Grain size affects the relationship between species richness and above-ground biomass in semi-arid rangelands

Anvar Sanaei, Íñigo Granzow-de la Cerda and Luis Cayuela

Abstract

Background: Discrepancies in the shape of the productivity–diversity relationship may arise from differences in spatial scale. We hypothesised that there is a grain size effect on the productivity–diversity relationship.

Aims: To determine the effect of three sampling grain sizes on the productivity–diversity relationship.

Methods: We applied generalised linear mixed effect models on community data from 735 vegetation plots in the Taleghan rangelands, Iran, sampled at three grain sizes (0.25, 1 and 2 m²) to ascertain plant productivity-diversity patterns, while accounting for the effects of site, plant community type, disturbance, and life form.

Results: Overall, relationships between biomass and plant species richness were unimodal at grain sizes of 0.25 and 1 m², and asymptotical at 2 m². The spurious occurrence of a single large shrub may overwhelm a small-sized sampling unit, resulting in a high estimate of the sample’s biomass relative to species richness. However, the relationship between biomass and species richness at larger grain sizes is more likely to reach an asymptote.

Conclusions: Shrubs are partly responsible for driving the relationship between plant biomass and species richness. Given that the frequency of shrubs is highly variable between small plots but not so in large plots, their presence may result in unimodal productivity–diversity relationships at small but not at large grain sizes.

Introduction

The relationship between productivity and species diversity has long been studied under different environmental conditions across various geographical extents: from local to continental. The unimodal pattern (humped-back function curve) proposed by Grime (1973) seems, to date, to be the one that best explains the productivity–diversity relationship (Grace 1999; Waide et al. 1999; Abrams 1995; Mittelbach et al. 2001; but see Adler et al. 2011). Such a hump-shaped curve indicates that species diversity in these landscapes is augmented at sites with low and intermediate productivity, but decreases at those with high productivity (Grime and Pierce 2012). Other patterns have also been reported for the productivity–diversity relationship: positive monotonic, negative monotonic, U-shaped (negative unimodal), null (i.e. no relationship, Hector et al. 2010; Graham and Duda 2011) and, more rarely, asymptotic (Chalcraft et al. 2009). Such discrepancies in the shape of the productivity–diversity relationship seem to arise from differences in spatial scale (Rosenzweig 1995; Pastor et al. 1996; Mittelbach et al. 2001; Whittaker et al. 2001; Chase and Leibold 2002; Scheiner and Jones 2002; Chalcraft et al. 2004; Espinar 2006; Bai et al. 2007; Ni et al. 2007; Whittaker 2010; Šimová et al. 2013; McBride et al. 2014). For example, some studies reported unimodal relationships at local extents (i.e. from hundred metres to a few kilometres) whereas they become monotonically positive at larger extents (Waide et al. 1999; Mittelbach et al. 2001).

In this context, we refer specifically to the different concepts by which spatial scale can be expressed: extent, grain and focus (Scheiner and Jones 2002). Extent refers to the area surveyed, grain refers to the size of the sampling unit, and focus to the area or inference space represented by each data point (i.e. the scale at which the grains are aggregated, Scheiner et al. 2000). In studies aiming to investigate the influence of ecological factors on biodiversity, the choice of grain size and extent of sampling is critical, since they can affect the magnitude (and even direction) of the
effect (Wiens 1989; Chase and Knight 2013). A number of studies have investigated the effect of scale on the relationship between productivity and diversity (e.g. Chase and Leibold 2002; Scheiner and Jones 2002; Chase and Ryberg 2004). While most of them have investigated the effect of geographical extent and focus (e.g. Scheiner and Jones 2002; Chalcraft et al. 2004; Jennings et al. 2005; Bai et al. 2007; Ni et al. 2007; Adler et al. 2011; Zhang et al. 2011; McBride et al. 2014), less attention has been paid to the role of grain size in such relationship (but see Braschler et al. 2004; Fraser et al. 2015). According to Braschler et al. (2004), different grain sizes result in different productivity-diversity curves. In contrast, Fraser et al. (2015) have concluded that the productivity–diversity relationship was irrespective of grain size, though the proportion of explained variance decreased with increasing grain size in addition to extent. Other factors such as species composition (Hector et al. 2011; Tilman et al. 2012) or disturbance regime (whether by grazing (Zhou et al. 2006) or management (Minden et al. 2016)) may also influence the shape of the productivity-diversity curve.

