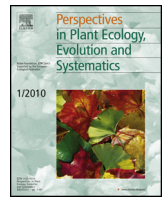




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Environmental correlates of species rank – abundance distributions in global drylands



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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. Lognormal SADs were 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 dryland 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 heterogeneous environments, allowing for more evenly distributed plant communities, or in 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.

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1. Introduction

Since its introduction by Raunkjær (1909), species abundance distributions (SADs) have been extensively studied by ecologists (reviewed in McGill et al., 2007; Matthews 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 characterised 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

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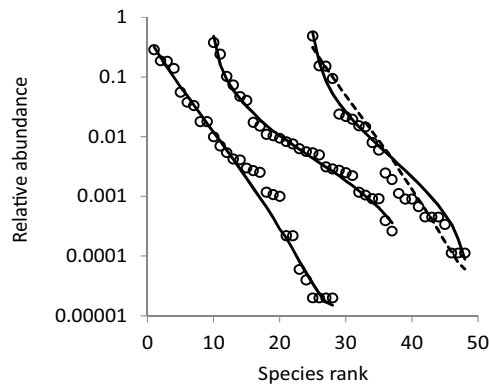


Fig. 1. Three examples of dryland SADs with best fits. From the left: a site from Argentina Pampas and the respective log-series fit, a site from China with the respective lognormal fit, and a site from Spain where both models fit nearly equally well.

more likely to be found in closed communities with low temporal and spatial species turnover and a high proportion of species with intermediate abundances (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 been theoretically linked to environmental conditions and gradients (reviewed in Magurran, 2004; McGill et al., 2007; Dornelas et al., 2011). Some authors assume that 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).

Our knowledge about plant species abundance distributions stems mainly from work done in forests (Hubbell, 1979; Morlon et al., 2009; Ulrich et al., 2016) and temperate grasslands (Bazzaz, 1975; Maire et al., 2012). With the exception of Whittaker (1965) classical report of a lognormal SAD for Arizona desert plants, similar distributions in arid, semi-arid and dry-subhumid regions (dry-

lands 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 (Safrieli 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 91 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, 1975; Hubbell, 1979). These assumptions lead to four basic starting hypotheses regarding dryland plant communities: (1) arid, and therefore low productive, communities are dominated by log-series SADs; (2) woodland communities, typically dominated by a few species (reviewed in Carson and Schnitzer, 2011), should follow log-series distributions; (3) lognormal SADs dominate in species rich communities; and (4) log-series SADs are linked to both increased environmental variability and decreased importance of habitat filtering.

2. Materials and methods

2.1. 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 three basic vegetation types (open 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 compro-

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