, which includes estimates of treatment effect sizes and significance

non-forested habitats (Dengler et al., 2020; Drakare et al., 2006).

Our study allowed us to examine small-scale patterns as reflected in the intercept of the SAR (log c) and the minimal area of coexistence (A_{min}). At this scale, our results showed wide variation in local diversity (as estimated by log c) and the minimal area of coexistence (A_{min}) among sites. This among-site variation was related to light availability and total site richness. Across all sites, nutrient addition reduced local diversity (log $c \downarrow$) (see also Borer et al., 2014b; Harpole et al., 2016; Midolo et al., 2019) and increased the minimal area of coexistence (A_{min}), which has not been previously reported to our knowledge. Nutrient-induced changes in local richness were strongest at sites with a larger number of species, as shown by Harpole et al., (2016) using many of these same sites. Finally, we found no consistent relationship in the influence of herbivore exclusion on local diversity measures, which in itself is consistent with other studies that find that herbivore effects on diversity depend on site context (Borer et al., 2014b; Koerner et al., 2018; Proulx & Mazumder, 1998). In our case, the effects of herbivores depended on light transmission, supporting the evidence for light as an important mechanism underpinning herbivore effects on richness (Borer et al., 2014b).

Contrary to the local-scale patterns, we found lesser variation in the scaling relationships, measured by SAR slopes (z). Although local diversity varied widely in unmanipulated control plots, SAR slopes were similar across sites. It is important to note that a wide array of processes govern SARs, and the consistent slopes do not necessarily indicate that the same processes govern diversity across these sites. We found mixed results in our tests of local environmental conditions predicted by theory to mediate SAR slopes. Although the expected negative correlation between SAR slope and evenness was not significant in our larger observational data set (30 sites), we found this in the subset of 16 sites at which we conducted the consumer–nutrient experiment. We did find some evidence for increased SAR slope at sites with large numbers of species in the observational data set. These mixed results mirror the