A recent study conducted in Iranian steppes has suggested a hump-shaped relationship between plant species richness (as a surrogate for diversity) and above-ground biomass (as a surrogate for productivity) (Ashouri et al. 2016). Here, we re-examine this assertion with data collected from 735 plots in the semi-arid steppes of the Middle Taleghan rangelands of northern Iran, each sampled at three nested sampling unit sizes, to specifically address the effect of grain size (0.25, 1 and 2 m$^2$), plant life forms (herbs, graminoids, shrubs), plant community type, and intensity of disturbance on the productivity-diversity curve. The strong structural unevenness due to the large differences in biomass – and most importantly, lifespan and growth – among plant life forms in these plant communities is expected to have an increased effect on the spatial arrangement of species and individuals, as the size of sampling units varies. Species composition and relative abundances are, ultimately, the determinants of diversity and biomass of a community. Such interplay between different life forms and spatial scale (in this case grain size) has so far seldom been addressed.

In this study we investigated how the productivity (biomass) and diversity (species richness) of a plant community were affected by community composition traits such as plant size and longevity (i.e. life forms), spatial scale (grain size) and an environmental/historical factor (grazing intensity). Specifically, we addressed the following research questions: (1) does grain size of the sampling unit affect the relationship between above-ground biomass and plant species richness? (2) do different plant life forms display the same biomass-species richness pattern, and how does grain size affect it? and (3) does the relationship between biomass and species richness remain invariant through different plant community types and disturbance levels? We hypothesised, in accordance with the results reported by Braschler et al. (2004), that there would be a grain size effect on the productivity–diversity relationship. In this paper we investigate this assertion and try to ascertain what ecological mechanisms cause such scale-dependent relationships. Understanding the scaling effects on species richness-biomass relationships would improve our awareness about sampling effects in natural communities and, therefore, can contribute to optimise observational and experimental sampling designs in ecological studies.

**Materials and methods**

**Study area**

The study was conducted in the middle Taleghan rangelands, Alborz Province, northern Iran (36°08'10" N; 50°43'10" E), between 1900 and 2500 m a.s.l. (Figure 1(a,b)). Annual precipitation ranged from 460 to 600 mm, in a typical semi-arid climate with a distinct dry season (Sanaei et al. 2018a, 2018b, 2018c). Absolute minimum temperature was recorded in December (~25°C) and maximum in June (35°C). Mean temperatures during the growing season ranged between 4°C (March) and 26°C (June) (Sanaei et al. 2018a, 2018b, 2018c). Geomorphologically, most of the study area was characterised by volcanic rock outcrops, compacted sandstone, limestone conglomerates and fine-grained calcareous marls that are low to moderately rich in gypsum and halite, resulting in regosols and cambisols (Sanaei et al. 2018a, 2018b, 2018c).

**Sampling method**

Thirty-five polygons were established within an area of ca. 3 km $\times$ 2.5 km, each one defined by a plant community type based on its floristic composition and vegetation structure. The abiotic attributes of individual polygons (e.g. slope, aspect, soil
type, elevation and disturbance regime) were considered to maximise physiognomic homogeneity within polygons (Figure 1(c)). Each polygon was assigned to one of the 18 existing plant community types defined by their floristic composition and relative abundance of dominant species (Sanaei et al. 2018a, 2018b, 2018c) (Table S1). Each one was also assigned one of five disturbance levels, based on the history of sheep grazing, soil erosion, soil depth, fraction of gravel, and range condition (Parker 1951; Table S1).

