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Environmental correlates of species rank – abundance distributions in global drylands

Werner Ulrich[1,*], Santiago Soliveres[2], Andrew D. Thomas[3], Andrew J. Dougill[4] & Fernando T. Maestre[5]

[1]Chair of Ecology and Biogeography, Nicolaus Copernicus University in Toruń
Lwowska 1, 87-100 Toruń, Poland, e-mail: ulrichw@umk.pl.
[2]Institute of Plant Sciences, University of Bern, Alterbengrain 21, 3013 Bern, Switzerland, e-mail: santiago.soliveres@ips.unibe.ch.
[3] Department of Geography and Earth Sciences, Aberystwyth University, SY23 3DB, UK, e-mail: ant23@aber.ac.uk
[4] School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK, e-mail: a.j.dougill@leeds.ac.uk
[5]Área de Biodiversidad y Conservación, Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain, e-mail: fernando.maestre@urjc.es.

***Author for correspondence (Phone: 0048 56 611 2649, e-mail: ulrichw@umk.pl)

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Abstract

Theoretical models predict lognormal species abundance distributions (SADs) in stable and productive environments, with log-series SADs in less stable, dispersal driven communities. We studied patterns of relative species abundances of perennial vascular plants in global dryland communities to: i) assess the influence of climatic and soil characteristics on the observed SADs, ii) infer how environmental variability influences relative abundances, and iii) evaluate how colonisation dynamics and environmental filters shape abundance distributions. We fitted lognormal and log-series SADs to 91 sites containing at least 15 species of perennial vascular plants. The dependence of species relative abundances on soil and climate variables was assessed using general linear models. Irrespective of habitat type and latitude, the majority of the SADs (70.3%) were best described by a lognormal distribution. The lognormal was associated with low annual precipitation, higher aridity, high soil carbon content, and higher variability of climate variables and soil nitrate. Our results do not corroborate models predicting the prevalence of log-series SADs in local ecological communities. As lognormal SADs were particularly associated with sites with drier conditions and a higher environmental variability, we reject models linking lognormality to environmental stability and high productivity conditions. Instead our results point to the prevalence of lognormal SADs in variable and stressful ecosystems, which are generally shaped by strong habitat filters and limited colonisation. This suggests that drylands may be resilient to environmental changes because the many species with intermediate relative abundances could take over ecosystem functioning if the environment becomes suboptimal for dominant species.

Running title: Rank – abundance distributions of dryland plants

Key Words: aridity, species abundance, competition, lognormal distribution, log-series distribution, habitat filtering, soil fertility, climate

Introduction

Since its introduction to ecology by Raunkiær (1909), species - abundance distributions (SADs) have been extensively studied (reviewed in McGill et al., 2007; Matthew and Whittaker, 2014, 2015). They provide an exhaustive description of the distribution of species abundances within an ecological community (Magurran, 2004; McGill et al., 2007; Dornelas et al., 2011; Matthews and Whittaker, 2015) and have been linked to differential resource use and competitive strength (Sugihara, 1980; Tokeshi, 1998; Pueyo, 2006), disturbance regimes (Gray and Mirza, 1979), stochastic processes (May, 1975, Šizling et al., 2009), or species-specific dispersal rates (Hubbell, 2001; Zillio and Condit, 2007).

SADs can be grouped into two particular classes of distributions: the log-series and the lognormal (Fig. 1; Connolly et al., 2005; Ulrich et al., 2010, 2016). The lognormal is characterized by a comparably high number of species with intermediate abundance and smaller numbers of very abundant and very rare species (Fig. 1). In turn, the log-series lacks a distinct group of very rare species (Fig. 1). Although it is difficult to relate these models to a particular underlying mechanism (cf. McGill et al., 2007; Ulrich et al., 2010; Cheng et al., 2012; Locey and White, 2013, but see Alonso et al., 2008), lognormal SADs are more likely to be found in closed communities with low temporal and spatial species turnover and a high proportion of species with intermediate abundances (that is the lognormal represents communities with a proper ‘middle class’ of species) (Magurran and Henderson, 2003) if they are shaped 1) by multiple stochastic processes, independent of niche differentiation, resource use, or competitive ability as predicted by the central limit theorem of statistics (Preston, 1948; May, 1975; Connolly, et al. 2005; Šizling et al., 2009), 2) by sequential niche partitioning, where competitive strength with respect to dominant niche axes governs the distribution of species abundances (MacArthur, 1957; Sugihara, 1980; Tokeshi, 1998; Pueyo, 2006), or 3) by environmental filters, such as climate and soil characteristics that select for certain species and species combinations and limit colonisation (Green and Plotkin, 2007; Zillio and Condit, 2007; Maire et al., 2012). On the other hand, log-series SADs are expected to occur 1) in open colonisation driven communities with high degrees of dispersal and species turnover (Volkov et al., 2005; Zillio and Condit, 2007; Hirao et al., 2012) or 2) in incomplete samples from larger species pools (Fisher et al., 1943).

