1      **Species Loss Due to Nutrient Addition Increases with Spatial Scale in Global Grasslands**

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78    **Abstract** The effects of human-induced changes to nutrient supplies and herbivore density on
79    species diversity vary with spatial scale because coexistence mechanisms are scale dependent.
80    This scale dependence may alter the species-area relationship (SAR), which describes changes
81    in species richness (S) as a power function of the sample area (A): $S=cA^z$, where c and z are
82    constants. We analyzed the effects of experimental manipulations of nutrient supply and
83    herbivore density on species richness across a range of scales ($0.01 - 75$ m$^2$) at 30 grasslands in
84    10 countries. We found that nutrient addition reduced the number of species that could coexist
85    locally, indicated by the SAR intercepts (log c), but did not affect the SAR slopes (z). As a result,
86    proportional species loss due to nutrient enrichment was constant across sampling scales, and
87    total species loss increased over threefold across our range of sampling scales.

**Introduction**

89     What determines the number of species at a location? This question lies at the core of
90     community ecology. The answer is inherently scale dependent (Arrhenius 1921; Godwin 1923;
91     Gleason 1926; MacArthur & Wilson 1967; Grace *et al.* 2011; Chase *et al.* 2018), because
92     different mechanisms influence diversity at different spatial scales (Chesson 2000; Leibold *et al.*
93     2004; Hart *et al.* 2017; Leibold & Chase 2017; Thompson *et al.* 2020). For example, non-spatial
94     coexistence mechanisms that depend on tradeoffs (e.g., in resource use efficiency or
95     susceptibility to consumers) or temporal variability (e.g., temporal storage effects) can lead to
96     coexistence at very small spatial scales (Hutchinson 1961; Tilman 1982; Holt *et al.* 1994;
97     Chesson 2000). In contrast, coexistence mechanisms that depend on spatial variability, e.g.,
98     dispersal limitation or competition-colonization tradeoffs influence diversity at larger spatial
99     scales (Godwin 1923; Gleason 1926; MacArthur & Wilson 1967; Hastings 1980; Chesson 2000;
100    Leibold *et al.* 2004; Vellend 2010). Furthermore, the size of individuals and the spatial
101    heterogeneity of the environment will determine the scales at which species interact and the
102    minimum possible scale of coexistence (Goldberg & Miller 1990; Oksanen 1996; Seabloom *et al.*
103    2005). For these reasons, differences in diversity observed in field studies, across space or in
104    response to environmental changes induced by ecological and anthropogenic drivers, will
105    reflect both sampling scale and the scale-dependence of coexistence mechanisms.
106    Nevertheless, most empirical studies sample and compare diversity at a single scale, leading to
107    an incomplete understanding of diversity responses to ecological drivers (Chalcraft *et al.* 2008;
108    Lan *et al.* 2015; Chase *et al.* 2018).

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

114                                                 $$S = cA^z$$                                                          (1a)

115    or equivalently

116                                          $$\log(S) = \log(c) + z\,log(A)$$                                          (1b)

117    in which S is the number of species and A is the area sampled (Arrhenius 1921; Flather 1996;
118    Fridley *et al.* 2005; Drakare *et al.* 2006; Dengler *et al.* 2020).

119    In this formulation, the y-intercept, log (c) is a measure of local diversity (proportional to $\alpha$
120    diversity when *A*=1), and the slope (*z*) is a measure of spatial heterogeneity in community
121    composition (proportional to some measures of $\beta$ diversity)(Crist & Veech 2006; Grace *et al.*
122    2011; Scheiner *et al.* 2011). While the SAR only attains a true asymptote at a global scale
123    (Williamson et al. 2001), saturation within sampling confines can be taken as a measure of the
124    available species pool ($\gamma$ diversity)(Grace *et al.* 2011; Chao *et al.* 2014). The x-intercept indicates

125    the Minimal Insular Area ($A_{min}$) (sensu, Heatwole 1975), the area at which only a single species
126    is found (S=1 or log(S)=0) and is a nonlinear function of c and z:

$$A_{min} = c^{-\frac{1}{z}} \qquad (2)$$

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

130    Understanding the patterns and determinants of diversity across scales has gained increased
131    relevance as human domination of the biosphere has altered many of the controls on species
132    diversity, leading to scale-dependent changes in diversity (Chase et al. 2019). For example,
133    humans have increased the supply of biologically-limiting nutrients and have changed the
134    density of herbivores in many ecosystems (Foley et al. 2005; Ripple et al. 2015; Steffen et al.
135    2015), both of which can alter plant diversity at a range of spatial scales (Chaneton & Facelli
136    1991; Olff & Ritchie 1998; Crawley et al. 2005; Bakker et al. 2006; Hillebrand et al. 2007;
137    Chalcraft et al. 2008; Leps 2014; Lan et al. 2015).