Within each of the 35 polygons, a single 2 m × 1 m plot was first established at random. Then, 20 additional plots were established at least 10 m from each other, following an approximate straight line across the polygon. A total of 735 plots (21 plots × 35 polygons) were thus established over the entire study area (Sanaei et al. 2018a, 2018b, 2018c). Each plot was parsed into three nested sampling units of 2 m², 1 m² and 0.25 m² (Figure 1(c)). Individual plants were identified in the field and separated into three life forms (Sanaei et al. 2018a, 2018b): annual and biennial herbs (Poacea and Cyperaceae excluded), grasses and sedges (henceforth graminoids), and shrubs. As a surrogate for primary productivity (Tilman et al. 2001), the entire annual above-ground biomass per sampling unit was collected between May and June 2014. Herbs and graminoids were clipped at ground level (Al-Mufti et al. 1977; Grime 1973); for shrubs, the current year’s branch growth and leaves were also collected. All (mostly recent) leaf-litter mass was added to the total above-ground biomass estimate for the entire sampling unit. Litter production is a function of annual net primary productivity in grasslands and can have profound effects on the structure and functioning of communities, as it can, among other effects, alter nutrient cycling or impede vegetative growth and seedling recruitment (Knapp and Seastedt 1986; Foster and Gross 1998). All samples were oven-dried at 70°C for 24 h and subsequently weighted.

**Statistical analyses**

The accumulated number of species accounted for >80% of the estimated regional species pool (Safaian et al. 2008). We explored the species-area relationship using random permutations of data by subsampling without replacement (Gotelli and Colwell 2001) at each grain size and verified that the sampling effort was sufficient as species-area curves approximated an asymptote at all grain sizes (Figure S1). We used generalised linear mixed models (GLMMs) to analyse the relationship between total above-ground vegetation biomass and species richness at all three grain sizes while accounting for different random effects, such as disturbance, plant community type, and site (i.e., polygon, nested within plant community type).
Disturbance and plant community type were defined as random factors because their levels were established ad-hoc and were of no particular interest for the study (Table S1). Disturbance showed an intermediate correlation with above-ground vegetation biomass at all grain sizes (Pearson’s correlation coefficient ranging between 0.37 and 0.59). Site represented an autocorrelation structure in our dataset because all 21 plots sampled within each polygon shared floristic and environmental conditions that could affect species richness and the shape of the biomass-species richness relationship.

For each grain size, we fitted models for all possible combinations of random and fixed factors. For fixed factors, we tested different curve functions to model the relationship between plant species richness and above-ground biomass: (1) null model; (2) linear model; (3) quadratic model; (4) log-linear model; and (5) log-quadratic model. For each random effect, we tried both intercept and random slope models. Intercept models estimate a random variance term that affects the mean response variable (e.g. species richness). For example, a random intercept effect of plant community type would indicate changes in mean species richness among plant community types. Slope random models, on the other hand, estimate a random variance term that affects the slope of the regression line. In our specific case study, it would imply that the relationship between richness and above-ground biomass could randomly change among levels of the random factor. In all models, we used a Poisson error distribution and a log-link function. Model assumptions were checked based on easily interpretable scaled residuals from best-fit models that were created using a simulation-based approach (Dunn and Smyth 1996). The key idea for this approach is that, if the model is correctly specified, then the observed data should look as if created from the fitted model. Hence, for a correctly specified model, all values of the cumulative distribution should appear with equal probability (Hartig 2017).

We used an information-theory rather than a frequentist-based statistical approach to make inferences about fixed and random effects (Richards 2005). Overall, we fitted 105 models for each response variable (i.e. overall species richness and richness for each plant life form at all three grain sizes) that were compared using the Akaike Information Criterion (AIC) (Table S2). Models with a difference in AIC >2 indicate that the worse model has virtually no support and could be omitted (Burnham and Anderson 2002). Models with differences in AIC ≤2 had equal support and were selected within a set of best-fit models. When multiple best-fit models, we compared model predictions to see if large discrepancies existed in the response curves between richness and above-ground biomass. If they were not, then the most complex model was selected to represent the results. Following Nakagawa and Schielzeth (2013), we estimated the R² of best-fit models. This approach allows two components of R² to be calculated: (1) a marginal R² (R²m) that only considers the variability explained by fixed effects; and (2) a conditional R² (R²c) that accounts for the variability supported by both the fixed and random effects. All these analyses were repeated for each plant life form: herbs, graminoids and shrubs.

All analyses were carried out in R (R Core Team, 2016), using the packages ‘vegan’ (Oksanen et al. 2017), ‘lme4’ (Bates et al. 2015), ‘MuMIn’ (Barton 2016), and ‘DHARMa’ (Hartig 2017).