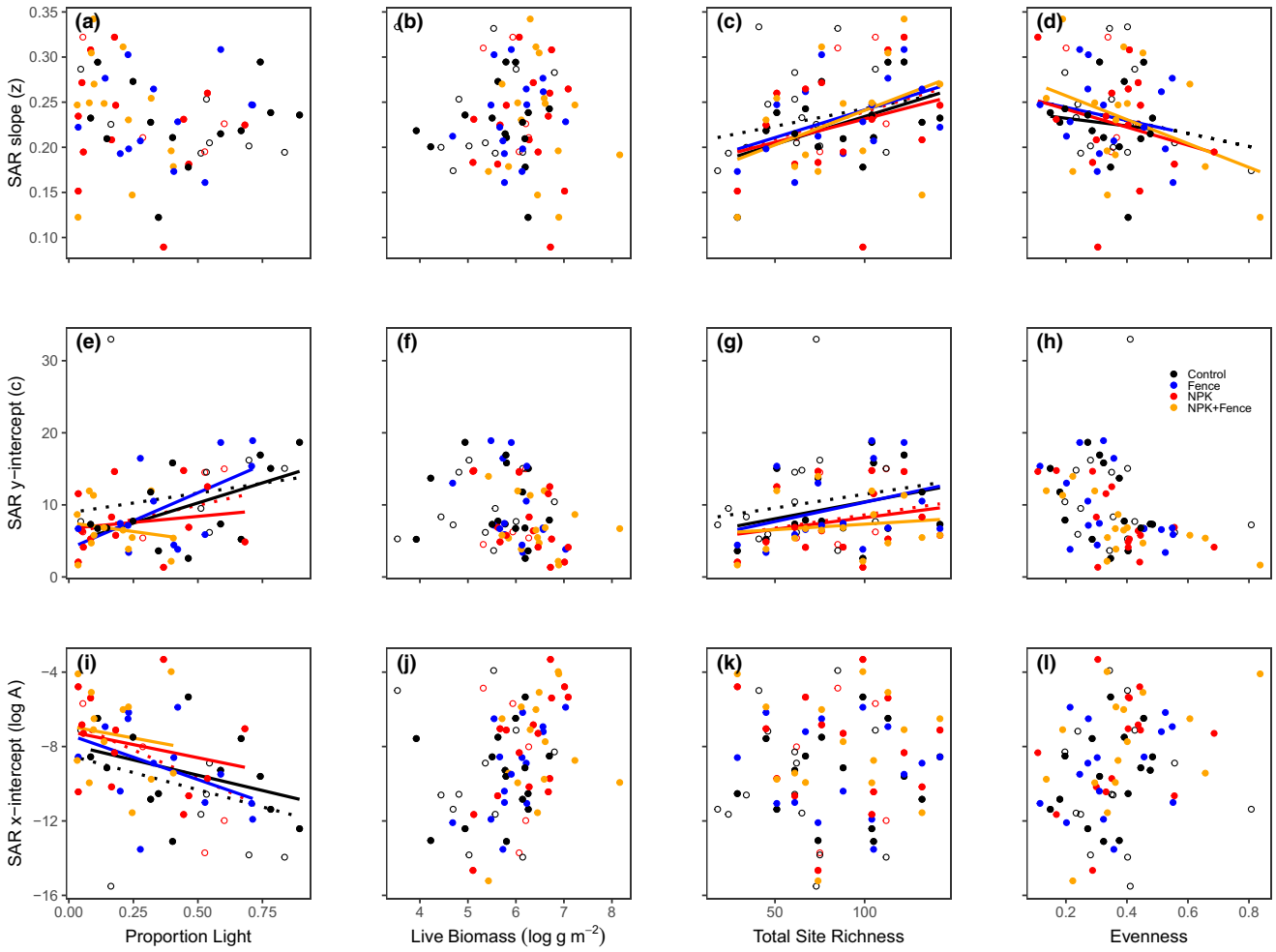

FIGURE 4 Effects of proportion light transmission, aboveground live biomass, site richness and evenness on the slope (z), (log c) and x-intercept (a) of the species–area relationships (SARs) in grasslands. Solid points show SAR parameters for the subset of sites with all fencing and nutrient addition treatments (16 sites). Open circles and dashed lines show SAR parameters from sites with control plots (black lines, 30 sites) and the subset of these with nutrient addition treatments but not fencing (red lines, 21 sites). Lines are shown only for significant regressions. Full analysis is presented in Table S5

literature. Some studies have found relationships between environmental parameters (e.g. productivity) and slopes of the SAR (e.g. Chiarucci et al., 2006; Moradi et al., 2020), whereas other multi-site studies failed to find strong relationships between SAR parameters and environmental characteristics (e.g. DeMalach et al., 2019; Dengler et al., 2020). Furthermore, relationships between diversity and environmental factors may vary in complex ways across scales and among different diversity metrics (Chalcraft et al., 2008; Chalcraft et al., 2004; Chalcraft et al., 2009). In summary, although slopes varied among sites, these scaling relationships were less variable than local diversity and minimal area of coexistence.

Changes in the scaling relationship (i.e. the slope of the SAR) due to external factors, such as nutrient addition or herbivory, also can provide important insights into the nature by which biodiversity responds to experimental treatments (reviewed in Chase et al., 2018). Across our study sites, nutrient addition did not systematically change the SAR slope (z), suggesting a constant proportional loss of species and, as a result, total species loss increased with area (Figure 1C,D). For example, addition of all nutrients in combination caused a mean loss of 0.9 species at the smallest scale (0.01 m^2) and 3.2 species at the largest scale (75 m^2). This is consistent with results from other studies that have manipulated nutrients (Lan et al., 2015), but others have shown either increases or decreases in z (and in some cases, β diversity, which is related to z) with nutrient addition (Chalcraft et al., 2008; Lan et al., 2015; Leps, 2014; Sandel & Corbin, 2012; Zhou et al., 2018). Likewise, we found no effect of herbivore exclusion on the scaling of diversity with area (z) whereas other studies have found positive, negative or neutral effects (Bakker et al., 2006; de Bello et al., 2007; Fernández-Lugo et al., 2011; Godo et al., 2017; Li et al., 2015). Taken in total, the variable results from other studies and the lack of a consistent directional shift in the SAR slope in our analysis indicates that nutrients

and herbivore effects on diversity scaling are highly variable and context dependent.