Species - abundance distributions have often been theoretically linked to environmental conditions and gradients (reviewed in Magurran, 2004; McGill et al., 2007; Dornelas et al., 2011). Some authors assume lognormal SADs prevail in stable, undisturbed environments, while log-series SADs will be found in disturbed habitats with higher temporal or spatial variability (e.g. Gray et al., 1979; Gray and Mirza, 1979; Hamer et al., 1997; Hill and Hamer, 1998; but see Nummelin, 1998). Whittaker (1975) and Hubbell (1979) linked lognormal SADs to higher environmental productivity. Consequently, log-series SADs should predominate at unproductive, e.g. arid, sites. However, the direct influence of environmental conditions on abundance distributions has been very rarely studied empirically. The few existing studies mainly focus on community recovery after severe disturbances (Mouillot et al., 2000), gradients of environmental pollution (e.g. Gray et al., 1979; Death, 1996; Qu et al., 2008), and successional stages (e.g. Whittaker, 1965; Bazzaz, 1975; Zaplata et al., 2013). Taken together, current evidence indicates that a directional shift from log-series towards lognormal SADs may occur with increasing intensity of interspecific competitive interactions and habitat stability (Tilman, 1982; Lan and Bai, 2012).

Environmental filters, like climate and soil characteristics, and biotic filters, such as facilitative and competitive interactions, tend to select for certain species and species combinations that are able to pass the respective filters (Bruno et al., 2003; Lortie et al., 2004). Consequently, species abundances should correlate with the strength of a particular filter (Maire et al., 2012). Indeed, theoretical sampling models predict habitat filtering will generate lognormal SADs if they limit colonisation probabilities (Green and Plotkin, 2007; Zillio and Condit, 2007; Ulrich et al, 2016).

Our knowledge about plant abundance distributions stems mainly from work done in forests (Hubbell, 1979; Morlon et al., 2009; Ulrich et al., 2015) and temperate grasslands (Bazzaz, 1975; Maire et al., 2012). With the exception of Whittaker's (1965) classical report of a lognormal SAD for Arizona desert plants, similar distributions in arid, semi-arid and dry-subhumid regions (drylands hereafter) have so far not been studied. Drylands, including a variety of habitat types like grasslands, scrublands and savannahs, occupy more than 40% of the terrestrial surface area (Safriel and Adeel, 2005) and are vulnerable to human disturbances (Maestre et al. 2012a) and changing climate (Körner, 2000; Reynolds et al., 2007; Dai, 2013), which in turn affect nutrient cycles (Maestre et al., 2012b). We do not know whether the abundance patterns observed in forests can be generalised to drylands, and how changes in environmental conditions affect the SADs of dryland communities. As plant abundances are directly related to important ecosystem functions in drylands, like primary production and nutrient cycling (Gaitán et al., 2014; Maestre and Escudero, 2009), such knowledge can also greatly contribute to our understanding of the consequences of global change on ecosystem functioning in these areas (Maestre et al., 2012a; Maire et al., 2012).

Here we evaluate how environmental factors affect the SADs of 230 dryland communities from all continents except Antarctica and from three different vegetation types obtained within an international, large-scale dryland survey (Maestre et al., 2012b, Delgado-Baquerizo et al., 2013). We focus on the gradient between the log-series and the lognormal type SAD. Based on the available knowledge, we assumed that highly variable environmental conditions would favour unstable and dispersal-driven communities (reviewed in Fraterrigo and Rusak, 2008), while water-rich, productive environments favour stable, competition driven communities (Whittaker, 1979; Hubbell,1979). These assumptions lead to three basic starting hypotheses regarding dryland plant communities:

(1) more arid, and therefore less productive, communities are dominated by log-series SADs,

(2) lognormal SADs dominate in species rich, communities, and

(3) log-series SADs are linked to both increased environmental variability and decreased importance of habitat filtering.

Materials and methods

Study sites and sampling protocol

Field data were obtained from 230 sites established across precipitation gradients in 17 countries from five continents (Argentina, Australia, Botswana, Brazil, Chile, China, Ecuador, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, USA and Venezuela). Sites were chosen to cover a wide spectrum of abiotic (climatic, soil type, slope) and biotic (type of vegetation, total cover, species richness) features characterizing drylands worldwide. These sites include the 224 sites used in Maestre et al. (2012b) plus six additional sites in Botswana surveyed in 2012. We restricted our study to arid, semi-arid and dry-subhumid ecosystems, defined as sites with an aridity index (precipitation/potential evapotranspiration) between 0.05 and 0.65. The sites cover all major biogeographic regions and four basic vegetation types (woodlands, savannahs, scrublands, and grasslands). All study sites were sampled quantitatively following the same protocol. At each site, we surveyed 80 1.5 m × 1.5 m quadrats along four 30-m long transects separated eight meters from each other (see Maestre et al. 2012b for full methodology). In each quadrat, we measured the cover of perennial plant species and used the total counts to construct the respective vectors of relative abundances. Thus all abundance distributions are based on complete censuses.