Results

A total of 168 plant species were identified across the 35 sites. Overall species richness ranged from 0 to 23 species (i.e. 0–18, 0–9 and 0–4 species of herbs, graminoids and shrubs, respectively) in 0.25 m² sampling units, 5–27 species (0–19, 0–9 and 0–5 species for each life form) in 1 m² sampling units, and 5–32 species (2–23, 0–10 and 0–5 species per life form) in 2 m² sampling units.

Total dry plant biomass ranged from 22.4 to 434.9 g m⁻² in 0.25 m² sampling units (i.e. 22.4–423.7 g m⁻² for herbs, 22.4–285.7 g m⁻² for graminoids, and 21.9–360.4 g m⁻² for shrubs); 46.9–441.0 g m⁻² in 1 m² sampling units (13.3–378.0, 12.7–314.4 and 11.7–165.4 g m⁻² per life form); and 27.5–425.7 g m⁻² in 2 m² sampling units (17.9–380.6, 11.1–265.7 and 10.4–222.2 g m⁻² per life form). In most plots, herbs had a low biomass (0–225 g m⁻²) in all three grain sizes, whereas biomass was intermediate (225–400 g m⁻²) or high (>400 g m⁻²) for graminoids and for shrubs (shrubs contributing in some cases to more than 60% of the total biomass) in all grain sizes. However, in the 0.25 m² grain size, biomass of shrubs was exceedingly variable (Figure 2). The proportion of bare soil was greatest in 0.25 m² sampling units (mean percentage of bare soil 44.8 ± 20.9%, with some sampling units entirely devoid of vegetation), whereas it was small in 1 m² (mean percentage of bare soil 2.0 ± 7.4%) and 2 m² sampling units (mean percentage of bare soil 0.2 ± 2.4%, many with 100% cover).
Grain size affects the relationship between above-ground biomass and species richness. The comparison of models for overall plant species richness identified one or more best-fit models at each grain size: four best-fit models for grain size 0.25 m$^2$, two for grain size 1 m$^2$, and one for 2 m$^2$ (Table S2). All best-fit models at grain sizes 0.25 and 1 m$^2$ included quadratic terms of the biomass, whereas at 2 m$^2$ the best-fit model contained a quadratic term of biomass on a log-scale (Table S2). For each grain size, different best-fit models produced similar predicted response curves. These revealed a change in the relationship between species richness and above-ground biomass as grain size increased: from unimodal (i.e. hump-shaped) in the 0.25 and 1 m$^2$ sampling units, to approaching asymptotic in 2 m$^2$ sampling units (Figure 3). The amount of variance explained decreased as grain size increased, from $R^2_c = 0.42$ in 0.25 m$^2$ sampling units to $R^2_c = 0.23$ in 2 m$^2$ sampling units (Table S2). To examine the influence of (the few) high biomass observations when fitting the curves, we

Figure 2. Mean percentage contribution to overall biomass of each plant life form (herbs, graminoids, shrubs) and litter for different levels of biomass, namely: low (0–225 gr/m$^2$), intermediate (225–400 gr/m$^2$), high (> 400 gr/m$^2$) at different grain sizes: (a) 0.25 m$^2$; (b) 1 m$^2$; and (c) 2 m$^2$. Error bars represent upper 95% confidence intervals.
re-fitted all models by removing plots with highest biomass values (2.5% of the total). The new model generated curves that were almost identical to the original ones (results not shown), thus revealing a consistency in the pattern not attributable to an excessive influence of a few high-biomass observations.

Different plant life forms have identical biomass-species richness patterns

Model selection for herbs, graminoids and shrubs were all consistent in their fixed-effects structure, which included the quadratic term of the biomass on a log-scale (Table S2). There were two or more best models, consistently, for all three life forms and grain sizes that varied in their random-effects structure (Table S2). Different life forms displayed slightly different relationships between species richness and above-ground biomass (Figure 4). For herbs and graminoids, the relationship was slightly unimodal with a tendency towards an asymptote in all three grain sizes (Figure 4(a, b, d–h)), particularly for herbs (Figure 4(a, d, g)), whereas it was unimodal for shrubs, (Figure 4(c, f, i)) with a tendency towards monotonically decreasing, most obvious in the smallest grain size (Figure 4(c)). As with the models for overall species richness, the amount of variance explained decreased as grain size increased, with shrubs having the most variance, followed by herbs, and graminoids the least (Table S2).