138    The effects of environmental change on diversity may shift with spatial scale, and this scale-
139    dependence may be reflected in diversity-scaling relationships such as the parameters of the
140    SAR (Chaneton & Facelli 1991; Olff & Ritchie 1998; Bakker et al. 2006; Chalcraft et al. 2008; Lan
141    et al. 2015; Chase et al. 2018). For example, in grassland ecosystems, increasing the supply
142    rates of biologically limiting nutrients like nitrogen (N) and phosphorus (P) often leads to
143    reduced plant diversity at local scales (i.e., lower log c and higher $A_{min}$; Figure 1) by reducing the
144    opportunity for coexistence through tradeoffs in soil resource use efficiency and increasing
145    competition for light (Goldberg & Miller 1990; Dybzinski & Tilman 2007; Harpole & Tilman
146    2007; Hautier et al. 2009; Borer et al. 2014b; Harpole et al. 2016; Midolo et al. 2019). While the
147    effects of nutrient addition and herbivory on local coexistence in grasslands have been
148    examined experimentally, it remains unclear how these effects will change with spatial scale.
149    Importantly, if environmental changes alter the SAR slope, diversity change measured at a
150    single scale may overestimate or underestimate diversity change at larger spatial scales (Figure
151    1)(Lan et al. 2015).

152    Changes in the scaling relationship will depend on the specific coexistence mechanisms (e.g.,
153    spatial versus non-spatial mechanisms) affected by nutrient enrichment or herbivore exclusion.
154    Furthermore, different mechanisms will be associated with the total biomass, light availability,
155    and size of the species pool (Bakker et al. 2006; Chalcraft et al. 2008; Borer et al. 2014b; Lan et
156    al. 2015; Harpole et al. 2016). For example, nutrient enrichment or herbivore exclusion may
157    increase biomass which can lead to thinning due to light competition, which would reduce the
158    SAR slope and intercept simply due to the presence of fewer larger individuals in each sample
159    (Lan et al. 2015). These treatments also may increase the dominance of a few species, and this
160    reduced evenness would be expected to reduce the SAR intercept but increase the SAR slope
161    (Lan et al. 2015)(Figure 1E). Treatments may also cause the extinction of specific species leading
162    to reduced species pool and lower SAR slope (Figure 1A) (Lan et al. 2015).

163    We have more specific expectations for cross-scale effects of nutrient addition than for
164    herbivore exclusion, because nutrient addition has more consistent effects on grassland plant
165    diversity, and nutrient effects have been examined across scales (Chalcraft *et al.* 2008; Borer *et*
166    *al.* 2014b; Lan *et al.* 2015). For example, if nutrient-induced light limitation reduces coexistence
167    opportunities for a consistent set of species through non-spatial processes such as reduced
168    niche dimensionality (Harpole & Tilman 2007; Harpole *et al.* 2016), then the local diversity loss
169    (log c $\downarrow$) will be accompanied by a reduced total species pool ($\gamma$ diversity $\downarrow$) (Harpole & Tilman
170    2007; Chalcraft *et al.* 2008; Lan *et al.* 2015)(Figure 1C & D). These effects would also be
171    associated with increased biomass and reduced light availability. In this case, the effects on the
172    SAR slope depend on the relative rate of species loss across scales (Lan *et al.* 2015). If there is a
173    constant proportional loss of species with increasing area, then the slope of the SAR would
174    remain constant (Figure 1C & D). In contrast, the slope would decline if there is greater
175    proportional loss at larger spatial scales (z$\downarrow$)(Figure 1A & B), resulting in a more spatially
176    homogeneous community. In a less extreme case, nutrient addition could increase the
177    dominance of species that favor high nutrient conditions without causing species extinctions. In
178    this case, nutrient addition would increase the SAR slope (z$\uparrow$) due to local diversity loss (log c
179    $\downarrow$), but the total species pool would remain unchanged (Figure 1A & B). This effect also would
180    be reflected in reduced species evenness (Lan *et al.* 2015).

181    Nutrient addition also could influence spatial coexistence mechanisms, such as competition-
182    colonization tradeoffs or mass effects by reducing dispersal and local recruitment (Hastings
183    1980; Tilman *et al.* 1994; Leibold *et al.* 2004; Vellend 2010). Reduced dispersal and colonization
184    would lower local diversity (log c$\downarrow$) but leave the total species pool unchanged, resulting in an
185    increased SAR slope (z$\uparrow$) in communities with low to moderate dispersal (Mouquet & Loreau
186    2003; Lan *et al.* 2015)(Figure 1A & B), although very high rates of dispersal may reduce both
187    local richness and the total species pool (Mouquet & Loreau 2003). Finally, nutrient addition
188    could increase individual plant size (Goldberg 1987; Oksanen 1996), thereby reducing local
189    diversity (log c$\downarrow$). As with reduced dispersal, increased plant size would not affect the total
190    species pool but would increase the SAR slope (z$\uparrow$) (Lan *et al.* 2015) (Figure 1E & F).

191    In any of these cases, a constant SAR slope indicates constant proportional change in species
192    with increasing spatial scale, whereas a change in the SAR slope indicates an increasing or
193    decreasing proportional change in the numbers of species with increasing spatial scale (Lan *et*
194    *al.* 2015). Importantly, if there is a constant proportional loss (or gain) of species, this means
195    that there is an increase in the total number of species lost (or gained) at larger spatial scales
196    (Lan *et al.* 2015) (Figure 1C & D).

197    In summary, as we expect nutrient addition to decrease local diversity in grasslands (log c$\downarrow$)
198    (Borer *et al.* 2014b; Midolo *et al.* 2019), the SAR slope will either increase (z$\uparrow$) or decrease (z$\downarrow$)
199    depending on the change in diversity at larger scales (Chalcraft *et al.* 2008; Lan *et al.*
200    2015)(Figure 1). While there are few specific predictions for the minimal area of coexistence
201    ($A_{min}$), we expect this to be negatively correlated with local diversity (log c) via the relationship
202    in Equation 2, such that the expected nutrient-induced reduction in c should lead to an increase
203    in $A_{min}$ depending on the change in z.

204    While the predictions for herbivore effects on diversity scaling are less well developed, the
205    effects should be mediated through changes in the same core processes governing nutrient
206    effects. For example, herbivores may reduce diversity if the community becomes dominated by
207    a few unpalatable species that are resistant to grazing (log $c\downarrow$), or they may increase diversity if
208    they reduce the abundance of dominant, competitive, or fast-growing species (log $c\uparrow$) (Olff &
209    Ritchie 1998; Viola *et al.* 2010; Lind *et al.* 2013; Koerner *et al.* 2018). Herbivores also may
210    increase diversity by increasing availability of a limiting resource (e.g., light) or increasing seed
211    dispersal and colonization rates (Olff & Ritchie 1998; Borer *et al.* 2014b). The presence of
212    herbivores also may change environmental variation, for example through localized deposition
213    of feces or urine (Olff & Ritchie 1998), which may increase the SAR slope ($z\uparrow$). As is the case
214    with nutrient effects, we expect herbivore effects on plant diversity to be related to evenness,
215    light availability, and plant biomass, such that herbivores will likely have positive effects on
216    diversity at light-limited, productive sites that are dominated by a few plant species (Bakker *et*
217    *al.* 2006; Borer *et al.* 2014b; Koerner *et al.* 2018).

218    Here we analyze species richness data from 30 grasslands or low-stature shrublands (hereafter
219    grasslands) spanning spatial scales of three orders of magnitude (0.01 – 75 m$^2$) in the context of
220    the Nutrient Network Distributed Experiment (NutNet, www.nutnet.org), a globally-replicated
221    experiment manipulating nutrient supply and herbivore density (Borer *et al.* 2014a; Borer *et al.*
222    2017). These sites are located in 10 countries on five continents and represent a wide range of
223    environmental conditions and ecosystem types including annual grasslands, deserts, tundra,
224    montane meadows, semi-arid and mesic grasslands, and old fields.  We use these data to
225    address the long-standing gap in our understanding of how environmental drivers affect
226    diversity across spatial scales (Chalcraft *et al.* 2008; Chase *et al.* 2018). Specifically, we quantify
227    variability among sites in the slope and intercept of the species-area relationship (SAR) and test
228    the effects of nutrient addition and herbivore exclusion on the SAR. In addition, we test
229    whether among-site differences in the SAR are correlated with evenness, light availability, plant
230    biomass, the size of the total species pool, and whether these covariates affect the strength of
231    the nutrient or consumer reduction treatments (Chalcraft *et al.* 2008; Lan *et al.* 2015).

232                                 **Materials and Methods**

233                        *Experimental Design and Data Collection*

234    We include data from 30 sites in 10 countries which are part of the Nutrient Network (NutNet)
235    distributed experiment (Borer *et al.* 2014a; Borer *et al.* 2017) (Table S1). All sites were
236    dominated by herbaceous or low-statured vegetation and spanned wide gradients including
237    elevation (6 to 3500 m), latitude (52° S to 69° N), mean annual precipitation (249 to 1877 mm
238    yr$^{-1}$), mean annual temperature (-3 to 23 °C), and mean aboveground live biomass (34 to 900 g
239    m$^{-2}$). Local richness (plot scale richness ranged from 4 to 43 species m$^{-2}$) and total site richness
240    (richness pooled across all sampled plots ranged from 18 to 142 species site$^{-1}$) were highly
241    variable among sites. We used data from control plots at 30 sites and from two experiments at
242    subsets of the sites: the Multiple-nutrient experiment (21 sites) and the Consumer-nutrient
243    experiment (16 sites). Experimental duration at the time of sampling varied from 3-11 years

244 (Table S1), but inclusion of duration in statistical models did not qualitatively change results.
245 While other studies have used this experiment to examine the influence of nutrients and
246 herbivores on patterns of local diversity and coexistence (Borer *et al.* 2014b; Harpole *et al.*
247 2016; Borer *et al.* 2017), there has been no examination of the potential influence of scaling
248 relationships and scale-dependence of treatment effects.

249 **Multiple-nutrient Experiment:** At 21 of the 30 sites, we replicated an experiment that
250 factorially combined three nutrient-addition treatments each at two levels (Control or
251 Fertilized): Nitrogen addition (10 g N $m^{-2}$ $yr^{-1}$ as timed-release urea), Phosphorus addition (10 g
252 P $m^{-2}$ $yr^{-1}$ as triple-super phosphate), and Potassium and Micronutrient addition (10 g K $m^{-2}$ $yr^{-1}$
253 as potassium sulfate and 100 g $m^{-2}$ $yr^{-1}$ of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B,
254 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn). N, P, and K were applied annually, and the
255 micronutrient mix was applied once at the start of the study.

256 **Consumer-nutrient Experiment:** At 16 of the 30 sites, we added an additional two treatments
257 using herbivore fencing: Fenced with no nutrients added and Fenced with all nutrients added.
258 Fences were 2.1 m tall and excluded aboveground, non-climbing, vertebrate herbivores. The
259 lower 0.9 m was composed of 1 cm woven wire mesh with a 0.3 m outward-facing flange
260 stapled to the ground to exclude digging animals. The top 1.2 m was composed of five equally
261 spaced rows of woven wire to prohibit large animals from entering the plots. In combination
262 with the unfenced control and unfenced plots with all nutrients added, we had a full factorial
263 combination of nutrient addition (Control or Fertilized) and vertebrate consumer presence
264 (Control or Fenced).

265 **Data Collection:** We estimated SARs using data collected at five spatial scales: 0.01 $m^2$, 1 $m^2$,
266 6.25 $m^2$, mean 25 $m^2$, and 75 $m^2$. To do this, we sampled plant community composition in 1 m x
267 1 m quadrats by visually estimating the areal cover of each species. The cover data allowed us
268 to estimate richness and Simpson's evenness at an area of 1 $m^2$ (Smith & Wilson 1996). We also
269 recorded the presence of all species in the entire 5 x 5 m plot (25 $m^2$), the 2.5 x 2.5 m subplot in
270 which the cover plot was located (6.25 $m^2$), and four 0.1 x 0.1 m quadrats placed at the corners
271 of the 1 $m^2$ cover quadrat (0.01 $m^2$). We used the mean richness of the four 0.01 $m^2$ in our
272 analyses. We excluded a small number of the 0.01 $m^2$ quadrats in which the mean species
273 richness was zero as log richness was undefined (0.1% of samples). We aggregated species lists
274 across the three replicate 5 x 5 m plots to estimate species richness at the 75 $m^2$ scale. This
275 among block estimate of richness was not nested and incorporates among block variability.
276 Nested and non-nested SAR's have similar slopes in non-forested terrestrial habitats (Drakare *et*
277 *al.* 2006), and our results were qualitatively similar when we only used the fully nested samples
278 with a maximum area of 25 $m^2$. One site did not collect species richness data at the 75 $m^2$ scale,
279 so the maximum scale was at this site (chilcas.ar) was 18.75 $m^2$ (area of three 2.5 $m^2$ plots).
280 Inclusion or exclusion of this site did not qualitatively change results. We calculated site
281 richness (i.e., site species pool) as the total number of species found across all sampled plots
282 and years at the site (Table S1).

283    We sampled aboveground plant biomass by clipping all aboveground biomass (live and dead) in
284    two 0.1 m x 1 m strips, sorting current year's biomass (live biomass) from previous year's
285    biomass (dead biomass), drying the biomass to a constant mass at 60 $^{\circ}$C, and weighing it to the
286    nearest 0.01 g. Within each 1 m$^2$ quadrat, we measured the proportion of photosynthetically
287    active radiation (PAR) reaching the ground level.

288    *Statistical Analyses*

289    All analyses were conducted using R version 4.0.2 (R Development Core Team 2010). We fit a
290    SAR for each treatment at each site using Equation 1b (Figures S1 – S4) with the lmList function
291    in the lmer4 R library (version 1.1-23), which fits linear models to subgroups of data (e.g.,
292    different sites). We used the site-level estimates of z, c, and $A_{min}$ in subsequent analyses. $A_{min}$
293    was natural log transformed due to a highly skewed distribution. We tested whether among
294    site differences in the SAR parameters were correlated with evenness, light availability, plant
295    biomass, the size of the total species pool.

296    While we focus on the SAR model in Equation 1, there are a wide range of potential models for
297    SARs (e.g., Flather 1996). As our goal was to compare parameters across sites, we fit the same
298    model to all sites. However, we also tested whether an alternate model could provide a better
299    fit to the data. To do this, we used a general three parameter model (a, b, c) which is
300    recommended in the absence of a specific theoretical basis (Flather 1996):

301    $$S = \frac{a+bA}{1+cA} \tag{2}$$

302    We fit this model to 30 sites with observational data, and compared the AIC and root mean
303    square error (RMSE) between the two SAR models (Equations 1 and 2). We also fit this model
304    separately to the 4 treatments (Control, Fertilized, Fenced, Fertilized & Fenced) at the 16 sites
305    that implemented the Consumer-nutrient Experiment.

306    For sites that implemented the Multiple-Nutrient or Consumer Nutrient experiments, we tested
307    whether experimental treatments altered the SAR parameters with Mixed Effects Models
308    (MEMs) using the lmer function in the lme4 R library with p-values generated using
309    Satterthwaite's degrees of freedom method using the lmerTest R library (version 3.1-2). We
310    included site as a random effect in these models, and model specifications are included in
311    Tables S2-S4. Inclusion of experimental duration as a random effect in these models did not
312    change any results and occasionally prevented models from fitting due to singularities.
313    We tested for effects of differential errors associated with the estimates of c and z at each site
314    by running weighted regression in which weights were the inverse of the standard error of site-
315    level estimate of c and z. Weighted regressions were nearly identical to unweighted regressions
316    and did not change interpretation of any results presented here. Here we present results of
317    unweighted regressions in the interest of parsimony and to give equal weight to each site.
318
319    In testing for interactions between treatment effects and covariates (evenness, light availability,
320    plant biomass, the size of the total species pool), we used site level treatment mean of
321    evenness, light availability, and plant biomass, while the total species pool has only a single

322    measurement per site. We note here that evenness (1 m$^2$), light (1 m$^2$), and plant biomass (0.2
323    m$^2$) are measured at different scales within each plot, while the total species pool is the
324    summed number of species across 30 1 m$^2$ plots. In these analyses, the correlation among
325    these covariates could lead to a suite of comparable models rather than a single best model. To
326    address this, we used a multi-model approach, as described in Grueber et al. (2011) using the
327    dredge and model.avg functions in the MuMIn library (version 1.43.17). We standardized the
328    input variables using the arm library (version 1.11-1). In the model averaging, we included all
329    models within 4 AIC$_c$ units of the best model.

## Results

331    We started by testing if the appropriateness of the two-parameter SAR formulation (Equation
332    1) relative to a more general three parameter model (Equation 2).). In paired t-test, the two-
333    parameter model fit the observational data (30 sites) better than the three-parameter model
334    based on AIC (t = -2.343, p=0.026) and RMSE (t = -2.231, p = 0.033). We also compared these
335    models using the 16 sites that implemented the Consumer-nutrient Experiment. As was the
336    case for observational sites, the three-parameter model did not provide a better fit based on
337    AIC and RMSE. Based on these analyses, we concluded that the two-parameter model was
338    appropriate for our analyses and our subsequent descriptions and discussion focus only on that
339    model.

340    Overall, sites showed more variability in SAR intercept (c) than in the SAR slope (z) (Figure S1).
341    The coefficient of variation (CV = standard deviation / mean) for z (0.19) was about 3 times
342    lower than for c (0.58). Across all sites (N=30) under ambient conditions (Control Plots), SAR
343    slopes ranged from 0.12 to 0.33 (mean=0.23 log(species)/log(m$^2$)) and the intercept ranged
344    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
345    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
346    used natural log transformed values of $A_{min}$ in our analyses, which ranged from -14.5 to -4.6
347    log(m$^2$) (Figures 2 & 3).

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

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

359    Nutrient addition reduced local diversity (log c) and increased the minimal coexistence area
360    ($A_{min}$) but did not affect the slope of the SAR (Figures 2 & 3; Tables S3 & S4). The lack of a

361  treatment effect on the SAR slope may reflect either a lack of change in the slope or high
362  variability in the estimates. As noted above, slopes did not vary widely among sites, and
363  variance among slope estimates among sites was not large within treatments (Figures 4 & 5).
364  For example, in our analyses of the experimental data, the standard error in the slope estimates
365  and treatment effects were close to 0.01 (Tables S3 & S4), suggesting that we could detect
366  small differences in slopes among sites and treatments.

367  Because slopes remained constant and species loss was proportional across scales, addition of
368  all nutrients in combination caused more absolute species loss at the largest scale (mean of 3.2
369  species lost at 75 $m^2$) than at the smallest scale (mean of 0.9 species lost at 0.01 $m^2$). The
370  nutrient effect on species loss was driven by the effects of N addition (Figure 3; Table S4).
371  Fencing did not have a consistent effect on any of the SAR parameters (Figure 2; Table S3).

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

378  Some of the focal environmental covariates that we measured at the plot scale, live biomass
379  and light transmission, were affected by experiment treatments. Nutrient addition, primarily N
380  & P addition, reduced light transmission and increased live biomass (Figure 5; Tables S6 & S7).
381  Evenness was unaffected by the experimental treatments (Figure 5; Tables S6 & S7). The
382  covariate, site richness is measured at the site scale, so does not vary among plot or treatments
383  within a site.

384                                        **Discussion**

385  We found that experimental addition of nutrients, and nitrogen in particular, reduced the SAR
386  intercept (log c), but did not have a consistent effect on the SAR slopes (z) across sites. As a
387  result, proportional species loss was constant across spatial scales, and total species loss
388  increased over 3.6-fold with spatial scale within individual sites (Figure 1C & D, 3, & 4).
389  Furthermore, we found that nutrient-induced loss of species was highest at sites with larger
390  species pools (i.e., site-level species richness)(Harpole *et al.* 2016), and that the effects of
391  fencing were mediated by light availability (Borer *et al.* 2014b)(Figure 5; Table S5). While our
392  maximum sample area was rather small relative to other studies, the SAR slopes in our data
393  (mean=0.23) were similar to those spanning much larger spatial scales in other terrestrial, non-
394  forested habitats (Drakare *et al.* 2006; Dengler *et al.* 2020).

395  Our study allowed us to examine small-scale patterns as reflected in the intercept of the SAR
396  (log c) and the minimal area of coexistence ($A_{min}$). At this scale, our results showed wide
397  variation in local diversity (log c) and the minimal area of coexistence ($A_{min}$) among sites. This
398  among-site variation was related to light availability and total site richness. Across all sites, we
399  found that nutrient addition reduced local diversity (log c↓) (Borer *et al.* 2014b; Harpole *et al.*

400    2016; Midolo *et al.* 2019) and also increased the minimal area of coexistence ($A_{min}$), which has
401    not been previously reported. Nutrient induced changes in local richness were strongest at sites
402    with a larger number of species, as has been shown by Harpole *et al.* (2016) using many of
403    these same sites. Finally, we found no consistent relationship in the influence of herbivore
404    exclusion on local diversity measures, which in itself is consistent with other studies that find
405    that herbivore effects on diversity depend on site context (Proulx & Mazumder 1998; Borer *et*
406    *al.* 2014b; Koerner *et al.* 2018). In our case, the effects of herbivores depended on light
407    transmission, supporting the evidence for light as an important mechanism underpinning
408    herbivore effects on richness (Borer *et al.* 2014b).

409    As opposed to the local-scale patterns, we found much less variation in the scaling relationships
410    indicated by SAR slopes (z). While local diversity varied widely in unmanipulated control plots,
411    SAR slopes were similar across sites. It is important to note that a wide of array of processes
412    govern SARs, and the consistent slopes do not necessarily indicate that the same processes
413    govern diversity across these sites. We found mixed results in our tests of local environmental
414    conditions predicted by theory to mediate SAR slopes. While we did not find the expected
415    negative correlation between SAR slope and evenness in our larger observational data set (30
416    sites), we found this in the subset of 16 sites at which we conducted the Consumer-nutrient
417    experiment. We did find some evidence for increased SAR slope at sites with large numbers of
418    species in the observational data set. These mixed results mirror the literature. Some studies
419    have found relationships between environmental parameters (e.g., productivity) and slopes of
420    the SAR (e.g., Chiarucci *et al.* 2006; Moradi *et al.* 2020), while other multi-site studies failed to
421    find strong relationships between SAR parameters and environmental characteristics (e.g.,
422    DeMalach *et al.* 2019; Dengler *et al.* 2020). Furthermore, relationships between diversity and
423    environmental factors may vary in complex ways across scales and among different diversity
424    metrics (Chalcraft *et al.* 2004; Chalcraft *et al.* 2008; Chalcraft *et al.* 2009). In summary, while
425    slopes varied among sites, these scaling relationships were less variable than local diversity and
426    minimal area of coexistence.

427    Changes in the scaling relationship (i.e., the slope of the SAR) due to external factors, such as
428    nutrient addition or herbivory, also can provide important insights into the nature by which
429    biodiversity responds to experimental treatments (reviewed in Chase *et al.* 2018). Across our
430    study sites, nutrient addition did not systematically change the SAR slope (z), suggesting a
431    constant proportional loss of species, and as a result, total species loss increased with area
432    (Figure 1C & D). For example, addition of all nutrients in combination caused a mean loss of 0.9
433    species at the smallest scale (0.01 m$^2$) and 3.2 species at the largest scale (75 m$^2$) . This is
434    consistent with results from other studies that have manipulated nutrients (Lan *et al.* 2015), but
435    others have shown either increases or decreases in z (and in some cases, $\beta$ diversity, which is
436    related to z) with nutrient addition (Chalcraft *et al.* 2008; Sandel & Corbin 2012; Leps 2014; Lan
437    *et al.* 2015; Zhou *et al.* 2018). Likewise, we found no effect of herbivore exclusion on the scaling
438    of diversity with area (z), whereas other studies have found positive, negative or neutral effects
439    (Bakker *et al.* 2006; de Bello *et al.* 2007; Fernández-Lugo *et al.* 2011; Li *et al.* 2015; Godo *et al.*
440    2017). Taken in total, the variable results from other studies and the lack of a consistent

441    directional shift in the SAR slope in our analysis indicates that nutrients and herbivore effects
442    on diversity scaling will be highly variable and context dependent.

443    Changes in z (or lack thereof) can be influenced by at least three different features in a regional
444    community (He and Legendre 2002, McGill 2011, Chase and Knight 2013, Chase et al. 2018): (1)
445    the density or abundance of individuals (including their size), (2) the relative abundance
446    (evenness) of species in the community, (3) the spatial clustering of species in the region (i.e.,
447    intraspecific aggregation, influencing beta diversity). Furthermore, each of these can be altered
448    by a number of environmental features, as well as experimental manipulations (e.g., nutrients
449    and herbivory), but not necessarily with the same effect on z. For example, nutrient addition
450    might simultaneously increase the size of individual plants, which may lead to higher z by
451    reducing local diversity (Lan *et al.* 2015), while concurrently reducing the size of species pool
452    resulting in a lower z (Lan *et al.* 2015); with the net result being no effect. Likewise, grasslands
453    differ considerably in their ambient conditions of the three components that may influence z
454    (DeMalach *et al.* 2019), and thus experimentally changing the biotic or abiotic environment
455    could, for example, lead to higher or lower spatial clustering depending on where they started,
456    which may obscure a general influence of experimental treatments on z. We did not collect the
457    spatially-explicit abundance data needed to fully resolve the importance of these processes
458    (Powell *et al.* 2013; McGlinn *et al.* 2019); making these measurements at a large number of
459    locations would provide greater mechanistic insight into the processes we describe here.

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

477    We note here that SARs arose out of empirical and theoretical work at biogeographical scales
478    (Arrhenius 1921; Godwin 1923; MacArthur & Wilson 1967), especially focused on variation
479    among islands or large habitat patches; however, these relationships have been conceptually
480    useful across a range of other spatial scales (Drakare *et al.* 2006; Dengler *et al.* 2020). Here, our
481    focus is on smaller scale variation within contiguous habitat, and our total species diversity

482   represents the species pool in a single grassland or meadow. Nevertheless, the slopes we
483   estimated are quite similar to SARs reported in similar habitats but spanning much larger spatial
484   scales (Drakare *et al.* 2006; Dengler *et al.* 2020). Despite this similarity in slopes, processes
485   governing diversity scaling at larger regional and biogeographic scales are different than those
486   acting at the scales we address here.

487   Understanding and measuring diversity is inherently scale-dependent (Godwin 1923; Gleason
488   1926; MacArthur & Wilson 1967; Vellend 2010; Grace *et al.* 2011; Chase & Knight 2013; Chase
489   *et al.* 2018), and we have shown that in grassland ecosystems this scaling is remarkably robust
490   to environmental gradients and experimental manipulations of nutrient supplies and herbivore
491   pressure. This result does not contradict the many studies that have shown the strong impacts
492   of nutrients in particular on grassland diversity (Borer *et al.* 2014b; Harpole *et al.* 2016; Midolo
493   *et al.* 2019). Rather, we build on this insight in showing that nutrient-induced diversity loss
494   often causes constant proportional loss across spatial scales. As a result, more species will be
495   lost at larger spatial scales, and existing estimates of nutrient-induced diversity loss are likely
496   too low, because they are typically based on a single, relatively small scale of sampling. More
497   generally, embracing the scale-dependence of diversity, and diversity loss in response to
498   different types of environmental change, is critical if we are to understand the impacts human
499   activities on the biodiversity of the Earth's ecosystems.

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676 **Acknowledgments**

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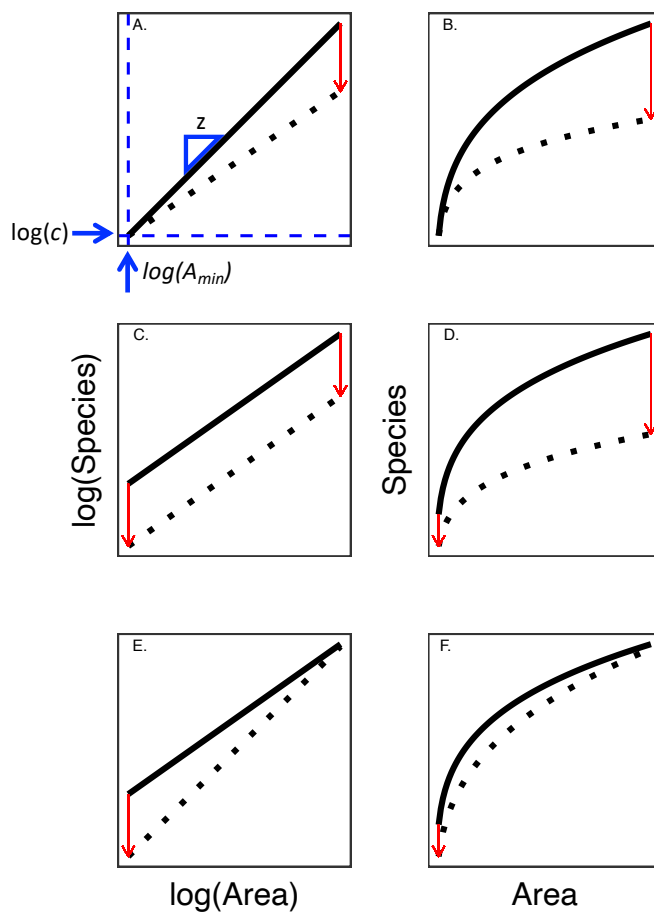699   but the slope is increased, such that species loss declines with area.



700

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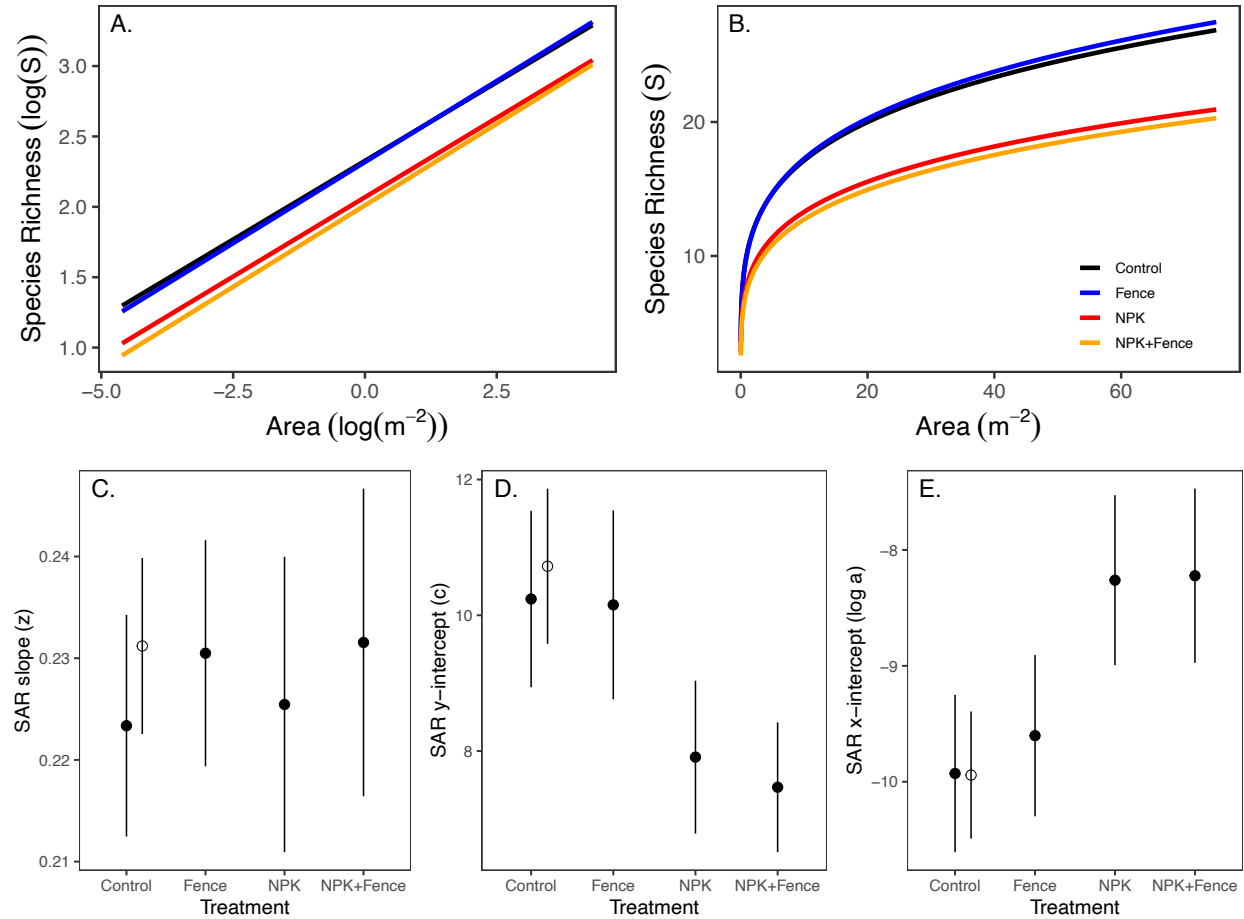706 Table S3, which includes estimates of treatment effects sizes and significance.



707

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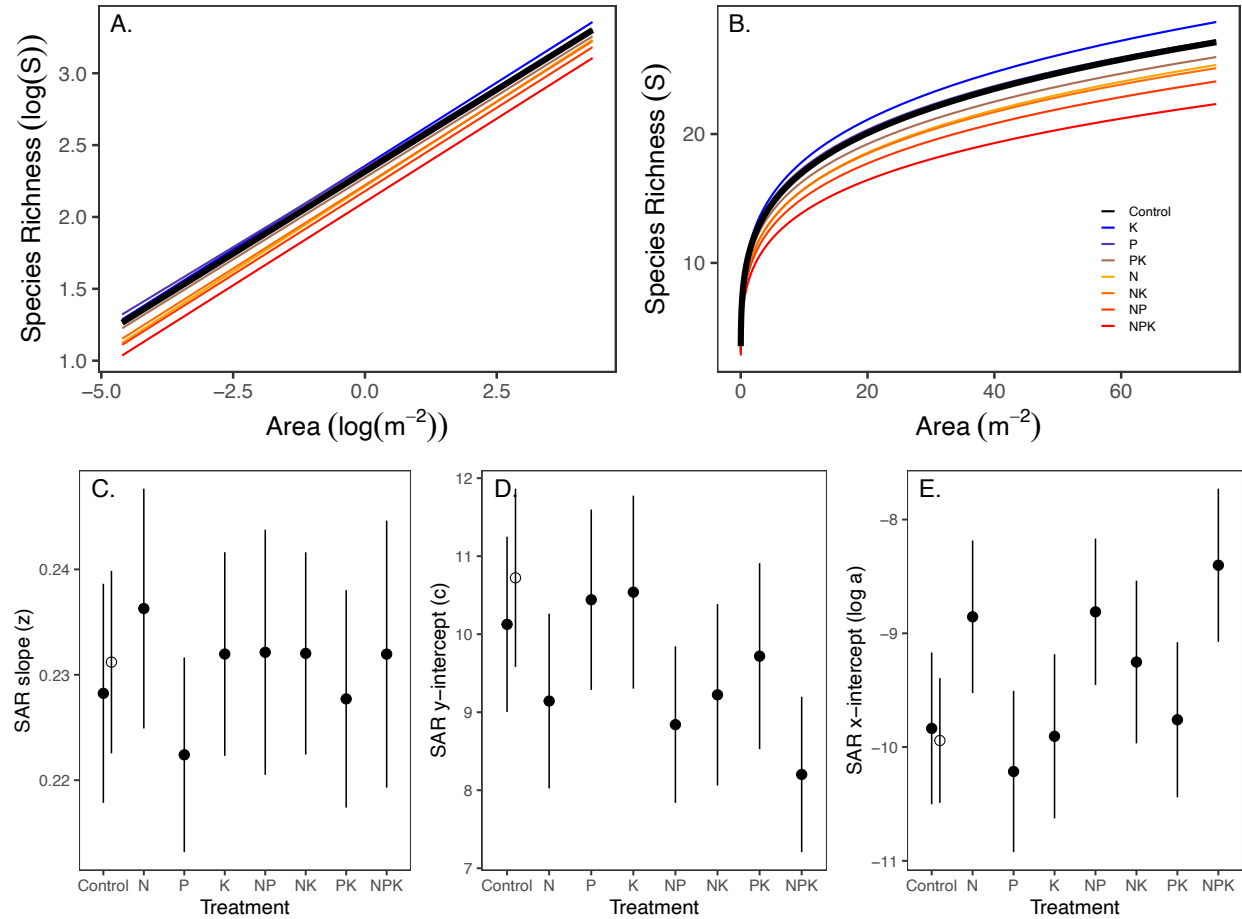713    includes estimates of treatment effects sizes and significance.



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715

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



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