A low number of species per site increases the noise in the SAD fits (Wilson et al. 1998), while selecting a high minimum number of species greatly reduces the number of sites (and vegetation types) considered making statistical inferences challenging. As a compromise, we retained 91 of the study sites, which had ≥15 species of perennial vascular plants. Nevertheless, and to assess the robustness of our analysis, we compared the results obtained from these sites with those obtained from an extended data set (166 sites) including at least 10 species (as recommended by Ulrich et al, 2010 as the lower limit for reliable fits) and from a reduced data set (55 sites) including at least 20 species per site. As the results from these three data sets were qualitatively similar, we only report the results obtained with the 91 sites having 15 species or more. We show the results obtained with the reduced and extended data sets in the electronic supplement.

Biotic and abiotic factors

Using a stratified sampling design, we sampled the top 7.5 cm of the soil from up to three different microhabitats per site. These microhabitats always included a location with bare soil (i.e. devoid of perennial vascular plants), as well as sites dominated by perennial vegetation (e.g. under trees, shrubs or grasses, depending on the dominant growth forms present within each site). Five samples were collected from each microsite, yielding between 10 and 15 samples per site. Soil samples were air-dried at room temperature, sieved (< 2 mm fraction) and analysed in the laboratory to obtain a range of physio-chemical analyses. In each soil sample we measured pH, organic carbon, available phosphorus, and nitrate content as described in Maestre et al. (2012b). These variables were selected because they are either appropriate surrogates of overall soil fertility and nutrient availability for plants in drylands (carbon and nitrogen variables; Whitford, 2002) or they are surrogates of abiotic variables that control nutrient transformations and availability in soils (e.g. pH; Reth et al., 2005). Thus, we expect them to be important factors influencing the relative abundance distributions of plant species. Soil variables were pooled to a single site-level value by weighting the values found underneath vegetation or in bare ground areas by their respective cover within the site (cf. Maestre et al., 2012b). As a measure of habitat variability, we calculated for the four soil variables their respective coefficients of variations based on the 10-15 samples obtained per site.

We also obtained climatic data for each site using Worldclim (http://www.worldclim.org; Hijmans et al., 2005). From this database, we extracted the altitude of each site, the mean annual temperature and precipitation, and their annual seasonality. As we expected to see changes in relative abundances along climatic gradients, particularly along the gradient from moist to dry, we calculated the UNEP aridity index as the quotient of annual precipitation and evapotranspiration. To give a more readily interpretable result, we used the aridity level (1- aridity), which is directly related to aridity (higher values indicate higher aridity conditions). Aridity was estimated using the Global Aridity Index (Global-Aridity) dataset (http://www.cgiar-csi.org/data/global-aridity-and-pet-database; Zomer et al., 2008; Trabucco and Zomer, 2009), which is based on the interpolations provided by the Worldclim database.

Fitting of relative abundances

We fitted lognormal (fit_{norm}) and log-series (fit_{lser}) models to the observed SADs as in Ulrich et al. (2010). For this task we used rank- log abundance (Whittaker) plots that show the log-transformed species abundances for each species ranked in declining abundance order (Fig. 1). These plots are superior to classical distribution (Preston) plots for fitting as they do not lose information and are not biased due to the grouping of species (Nekola et al., 2008, Ulrich et al., 2010). For each rank – log abundance plot we used a maximisation algorithm (implemented in the software application RAD 2.0, Ulrich 2013) that iteratively encapsulates parameter values to find the ones that minimise the average least square differences of observed and predicted relative abundance, respectively

$$fit = \frac{\sum_{i=1}^{S}\left(lnA_{i,obs} - lnA_{i,pred}\right)^2}{S} \qquad (1)$$

where $A_{i,obs}$ and $A_{i,pred}$ are the respective relative abundances of species i in the community of S species. Fits for all communities are contained in the electronic supplement. We used least squares differences for fitting as they put comparably high weight on rare and abundant species (Connolly and Dornelas, 2011) thus increasing the power to discriminate between the lognormal and the log-series models (Ulrich et al., 2010). In this respect, we note that major axis and reduced major axis have less discriminative power in the present context as both methods put higher weight on species with intermediate abundance.

As fit (eq. 1) x`equals the residuals sums of squares we compared the relative fits of both distributions using the corrected Akaike information criterion in the form

$$AICc = 2k + S\ln fit + \frac{2k(k+1)}{S-k-1} \qquad (2)$$

The lognormal SAD has k = 3 free parameters (richness S, shape, and error), the logseries is a four parameter model (S, α, X, and error). We used ΔAIC_c to identify the better fitting model and assigned models with $\Delta AIC_c > |10|$ as fitting significantly better (Burnham and Anderson 2002). As species differ in the probability to obtain particular least squares values (Connolly and Dornelas, 2011), least squares fitting applied to non-linear data might introduce a statistical bias when comparing SADs of different species richness. We minimized this possible bias two-fold: first, we always compared the two model fits for the same community and second, we included species richness as an extra predictor in our analyses. Locey and White (2013) highlighted the problem of comparing SADs from communities with different species richness and total abundance. Here we minimize this problem as we always fit both models to the same community and subsequently compare the respective relative fits among communities.