Biomass-species richness relationship across different plant community types and disturbance levels

In addition to the effect of site in all best-fit models for overall species richness, there was an effect of plant community type and disturbance level on the main response (intercept effect) at all grain sizes, as well as of plant community and site on the relationship between richness and above-ground biomass (slope effect) at grain size 0.25 m² (Table S2). The amount of estimated variability explained by random factors ($R^2_m$) decreased – both in absolute and relative terms – as grain size increased; thus, random factors contributed to ca. 50% of the overall explained variance at grain size 0.25 m² (i.e. 0.19/0.42), 36% at grain size 1 m², and only to 26% at grain size 2 m² (Table S2).

Discussion

The relationship between diversity and productivity remains a contentious issue in ecology. For terrestrial vascular plants, hump-shaped relationships predominate at any geographical extent below continent (Scheiner and Jones 2002). Although it has been questioned whether competition is truly associated with productivity (Reader et al. 1994), hump-shaped relationships in arid shrubland communities have been explained by competitive exclusion at low (e.g. Goldberg et al. 1999) as well as high productivity (Wilson and Keddy 1986; Sammul et al. 2000; Olofsson et al. 2002). Our study supports the existence of a hump-shaped relationship at small grain size (0.25 and 1 m²) which becomes asymptotic at larger grain size (2 m²) (Figure 3). This is partially in agreement with the results reported by Braschler et al.
(2004) for calcareous soil grasslands, where a unimodal relationship between herb species richness and productivity was found at sampling unit size of 0.25 m², but became negative as grain size increased. Such changes may be the result of sampling limitation because grain sizes that are too small may not adequately capture local diversity (Oksanen 1996). However, these discrepancies could also be suggesting scale-dependent ecological mechanisms that shape the productivity–diversity relationship. Scheiner and Jones (2002) pointed to the inadequacy of sampling at excessively low grain sizes as an explanation for a bias in the grain size-dependent productivity–diversity relationships. Their results, however, revealed the opposite pattern: hump-shaped relationships were more common as grain size increased (Wiens 1989).

Plant life forms display different patterns of biomass-species richness and different responses to the effect of grain size. Herbs in our study constituted the largest share of the species pool (136 out of 169 species), whereas shrubs were the most species-poor (10 species). The relationship between productivity and species richness within each life form tended to be asymptotic for herbs and graminoids, yet unimodal for shrubs at all grain sizes (Figure 4). How does this contribute to explaining the observed patterns of overall species richness? At small grain sizes, even the accidental presence of a single individual shrub – perhaps only partially occupying the plot – may dominate the corresponding entire sampling unit (Figure 2), thus contributing disproportionally to the biomass of the plot, compared to its small contribution to species richness. This may explain the sharp decrease in species richness in spite of high biomass values when sampling using a fine grain (small-plot) schema. When grain is of the appropriate size (i.e. large enough, like the 2 m² unit size in our study) it better captures local heterogeneity. At this size, the area within a sampling unit is large enough for shrubs (with their greater biomass and

