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Plant species-area relationships are determined by evenness, cover and aggregation in drylands worldwide

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Abstract

Aim—Species-area relationships (also known as ‘species-area curves’ and ‘species accumulation curves’) represent the relationship between species richness and the area sampled in a given community. These relationships can be used to describe diversity patterns while accounting for the well-known scale-dependence of species richness. Despite their value, their functional form and parameters, as well as their determinants, have barely been investigated in drylands.

Location—171 drylands from all continents except Antarctica.

Time period—2006–2013

Major taxa studied—Perennial plants

Methods—We characterized species-area relationships of plant communities by building accumulation curves describing the expected number of species as a function of the number of sampling units, and later compared the fit of three functions (power-law, logarithmic and Michaelis-Menten). We tested the prediction that the effects of aridity, soil pH on SAR are mediated by vegetation attributes such as evenness, cover, and spatial aggregation.

Results—We found that the logarithmic relationship was the most common functional form (c. 50%), followed by Michaelis-Menten (c.33%) and power-law (c.17%). Functional form was mainly determined by evenness. Power-law relationships were found mostly under low evenness, logarithmic relationships peaked under intermediate evenness and the Michaelis-Menten function increased in frequency with increasing evenness. The SAR parameters approximated by the logarithmic model (‘small-scale richness’ (b_0) and ‘accumulation coefficient’ (b_1)) were determined by vegetation attributes. Increasing spatial aggregation had a negative effect on the small-scale richness and a positive effect on the accumulation coefficient, while evenness had an opposite effect. In addition, accumulation coefficient was positively affected by cover. Interestingly, aridity decreased small scale richness but did not affect the accumulation coefficient.

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Data Accessibility

Data are available on Figshare

Main conclusions—Our findings highlight the role of evenness, spatial aggregation and cover as main drivers of species area relationships in drylands, the Earth’s largest biome.

Keywords

species accumulation curves; species-area curves; species richness; aridity; scale-dependence; pH; biodiversity

1 Introduction

Understanding how biodiversity varies in space and time is one of the main ecological challenges of this century (Sala *et al.*, 2000). Species richness, the number of species in a given area, is the simplest and most used biodiversity index (e.g. Vellend *et al.* 2013, Soons *et al.* 2017). However, species richness is extremely sensitive to the spatial scale (extent and grain size) considered (Whittaker *et al.*, 2001; Rahbek, 2005; Scheiner *et al.*, 2011; May *et al.*, 2018), and this scale-dependence is a major source of divergence among studies (Weiher, 1999; Mittelbach *et al.*, 2001; Chiarucci *et al.*, 2006). A possible solution to overcome this scale-dependence is to characterize communities across multiple scales using “Species-Area Relationships” (hereafter SAR, also termed ‘Species-Area Curves’). The species-area relationship describes how the total number of species varies as the sampled area increases (Scheiner, 2003; Dengler, 2009). Here, we focus on SAR type IIIB (Sensu Scheiner 2003), which describes the expected (mean) number of species as a function of the number of (non-contiguous) sampling units. The expected richness of this SAR type is computed based on all possible combinations of sampling units disregarding their spatial location within a site. Some authors refer to this SAR type as ‘species accumulation curve’ (Ugland *et al.*, 2003; Gray *et al.*, 2004; Harvey & MacDougall, 2018) or ‘species sampling curve’ (Dengler, 2009).

Ecological communities may vary in the type of function that best characterizes their SAR (hereafter ‘Functional form’) and in the parameter values of that function (hereafter ‘SAR parameters’). The functional form of the SAR could be described by various functions (Tjørve, 2009; Williams *et al.*, 2009) but the simplest ones are power law (‘Arrhenius’), logarithmic (‘Gleason’) and Michaelis-Menten (‘Monod’). All these functions are convex (see formulas in the methods section), but the slope of the power law often shows the smallest decrease with increasing area in contrast with the asymptotic Michaelis-Menten function (Tjørve, 2009; Williams *et al.*, 2009). The logarithmic function is intermediate between the two other forms, but never approaches an asymptote (Figure 1).

The two main proximate factors that determine SAR shape are species abundance distribution and spatial aggregation (He & Legendre, 2002; Tjørve *et al.*, 2008). Furthermore, Chase and Knight (2013) separated the effects of species abundance distribution on SAR into three components namely, density, evenness and species pool size. Both density (number of individuals per area) and evenness (similarity in relative abundance among species) increase richness at small spatial scales by increasing the probability of species detection (He & Legendre, 2002; Tjørve *et al.*, 2008). Nonetheless, their effect on richness declines with increasing the number of sampling units (Chase & Knight, 2013).

Spatial aggregation (intraspecific clustering in spatial distribution) decreases richness at small scales because aggregated species are less likely to be sampled, but this effect decreases as more sampling units are incorporated (He & Legendre, 2002; Tjorve *et al.*, 2008; Chase & Knight, 2013). Species pool size (the number of species that could colonize a site as determined by evolutionary and historical processes) has a positive effect on richness at all scales, although its relative importance should increase as more sampling units are added (Chase & Knight, 2013).