Ulrich et al. (2010) studied a third basic shape, the power function, and found it to be rarely realised in natural communities except for some forest tree data. Nevertheless, we checked the frequency of power function SADs in the global dryland data set. Our data confirmed the results of Ulrich et al. (2010) and revealed a low power to discriminate between log-series and power function shapes. Thus, we did not consider this model here, but present respective numbers of best and worst fits of all three models (lognormal, log-series and the power function) in the electronic supplement (Table A9).

An auxiliary measure of model fit is the skewness of the abundance distribution (γ). The symmetrical lognormal is not skewed. Unsymmetrical lognormal SADs have nearly always an excess of rare species, and consequently a negative skewness (McGill, 2003). The log-series has an excess of relatively abundant species (associated with a positive skewness) mostly in the case of incomplete sampling. An excess of relatively rare species (negative skewness) has been theoretically linked to communities characterised by high colonisation dynamics (Zillio and Condit, 2007).

As an approximate measure of SAD variance, the concept of evenness is closely related to the distribution of relative abundances (McGill et al., 2007). We assessed the evenness (E) in species abundances using the Shannon diversity metric H: $E = H/\ln(S)$. p_{norm}, skewness, and evenness values for each site are available from figshare (Maestre et al., 2015).

Statistical analyses

We used ordinary least squares general linear model analysis (GLM) in AICc model selection to link the ΔAIC_c scores (eq. 2) to environmental data. Thus, we selected as the most parsimonious models those with the lowest AICc, using the model selection routine of SAM 4.0 (Rangel et al., 2010). To verify our first to starting hypotheses on the dependence of abundance distributions on environmental states we related ΔAIC_c, skewness, and evenness to latitude (and squared latitude), climatic and soil variables. As our third starting hypothesis is about the influence of environmental variability we run separate models using the coefficients of variation of these environmental variables as predictors. Pearson correlation coefficients between predictor variables were always lower than 0.7, and therefore multicollinearity problems in our analyses are unlikely. Because vegetation type is strongly linked to temperature and precipitation, we did not include vegetation type as a categorical variable into the regression models to avoid multicollinearity problems. To account for possible non-linearity and non-normal error structures, we compared these results with those obtained from generalised linear modelling using log-link functions and Poisson error structure. As this latter approach did not improve our results and was largely consistent with the main analyses shown here, we only present them in the electronic supplement (Tables A7 and A8).

Our SAD fits and predictors were moderately spatially autocorrelated (Moran's $I < 0.5$). However, the global distribution of sites studied would cause any spatially explicit modelling, like simultaneous autoregression modelling or similar techniques, to artificially concentrate a large part of the variance in environmental data in the spatial distance matrix, masking thereby the underlying influences of the environment

(Hawkins, 2012). However, and to account for the spatial structure present in our data, we included the dominant eigenvector of the associated geographical distance matrix as an additional predictor in the GLM analyses (Hawkins, 2012). This dominant spatial eigenvector covered the large scale spatial structure of the sites and explained 85% of total variance in the geographical distance matrix. Species richness and elevation served as additional covariates. We used additive variance partitioning to assess the effects of single environmental predictors on ΔAIC_c, skewness, and evenness. The data used for the present study are available from figshare (Maestre et al., 2015).

Results

At the global scale the lognormal model fitted better ($\Delta AICc > 0$) for 64 (70.3%) and definitely better ($\Delta AICc < -10$) for 58 of the 91 communities with at least 15 species (40.7%; Table 1). Only 10 communities (10.0%) were definitely better fitted by a log-series ($p_{norm} > 10$) while 23 communities (25.3%) scored intermediate ($-10 \leq p_{norm} \leq 10$). Although we found a prevalence of lognormal distributions in each vegetation type (Table 1), there was slight indication that these differ with respect to SAD fit (one-way ANOVA: $F_{3,87} = 3.7$, $P = 0.02$). Tukey post-hoc comparisons point to grasslands as having a lower proportion of lognormal type communities (Table.1). Including sites with as few as 10 species made the results increasingly noisy (electronic supplement Table A1) while at ≥20 species per site (Table A2) results were qualitatively identical to those presented above.

There was a significant latitudinal gradient in $\Delta AICc$ indicating better fits of the lognormal in the Mediterranean communities (GLM $r^2 = 0.17$, $P < 0.01$). South American communities tended to be better fitted by the log-series than Old World communities (GLM $r^2 = 0.11$, $P < 0.05$). Evenness peaked around the equator and decreased with increasing latitude (GLM quadratic regression $r^2 = 0.08$, P [quadratic regression term] = 0.01), while skewness did not significantly vary with latitude ($r^2 = 0.03$, n.s.). After accounting for the effects of species richness and spatial autocorrelation, average annual precipitation was negatively linked to the fit of the lognormal model (Table 2, Table A4), and explained 8% of the variance in $\Delta AICc$. Communities best described by a log-series occurred along the whole gradient of precipitation while better fits of the lognormal were largely restricted to values of annual precipitation below 650 mm (Fig. 2a, ANOVA $F_{1,89} = 5.1$, $P < 0.05$, Fig. A2).