Figure 4. Predicted relationship between aboveground dry biomass and species richness for three plant life forms: herbs, graminoids and shrubs at the three grain sizes studied: (a), (b) and (c) herbs, graminoids and shrubs, respectively, in 0.25 m² sampling units; (d), (e) and (f) in 1 m² sampling units and (g), (h) and (i) in 2 m² sampling units. Biomass was re-scaled to the 1 m² sampling unit to improve comparison between the three grain sizes. Grey areas represent 95% confidence intervals upon model predictions, whereas light grey areas represent predictions outside the range of observed biomass values.
ability to otherwise outcompete other species/life forms for light) to co-exist with graminoids and/or herbs, thus contributing to both, biomass and species richness in a comparable degree. Sampling at a sufficiently large grain size will therefore reduce the probability of disproportionately contributing to biomass, while not (or dramatically less) to diversity, an error to which shrub clumped distributions can potentially lead (Kenkel et al. 1989). Such disparity in contributions (biomass over diversity) would ultimately alter the productivity–diversity relationship. This can help explaining why the productivity–diversity relationship reaches an asymptote at the largest grain size 2 m², where the clumping of shrubs is expected to have little effect on limiting the presence of other plant life forms, so biomass would therefore not overwhelm diversity. Because the frequency of shrubs varies greatly in small but not so in large sampling units, unimodal productivity–diversity relationships are to be expected at small grain sizes but not at large ones. Hence, it seems that shrubs become the main mechanism driving productivity–diversity relationships rather than a source of bias, as pointed out by other authors (Scheiner and Jones 2002). Caution should therefore be exercised when interpreting and comparing the results of many published ecological studies, as the mechanisms causing the patterns observed may not be the same depending on grain size. For instance, when reviewing studies that analyse the productivity–diversity relationship in grasslands, we most often found that: (1) studies using sampling units smaller than a 1 m² consistently detected a unimodal pattern (Al-Mufti et al. 1977; Guo and Berry 1998; Grytnes 2000; Braschler et al. 2004; Frank 2005; Espinar 2006; Šimová et al. 2013; Wu et al. 2014); (2) studies using a grain size of 1 m² quite often also detected a unimodal relationship (Bhattarai et al. 2004; Jennings et al. 2005; Noor Alhamad 2006; Bai et al. 2007; Zhang et al. 2011; Axmanova et al. 2013; Ashouri et al. 2016), while some studies reported alternative patterns: from a linear relationship (Zhou et al. 2006; Bai et al. 2007; Ni et al. 2007; Zhang et al. 2011) to an asymptotic relationship (Chalcraft et al. 2009), as well as no relationship (Bai et al. 2007; Adler et al. 2011; Zhang et al. 2011); (3) only the study by Braschler et al. (2004) analysed sample grain sizes larger than 1 m² for grasslands at geographical extents smaller than continent (but see Fraser et al. (2015) for an example at a continental extent), which reported non-unimodal relationships at these grain sizes.

How does the relationship between productivity and species richness vary with plant community type and disturbance regime? When analysing the relationship between productivity and diversity, it is important to consider the overall effect of possible autocorrelations among data that are grouped according to one or more classification factors (Pinheiro and Bates 2000). Ignoring these autocorrelations could lead to confounded patterns (Guo and Berry 1998). In the particular case of plant community types, the productivity–diversity relationship has been shown to be sensitive to specific community composition (Guo and Berry 1998; Grytnes 2000; Wu et al. 2014; Yuan et al. 2015; Minden et al. 2016), which implies that different species assemblages do have different average levels of species richness. Disturbance is known to affect species diversity and, as a result, may also affect the productivity–diversity relationship. In our study, we were neither interested in quantifying the particular effect of disturbance levels on either species richness (e.g. in agreement with the Intermediate Disturbance Hypothesis of Connell (1978) and Huston (1979)) nor on the relationship between species richness and biomass per se, since disturbance levels were defined ad-hoc based on the particular existing characteristics of the polygons in the study.

Our results point to a marked effect of plant community type and disturbance on species richness (Table S2), in addition to autocorrelation structures attributable to purely spatial site effects. Overall, the variability explained by random effects decreased as a function of explained overall variability with grain size increase. The productivity–diversity relationship was nonetheless affected by plant community type only at the smallest grain size. This may suggest a more stable (and therefore tractable) relationship between productivity and diversity as grain size increases. In other words, the relative effect of local factors (such as community composition or disturbance) on the response of species richness to aboveground biomass is greater (or at least becomes more obvious) as grain size increases.

Conclusions

Grain size-mediated effects in the productivity–diversity relationship, as reported by previous studies (Braschler et al. 2004), may be the result of superior competing ability of shrubs for light, this becoming overbearing at small grain size. Sampling size for field data collection should be carefully chosen as the resulting patterns may be pointing to several different ecological mechanisms that may
underlie the productivity–diversity relationship. Other factors, such as species composition (Hector et al. 2011; Tilman et al. 2012) or disturbance by grazing (Zhou et al. 2006) and management (Minden et al. 2016), may also influence the shape of the productivity–diversity curve, so they should be taken into account when assessing the true relationship between productivity and diversity. Mixed modelling and the inclusion of random factors are a reasonable way to achieve this, while maintaining the focus on the productivity–diversity relationship.

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Anvar Sanaei has recently obtained his Ph.D. in range management. This study was part of his doctoral thesis.

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References