Changes in the SAR slope (or lack thereof) can be influenced by at least three different features in a regional community (He and Legendre 2002, McGill 2011, Chase & Knight, 2013; Chase et al., 2018): (a) the density or abundance of individuals (including their size), (b) the relative abundance (evenness) of species in the community and (c) the spatial clustering of species in the region (i.e. intraspecific aggregation). Furthermore, each of these can be altered by a number of environmental features, as well as experimental manipulations (e.g. nutrients and herbivory) but not necessarily with the same effect on z. For example, nutrient addition might simultaneously increase the size of individual plants, which may lead to higher z by reducing local diversity (Lan et al., 2015), while concurrently reducing the size of species pool resulting in a lower z (Lan et al., 2015); with the net result being no effect. Likewise, grasslands differ considerably in their ambient conditions of the three components that may influence z (DeMalach et al., 2019), and thus experimentally changing the biotic or abiotic environment could, for example, lead to higher or lower spatial clustering depending on where the grassland started, which may obscure a general influence of experimental treatments on z. We did not collect the spatially explicit abundance data needed to fully resolve the importance of these processes (McGlinn et al., 2019; Powell et al., 2013); making these measurements at a large number of locations would provide greater mechanistic insight into the processes we describe here.

The lack of a consistent change in the diversity–scaling relationships (i.e. the slope of the SAR) to nutrient addition and herbivore exclusion could arise if these treatments primarily reduce non-spatial (local) rather than spatial coexistence mechanisms (but see Chalcraft et al., 2008). Non-spatial mechanisms, such as trade-offs among different resource use efficiency or susceptibility to consumers, should have consistent effects across scales. For example, nutrient addition has frequently been implicated in a loss of non-spatial coexistence mechanisms; the addition of limiting resources leads to a reduction in niche dimensions or switch to single-factor limitation such as light (Borer et al., 2014b; Dybzinski & Tilman, 2007; Goldberg & Miller, 1990; Harpole et al., 2016; Hautier et al., 2009). With respect to spatial mechanisms, a lack of consistent response in the slope of the SAR could be due to one of three possibilities. First, spatial coexistence mechanisms may not be particularly strong in these systems, at least at the scales as which we sampled (<75 m^2). Second, nutrient additions may not have a strong effect on these mechanisms. For example, dispersal limitation and local feedbacks may be more likely to structure coexistence of rare species, and these dynamics may be less strongly influenced by the effect of dominant species. Finally, there may be a lag in diversity responses at larger spatial scales, as has been shown in models with a trade-off between competition and dispersal (e.g. the extinction debt; Tilman et al., 1994).

We note here that the SAR concept arose out of empirical and theoretical work at biogeographical scales (Arrhenius, 1921; Godwin, 1923; MacArthur & Wilson, 1967), especially focused on variation among islands or large habitat patches; however, these relationships have been conceptually useful across a range of other spatial scales (Dengler et al., 2020; Drakare et al., 2006). Here, our focus is on smaller-scale variation within contiguous habitat, and our total species diversity represents the species pool in a single grassland. Nevertheless, the slopes we estimated are quite similar to SARs reported in similar habitats spanning much larger spatial scales (Dengler et al., 2020; Drakare et al., 2006). Despite this similarity in slopes, processes governing diversity scaling at larger regional and biogeographic scales are different than those acting at the scales we address here.

Understanding and measuring diversity is inherently scale-dependent (Chase & Knight, 2013; Chase et al., 2018; Gleason, 1926; Godwin, 1923; Grace et al., 2011; MacArthur & Wilson, 1967; Vellend, 2010), and we have shown that in grassland ecosystems, this scaling is remarkably robust to environmental gradients and experimental manipulations of nutrient supplies and herbivore pressure. This result does not contradict the many studies that have shown the strong impacts of nutrients, in particular on grassland diversity (Borer et al., 2014b; Harpole et al., 2016; Midolo et al., 2019). Rather, we build on this insight in showing that nutrient-induced diversity loss often causes constant proportional loss across spatial scales. As a result, more species will be lost at larger spatial scales, and existing estimates of nutrient-induced diversity loss are likely too low, because they are typically based on a single, relatively small scale of sampling. More generally, embracing the scaling of diversity and its change in response to environmental change is critical if we are to understand the impacts human activities on the biodiversity of the Earth's ecosystems.

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AUTHOR CONTRIBUTIONS

EWS wrote the first draft of the manuscript, and all authors contributed substantially to revisions. EWS analysed the data with contributions from PBA, EB, SB, JMC, LMH, WSH, JLM and TO. Detailed author contributions are presented in Table S8.

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DATA AVAILABILITY STATEMENT

Data are publicly available on the Environmental Data Initiative platform. https://doi.org/10.6073/pasta/404d2e721eb71f15feb65491853d5d42.

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SUPPORTING INFORMATION

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

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