However, within the highly arid communities (aridity level > 0.5) there was a trend towards log-series-distributed SADs at increased arid environments (Fig. 2b, GLM $r^2 = 0.05$, $P < 0.05$). This trend was supported by the reduced data set (at least 20 species per site included: Fig. A2, GLM $r^2 = 0.16$, $P < 0.01$). Among the soil variables, only carbon was consistently included in the regression models for ΔAICc (Table 2, Tabs. A3, A4), and explained 6% of the variance. ΔAICc decreased with increasing soil carbon content (Table 2) indicating a better fit of the lognormal in richer soils. This carbon influence was also corroborated by GLM Poisson regression (Table A7). Finally, we found ΔAICc to be positively linked to available phosphorus (Table 2, 6% variance explanation, and Table A7).

Positive and negative skewness measure the proportions of abundant and rare species, respectively. AICc model selection pointed to carbon content (Table 2) as affecting skewness, although this variable explained less than 5% of variance and consequently was insignificant in the reduced data set (Table A4) and the GLM Poisson model (Table A7). Evenness was negatively linked to soil carbon content (11% of variance explained) and these results were consistent regardless of the data subset used (Table 2, Tables A3, A4, A6).

The relative fit of the lognormal model increased with increasing seasonality in temperature (Table 3, A5, A6, A8) while seasonality in precipitation had no significant effect (Table 3, Tables A5, A6, A8). Despite of the lack of clear regressive trends linking AICc and soil variability (Table 3, Tables A5, A6, A8), our data indicate a distinction of model fit with respect to nitrate variability (Fig. 3a, Fig. A4A). Communities fitted better by a log-series were largely restricted to low nitrate variability. Further, lognormal communities significantly decreased in skewness (Fig. 3b, $r^2 = 0.17$, Fig. A4B) and increased in evenness (Fig. 3c, $r^2 = 0.16$, Fig. A4C) at higher nitrate variability, while there were no such trends for log-series communities (Figs. 3b, c).

Discussion

Basic patterns

Contrary to our first starting hypothesis (arid communities should be dominated by log-series SADs), our study adds dryland plants to the group of communities with a prevalence of lognormal abundance distributions (e.g. Tokeshi, 1998; Magurran and

Henderson, 2003; Connolly et al., 2005; Ulrich et al., 2010). Irrespective of dryland habitat type (Table 1), we found that nearly 2/3 of the communities studied were fitted better by the lognormal model, which predicts a relative excess of species with intermediate abundance. This finding is in line with the only comparable study by Whittaker (1965) on desert plant communities, but contrasts to results obtained with forest tree communities (Ulrich et al. 2010). Also Leigh (1999), Morlon et al. (2009), and Ulrich et al. (2016) have reported log-series abundance distributions to prevail particularly in tropical forest communities. Our results do not exclude the possibility that abundance distributions of dryland vegetation types, in general, differ from more humid forest communities. Therefore our results demand caution about the generalisation of abundance patterns obtained from single ecosystems types and their transfer to dryland ecosystems.

The contrasting results from forest and the present dryland studies call for a mechanistic explanation. The forest data studied by Morlon et al. (2009) and Ulrich et al. (2015) represent to a large extent secondary succession forests and plantations. These are generally characterised by small numbers of highly abundant and larger numbers of rare species, and thus lack the group of intermediately abundant species that characterizes a lognormal distribution (Preston, 1948). Such communities show a comparably low degree of evenness and this community organisation is more in line with a log-series. Studies on boreal forests, containing a relatively low number of very abundant species (often even mono-stands) also reported log-series distributions (Whittaker, 1960). Similarly, in species-rich coral reefs (Connolly et al., 2005) and in tropical and relatively pristine forest communities (Hubbell, 1979; Volkov et al., 2003; Cheng et al., 2012) lognormally organised communities seem to prevail. While our study sites comprise areas with different degrees of human activities, none of the studied sites are subject to intensive management areas such as cropping, fertilization or planting of species (Maestre et al., 2012b). Thus, our results and those from the literature indicate that less impacted ecosystems have a higher probability to follow lognormal species abundance distributions. Consequently, these dryland systems tend to accumulate a ‘middle class’ of species with intermediate relative abundances. Having such a class may make these systems more resistant to functional disturbance because these species might take over ecosystem functioning if the environment becomes suboptimal for the dominant ones, potentially enhancing the resilience to environmental changes (Walker et al., 1999).