A full understanding of SAR drivers includes a ‘causal cascade’ where the ultimate abiotic factors affect the proximate factors (e.g. pH affects evenness), thereby affecting SAR functional form and parameters (Chase & Knight, 2013). Recently, ecologists have started investigating how different proximate factors affect scale-dependent richness responses in reef fish (Blowes *et al.*, 2017) and invaded plant (May *et al.*, 2018) communities. Here, we focused on ultimate and proximate factors explaining SARs using vegetation data gathered from 171 drylands from six continents (Maestre *et al.*, 2012; Ochoa-Hueso *et al.*, 2018). Drylands, regions where the ratio between precipitation and potential evapotranspiration is lower than 0.65 (Hassan *et al.*, 2005), cover 45% of Earth’s land surface (Pr v lie, 2016) and support over 38% of the human population (Reynolds *et al.*, 2007). They are threatened by global land-use and climate changes that may further decrease water availability (D’Odorico *et al.*, 2013). Previous investigations of this database have revealed that abiotic factors such as aridity and pH determine the diversity (Soliveres *et al.*, 2014; Ulrich *et al.*, 2014) and spatial distribution (Saiz *et al.*, 2018) of plant communities, but their effect on SAR has never been investigated. Hence, in this contribution we studied the SAR patterns of perennial plant communities, focusing on the following questions:

- (1) What is the relative role of different proximate factors (evenness, density, and spatial aggregation and species pool) in determining SAR patterns?
- (2) How do proximate factors mediate the effect of aridity and pH on SAR?

2 Methods

(a) Study area and fitting species area relationship

The study includes sites representative of the major types of dryland vegetation from all continents except Antarctica, which cover a wide range of environmental conditions (mean annual temperature and precipitation ranged from -1.8 to 28.2 °C, and from 66 to 1219 mm, respectively). In all sites, vascular perennial vegetation was sampled using a standardized protocol (Maestre *et al.*, 2012). The sampling design included four 30-m length parallel transects comprised of 20 contiguous 1.5 x 1.5m sampling units (with eight meters distance between transects), where the cover of each perennial species was estimated. The SARs obtained from this type of sampling design are at the borderline between ‘Type IIB’ (contiguous sampling units) and type IIIB (non-contiguous sampling units) according to Scheiner (2003). Still, because the sampling units are not entirely contiguous (there was an 8 m distance between transects surveyed at each site), we refer to the SARs in this manuscript as type IIIB hereafter.

The mean and coefficient of variation (hereafter CV) in soil pH were estimated based on 10-15 soil cores of 145cm³ obtained at each site (see Maestre *et al.* 2012 and Supporting Online Material for details). We calculated the Aridity Index (AI, defined as precipitation/potential evapotranspiration) of each site as described in Zomer *et al.* (2008), who used data interpolation obtained from WorldClim (Hijmans *et al.*, 2005; Zomer *et al.*, 2008). Since higher values of AI correspond with more mesic sites (less arid), we used 1-AI (hereafter ‘aridity’) as a surrogate of aridity to facilitate the interpretation of our results. Both aridity and soil pH has been found to be important drivers of the structure and functioning of dryland ecosystems (Maestre *et al.*, 2012; Le Bagousse-Pinguet *et al.*, 2017). We used 171 sites out of the 236 original sites of the database (Ochoa-Hueso *et al.*, 2018) because we excluded sites with less than 10 perennial plant species (after this exclusion species richness in the study sites varied from 10 to 49).

For each site, a species area relationship (SAR) was built using the function ‘specaccum’ of the ‘Vegan’ R package (Oksanen *et al.*, 2013). This accumulator function calculates the expected number of species as a function of the number of sampling units using the algorithm suggested by Ugland *et al.* (2003). Then, each site-specific relationship was fitted to the following functions:

- (1) Power-law function: $S = b_0 \cdot A^{b_1}$
- (2) Logarithmic function: $S = b_0 + b_1 \cdot \log(A)$
- (3) Michaelis-Menten function: $S = \frac{b_0 \cdot A}{b_1 + A}$

In all functions, S is the number of species (the dependent variable), A is the number of sampling units (the independent variable) and b_0 and b_1 are the two (estimated) parameters. The best function for each site was chosen based on the lowest corrected Akaike Information Criterion (AICc) of the fitted model (Grueber *et al.*, 2011).

(b) Proximate drivers of species area relationship

We estimated the effect of proximate drivers of SAR (spatial aggregation, evenness, density) using several indices. As an index for spatial aggregation, we calculated the slope of the relationship between the incidence (proportion of the sampling units where the species was found) and the log abundance of each species. The steeper the slope, the more aggregated the plant community (Wright, 1991; