Letters

The influence of sampled biomass on species–area relationships of grassland plants

Understanding scaling relationships in ecology can foster the development of valuable predictive tools and also pave the ground towards the formulation of better mechanistic models. The species–area relationship (SAR) is a classical example of an empirical relationship between species richness (S) and sampling area (A). This relationship arises from the combined effects of higher detection likelihood due to sampling effects as larger areas are sampled and differential niche effects attributed to the habitat heterogeneity of larger areas (Cam *et al.*, 2002). It has also been argued that SARs could arise from other factors such as dispersal constraints (Rosindell & Cornell, 2007).

The SAR is a particularly useful concept in conservation biology as it can provide informative estimates of the recommended size of reserves (e.g. Gitay *et al.*, 1991) but also in extinction ecology where it can be used as a basis to calculate species extinctions following habitat loss (Halley *et al.*, 2013). A frequent issue involving the SAR is how it might be affected by net primary productivity. For annual grasslands sampled biomass (SB) may be a good proxy of net primary productivity but for perennial systems, and particularly those that are dominated by woody plants, the relationship between SB and net primary productivity may be weak. While standing biomass in many cases may be a poor indicator of net primary productivity (for example grasslands may be more productive than forests), for sites sharing comparable seral stages it can still represent a good proxy. For example, intuitively one might expect species richness to increase with SB but there are numerous counter examples such as the tendency for nitrogen enrichment to reduce biodiversity (Stevens *et al.*, 2004) or the low net primary productivity of many rainforest soils following deforestation (Kontowska *et al.*, 2015). While cross-habitat heterogeneity may occasionally compromise SARs (Báldi, 2008) there is compelling evidence that combining data from multiple small-scale quadrats yields robust SARs (Harte *et al.*, 1999).

In this paper we address the species accumulation curves of (typically nested) sample areas. Collecting data to fit SAR can be an exceptionally laborious task and it is often the synthesis of existing studies that permits comparison across sites. Sólymos & Lele (2012) synthesized existing data to estimate a mean power-law slope (z) of 0.205 and an intercept (c) for 1 km^2 plots of 3.209 (c. 25 plants per km^2) for vascular plants, globally. However these estimates may vary considerably across different systems. Pastor *et al.* (1996) fitted Arrhenius-relationship parameters (as power law scaling factors) to nested quadrats in six grassland plots in

Minnesota finding that zeta parameters declined with SB whereas c parameters increased. To the best of our knowledge relationships between SAR parameters and SB have not been tested anywhere else. Fraser *et al.* (2015) established a global network of 30 grassland sites in 19 countries to study SB–diversity relationships. Analysis of their 157 grids each consisting of 64 1 m × 1 m quadrats within an 8 m × 8 m area revealed humped overall SB–diversity relationships at 1, 2, 4, 9, 16, 25 and 64 m^2 scales, but explanatory power of SB diminished with increasing scale. However, the way species–area parameters scale with environmental factors can be counter-intuitive; for example when the relationship between richness and productivity within sites is negative but the more productive sites host richer species assemblages (Scheiner *et al.*, 2000).

The unique dataset of Fraser *et al.* (2015) offers great opportunities to better understand SARs. We reanalyzed the dataset to assess the way SAR parameters scale with SB. We expected that at high SB plants compete for a single resource (light) instead of nutrients and water and this would lead to competitive exclusion of rare taxa (Stevens *et al.*, 2004). We thus hypothesized a monotonic negative response of z_0 (maximum slope) with SB. We further hypothesized that higher SB would increase c (intercept) as was shown by Pastor *et al.* (1996).

In our analysis we considered both standing plant biomass and litter as constituents of SB. Traditionally SARs were modeled as a Arrhenius equation: a linear relationship between $s = \log S$ and $u = \log A$ with a slope of z and an intercept of c. However, it is well known that z is not constant but changes with scale. Harte *et al.* (2009) proposed a framework through which a global curvature constant (η) could be calculated. In this case fitting a SAR once the curvature is assessed requires regression with a modified response variable $y(u)$ for species richness, to find parameters z_0 (maximum slope value for 1 × 1 m^2 quadrats) and c (Supporting Information Methods S1):

$$y(u) = c + z_0 \cdot u, \quad y = s - b \cdot u^2, \quad b \approx \left(1 + (\bar{z})^2\right)^{3/2} \cdot \eta$$

Eqn 1

We first assessed a global curvature constant, η through combining local curvature information across all grids (Harte *et al.*, 2009). To estimate independently the parameters z_0 and c for each grid we assembled virtual quadrats continuous in space of desired sizes through combining data from the 1 × 1 m^2 quadrats (Harte *et al.*, 1999). We used for this purpose 100 bootstrap replicates of each of the quadrat sizes (1, 2, 4, 8, 16, 32 m^2) and recorded the two parameters through fitting two nonlinear models that combined all grid data following a log–log transformation with richness as a response variable and area as a predictor (Methods S1). To assess the way the parameters z_0 and c varied with SB across sites we first fitted for each parameter a mixed-effects linear model (site was used as a random effects factor) with and without quadratic

terms. For the parameter *c* the quadratic term (as well as the linear) was significant and we further fitted a segmented regression and assessed significance of the two resulting line segments (before and after the breakpoint). To assess the way the two parameters varied with SB within sites, we paired grids within sites and identified log-response ratios (RR) of biomass, zeta parameter estimates and *c* parameter estimates. A tendency of the RR for either parameter to obtain bigger values when the SB RR was larger would manifest as a positive relationship of within-site SB and the parameter and *vice versa*. Before fitting any models we transformed our data to meet the assumptions of homoscedasticity and normality.

Our mean z_0 value of 0.485 was higher than that reported for plants in Sólymos & Lele (2012). Our *c* value for 1–m^2 plots was 3.34. The parameter z_0 was monotonically positively influenced by SB (Fig. 1a). By contrast, we detected a negative relationship between SB and *c*. When we added to this model quadratic terms both linear and quadratic terms were significant and the model became more parsimonious based on Akaike Information Criterion estimates. We further explored this relationship with segmented regression. The breakpoint of the segmented regression was for an SB of *c.* 292 g m^{-2}. Both the mixed effect linear models for the SB gradient above and below the breakpoint were significant suggesting that the parameter *c* increases with SB up to an optimal
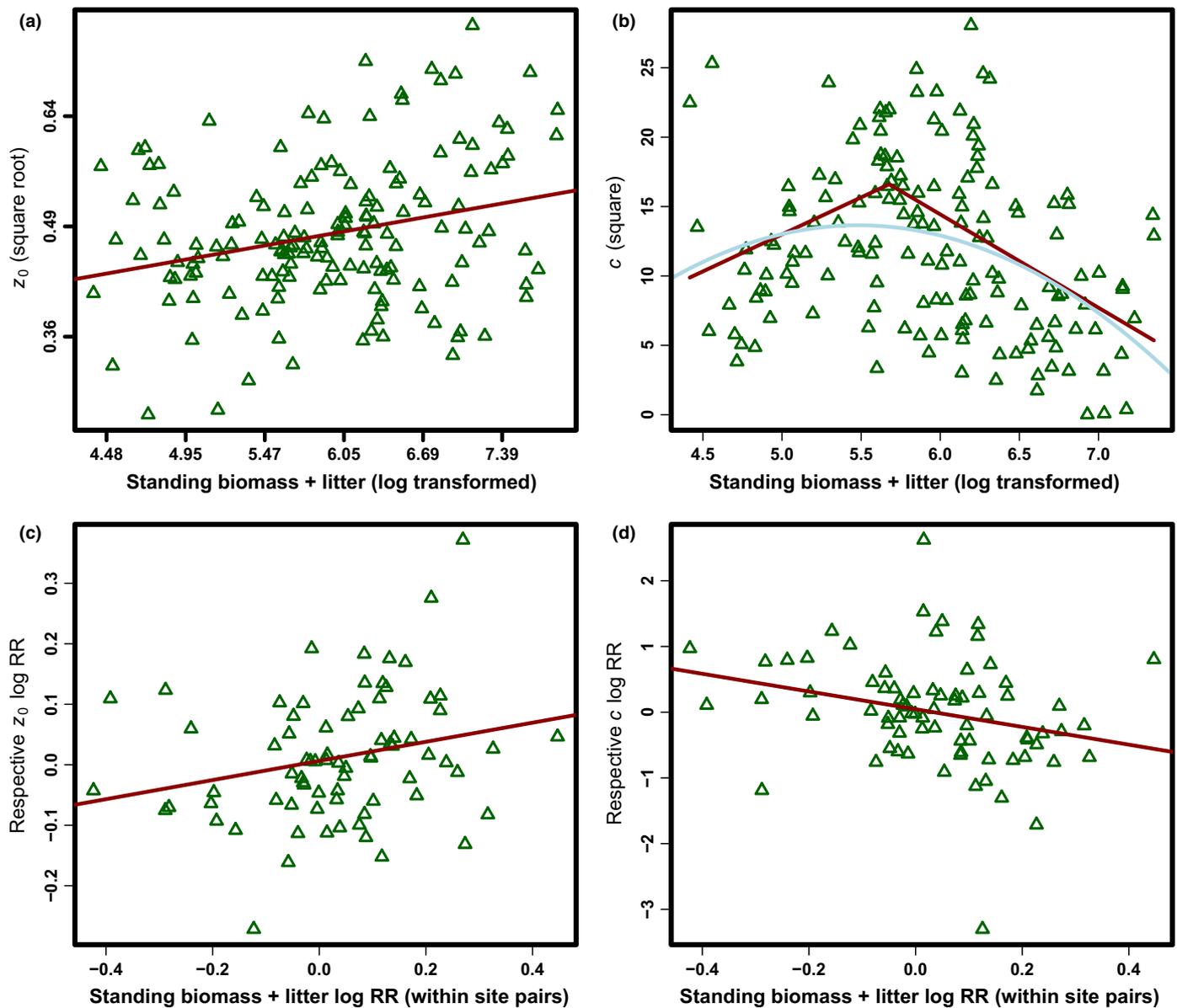
Fig. 1 (a) Relationship between standing biomass + litter (in the text sampled biomass) and the maximum observed slope of the species–area relationship (SAR) – z_0 across sites overlayed with the best fit line based on a mixed effects model; (b) relationship between standing biomass + litter and the intercept of the SAR relationship – *c* with overlayed best fit quadratic line (light blue) and the first order lines that were derived from segmented regression – all lines were significant; (c) a significant correlation was found between the log response ratios (RR) of within-sites standing biomass + litter differences over z_0 differences; (d) the respective relationship for *c* was also significant. For the specific linear models z_0 was square root transformed and *c* was square power transformed.

level of SB but then declines (Figs 1b, S1). Within-site comparisons of response ratios of SB vs z_0 were significant ($r = 0.49$, $P < 0.001$; Fig. 1c). We also found significance for within-site comparisons of RR of SB vs c but this time the relationship was negative ($\tau = -0.24$, $P = 0.002$, Figs 1d, S3). Detailed statistics for the tests are provided in Methods S1.

Our results support the idea of a humped relationship between the parameter c and SB gradients across sites but a negative relationship within sites. Observed differences on the effect of SB on c between and within sites may relate to the fact that the SB differences within sites were considerably smaller or resulted from within-site differences in biotic and abiotic parameters being less pronounced than between-sites. Alternatively SB may only promote c values over a narrow range of low-SB systems; in our within-sites analysis these SB sites did not cluster with each other and these effects were masked by the considerably more numerous higher SB sites. The nonmonotonic relationship we detected with regards to z_0 is incongruent with our hypotheses. The positive relationships (within and between sites) with regards to the parameter z_0 were also inconsistent with the existing literature and our hypotheses. When projecting our SAR estimates in agreement with the literature (Gillman & Wright, 2006; Fraser *et al.*, 2015) we find humped-shaped SB–diversity relations for small grassland plots with a trend towards producing positive relations for large-grassland areas (Figs S2, S4).

How could our results be informative from a policy-making perspective? It has been argued that a high parameter z reflects a greater number of endemic or geographically limited species (Harte & Kinzig, 1997). Because most grassland species have wide geographic distributions, it is the geographically-limited species that are of high conservation priority. Thus, contrary to intuition, conserving high-SB grasslands might optimize our conservation strategy. In fact, if realized species richness declines after some threshold of SB (e.g. Fraser *et al.*, 2015) then conservation efficiency could rely on a tradeoff between the higher probability of encountering rare taxa in productive sites and the high realized species richness of intermediate SB sites. The SLOSS controversy (Single Large Or Several Small; Wilson & Willis, 1975) asks whether it is better to invest in numerous small reserves or a large one of equivalent size. Our analysis suggests that conservationists should stratify grassland habitats based on their SB and disperse their conservation efforts to representative habitats across these strata.

Assessing the effect of environmental variables on the scaling parameters of SAR offers a contrasting approach to traditional correlational ecology perspectives on the assembly of plant communities. SB appears to be a key determining factor of the value of the power-law exponent of such relationships and should be considered in future studies. Testing relationships with other environmental variables may represent a promising avenue of further advancing ecology.

Author contributions

S.D.V. conceived the project and S.D.V. and J.M.H. carried out the analysis. S.D.V. and J.M.H. wrote the manuscript with the help of M.C.R. and L.H.F.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Exploratory analysis of square transformed parameter *c*.

Fig. S2 Projected productivity–diversity relationships.

Fig. S3 Exploratory analysis of square root transformed parameter z_0.

Fig. S4 Estimated values for the c parameter compared to observed richness values.

Methods S1 Detailed description of the materials and methods used for the analysis and statistics on the models used.

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