About a quarter of the communities (25.3%, Table 1) were roughly equally fitted by both models. This pattern is in line with previous reports (e.g. Hughes, 1986; Magurran and Henderson, 2003; Ulrich and Ollik, 2004; Dornelas and Connolly, 2008; Vergnon et al., 2012), who observed that SADs may be compound functions that capture contrasting parts of local communities and patterns of community assembly. These SADs might comprise on one side the stable elements of resident species following a lognormal distribution and on the other site so-called satellite species having a high temporal dynamic and thus being best described by the log-series (Magurran and Henderson, 2003). Surprisingly, up to now there is no systematic empirical study on how well the compound model fits to SADs in communities across a variety of habitat-types and differing environmental conditions. Apart from the dynamics model of Hughes (1986) and recent work on speciation driven neutral communities (Vergnon et al., 2012) and hidden niche models (Barabás et al., 2013) focusing on multimodality, there is also no explicit theoretical model to predict the precise SAD shape.

The large proportion of intermediate SADs also indicates that lognormal and log-series SADs rather mark both endpoints of a continuum within which very different dominance structures might be realised (Magurran and Henderson, 2003). We speculate that the position within this continuum provides information about the trade-off between species interactions and colonisation – extinction dynamics by which a focal community is shaped. This trade-off should be triggered by the regional species pool size (the colonisation pressure), but also by environmental drivers that act as filters for potential colonisers. Both processes position a focal community into this continuum of SAD shapes. The fact that nearly half of our communities ranked intermediate on this continuum makes it probable that dryland communities are assembled by the interplay of colonisation dynamics and competitive interactions.

Environmental triggers

Based on the global positive co-variation of species richness and productivity (Whittaker, 1975; Currie, 1991, but see Adler et al., 2011), Whittaker (1975) and Hubbell (1979) initiated the idea that SADs are linked to productivity gradients, with increasing lognormality at higher levels of productivity. Therefore, we expected to see a negative correlation of our AICc measure with average precipitation and a respective positive correlation with aridity (hypothesis 2), as plant cover and productivity decrease with increasing aridity (Safriel and Adeel, 2005; Delgado-Baquerizo et al., 2013). This was not the case, as rather we found the opposite pattern between AICc and annual precipitation (Table 2, Fig. 2a), and also a slightly negative effect of species richness on AICc (Table 2). Interestingly, Ulrich et al. (2015) reported a similar negative correlation of the fit of the lognormal distribution with precipitation and also with evapotranspiration in global forest communities. Therefore, both results do not corroborate the productivity hypothesis.

This finding links the occurrence of lognormally distributed communities to sites with higher environmental (in this case water) stress. Ecological theory mainly predicts a connection of stress with the log-series, although we note that existing evidence for this assumption is scarce (Gray et al., 1979; Gray and Mirza, 1979; Death, 1996; McGill et al., 2007; Qu et al., 2008). Our results point to strong effects of habitat filtering, and consequently limited dispersal in stressful environments as the major process shaping SADs. Average conditions filter specific sets of species (Wiens and Graham, 2005), and the abundance rank orders are established in a subsequent step by the interplay of species interactions, reproductive success, and local extinction (McGill et al., 2007). Therefore, variability in environmental conditions appears to be more important for the variation in species composition and abundances between sites than average conditions (Violle et al., 2012). Indeed, we found significant, albeit contrasting, relationships between AICc and the variability in temperature (Table 3). These results are partly in accordance with our third hypothesis (i.e. log-series SADs should be linked to both increased environmental variability and decreased importance of habitat filtering), and indicate the existence of trade-offs in habitat variability with regard to certain abundance distributions, thus complicating the simple environmental variability – lognormal view (Gray et al., 1979; Hamer et al., 1997; Hill and Hamer, 1998).

Only variability in soil carbon content entered the best fit regression model, and thus soil variability appeared to be much less influential than climate variability as a driver of the variation found in the SADs. However, nitrate variability (Fig. 3) might act differently, determining thresholds for community structure. We were surprised to find log-series SADs to be limited to soils with low nitrate variability (Fig. 3a). As nitrate variability also caused a negative skewness (Fig. 3b) and an increased community evenness (Fig. 3c), it apparently forces communities towards lognormal abundance structures with a small number of very rare species. These SADs are not predicted from colonisation driven models that possess a heavy tail of relatively rare species, for instance neutral models without dispersal limitation (Hubbell, 2001; Zillio and Condit, 2007). Our results thus clearly point to variability as a mechanism promoting the emergence of lognormal distributions (Fig. 3a) and limiting local colonisation dynamics (Figs. 3b, c). Consequently, our findings do not corroborate the opposed variability – log-series model that predicts disturbed or unstable sites to have log-series distributed communities (Gray et al., 1979; Zillio and Condit, 2007). A mechanistic explanation for this result invokes that high small-scale soil variability induces the development of a patchy community organisation with many intermediate and low abundant species that, when pooled to samples, nevertheless exhibit a higher evenness than expected from a homogeneous environment (equivalent to statistical averaging, Lehman and Tilman, 2000). Such a patchy distribution of soil nutrients is often exacerbated by even light levels of grazing and shifts seen towards increased shrub canopy cover (Berkeley et al., 2005). Further this patchy distribution prevents species from becoming locally very abundant, thus reducing the number of dominant species in line with the spatial storage effect (Sears and Chesson, 2007). Therefore, the trigger for the negative skewness is not only an increased number of very rare species but also the low number of very abundant species. Indeed, small-scale soil variability is known to induce vicariant plant species composition and phylogenetic structure (Schreeg et al., 2010; Ulrich et al., 2014), reducing the dominance of the most competitive species. In turn, dispersion-driven variability in species composition favours log-series abundance distributions. Thus variability in community composition induced by environmental factors and dispersal might act in opposite directions. We hypothesise that if environmental variability also affects composition, the outcome might be unpredictable and often intermediate between both types of dominance order.

The above picture is complicated by the fact that our environmental variables accounted for at most 35% of the variances in dominance structure (Table 3). This is the point where biotic interactions might step in. As the species found within each plot had already passed the abiotic habitat filters captured by our environmental variables, observed species composition and dominance structure already contain part of the environmental variance, leaving species interactions to explain the residual variance in

SAD shapes. In this respect, dryland plant communities worldwide are predominantly shaped by mutualistic, particularly facilitative, interactions (Soliveres and Maestre 2014). Interestingly, mutualistic interactions have been largely neglected in the SAD literature, which has focused on competition as the major process shaping dominance structures (McGill et al., 2007). Many competition based models (reviewed in Tokeshi, 1998; but see Mouillot et al., 2000) predict lognormal type SADs. As there are no models that include the interplay of competition and mutualistic species interactions, it remains unclear whether and to what degree the observed residual variance in SAD shapes (> 65%) can be explained by both types of interactions.

However, a low impact in terms of variance explanation does not mean that an environmental predictor is of low or even no influence. This predictor might severely and selectively constrain species abundance and also filter for possible species combinations. Consequently, such predictors might invoke strong selective pressures on species causing the long-term reshaping of community structure. Unfortunately respective long-term effects of low impact environmental drivers are not well known. In this respect we need data on the temporal change in abundance distributions in habitats of stable environmental conditions. Such data might allow for an assessment of the real impact of environmental drivers on community structure.

Conclusions

Composition and dominance orders of dryland plant communities are influenced by a manifold of possible drivers. Our results do not point to productivity as a driver towards lognormal abundance distributions in drylands. Rather, we identified the small scale variability in soil characteristics to be of major importance for the maintenance of community evenness and the type of SAD. This variability, in combination with arid habitat conditions, is supported by the presence of a proper ‘middle class’ of abundances. Factors increasing this small-scale soil variability might therefore also contribute to the stability of dryland plant communities.

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Online resources

Electronic supplementary material

Results from the additional analysis using the extended data set (sites with at least 10 species) and the reduced data set (sites with at least 20 species)

Table 1. Numbers of better fits of the log-series (ΔAICc > 10) and lognormal (ΔAICc < -10) SAD models for the vegetation types included in the present study. Intermediate fits refer to $-10 \leq \Delta\text{AICc} \leq +10$.

Vegetation type	Better fit of		
	log-series	lognormal	intermediate
Grasslands	4	22	8
Scrublands	6	21	14
Woodlands	0	15	0
Savannah	0	0	1
Total	10	58	23

Table 2. Ordinary least squares (OLS) models to identify relationships between environmental variables and the relative fits of the lognormal model (ΔAICc), SAD skewness, and evenness The variables included in the best fit models (lowest AICc) are in bold type Model beta values and r^2 refer to the beta values and the explained variance of the respective model N = 91

Variable	ΔAICc	Skewness	Evenness
Spatial eigenvector	-0.03	**-0.26**	**0.25**
Elevation	0.01	0.03	0.15
Species richness	**-0.24**	0.09	**0.16**
Temperature	0.06	**-0.20**	0.07
Precipitation	**0.17**	**0.23**	-0.12
pH	0.07	-0.11	0.07
Available phosphorus	**0.20**	-0.01	0.01
Organic carbon	**-0.21**	**0.17**	**-0.39**
Nitrate	-0.09	-0.02	0.03
r^2 (OLS total model)	0.18	0.15	0.28
r^2 (OLS selected model)	0.16	0.14	0.25

Table 3. Ordinary least squares (OLS) models to identify relationships between soil and climatic variability and the relative fits of the lognormal model (ΔAICc), SAD skewness, and evenness The variables included in the best fit models (lowest AICc) are in bold type Model parameters and r^2 refer to the beta values and the explained variance of the respective model N = 91

Variable	ΔAICc	Skewness	Evenness
Spatial eigenvector	-0.06	**-0.28**	**0.28**
Elevation	-0.04	0.07	-0.03
Species richness	**-0.21**	0.03	**0.24**
Temperature seasonality	**-0.22**	0.01	0.01
Precipitation seasonality	-0.07	**0.14**	0.15
CV pH	-0.04	0.06	-0.12
CV available phosphorus	-0.05	-0.10	0.07
CV organic carbon	**0.13**	0.15	**0.17**
CV nitrate	-0.08	**-0.39**	**0.45**
r^2 (OLS total model)	0.14	0.26	0.38
r^2 (OLS selected model)	0.12	0.23	0.35

Figure 1. Three examples of dryland SADs with best fits. From the left: a site from Argentina Pampas and the respective log-series fit, a site from China with the respective lognormal fit, and a site from Spain where both models fit nearly equally well

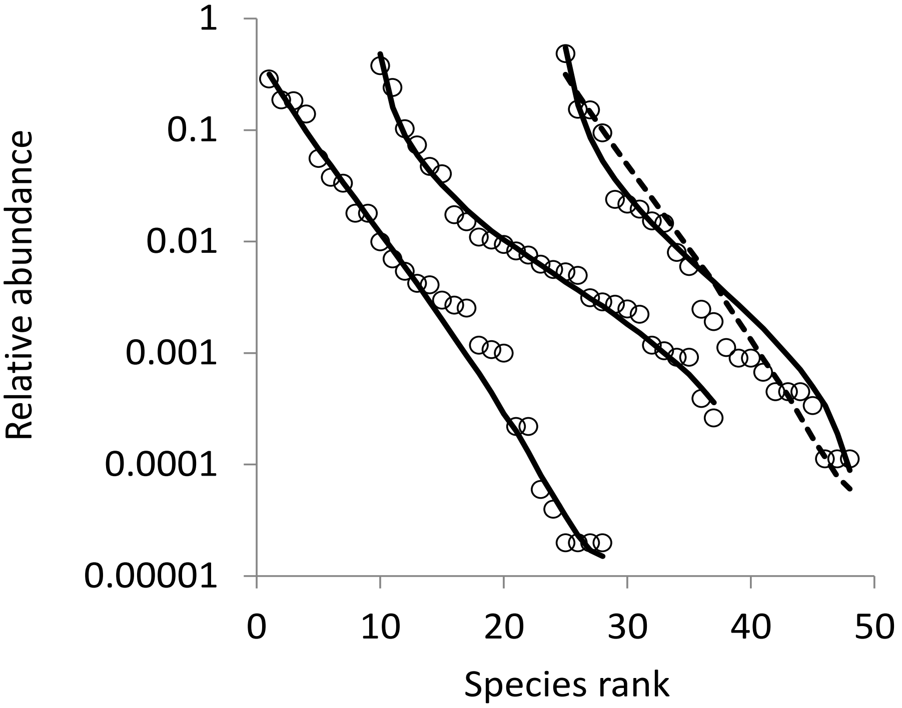

Figure 2. Better fits of the log-series SAD model (open dots) were independent of the degree of precipitation (a) while the lognormal model (black dots) generally fitted better (two exceptions) below 600 mm annual precipitation. Lognormal SADs were found predominately at higher levels of aridity (b).

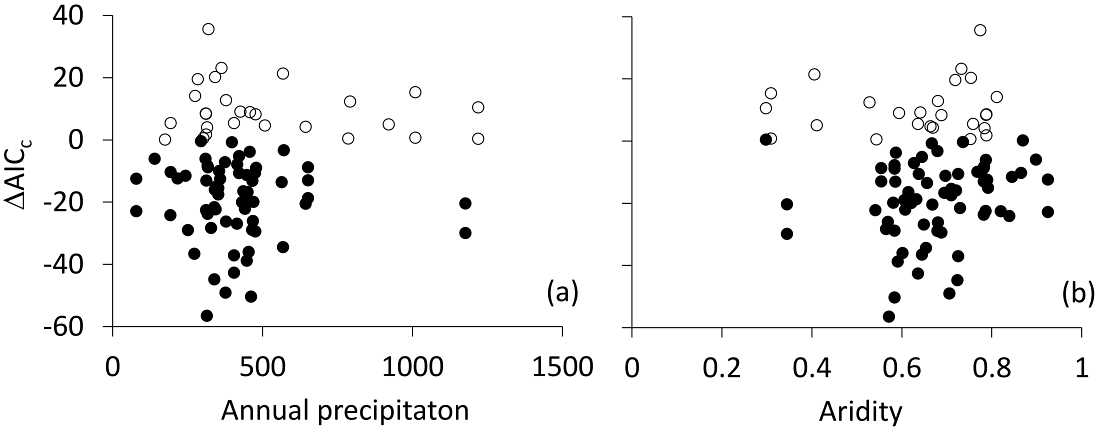

Figure 3. Scatter plots of the effect of soil nitrate variability (CV N) on p_{norm} (A), SAD skewness (B), and evenness (C) of the 91 sites having at least 15 species Black and open circles denote sites better fitted by the lognormal SAD and the log-series SAD, respectively. Regression lines for black circles: B: $r^2 = 0.21$, $P < 0.001$, C: $r^2 = 0.25$, $P < 0.001$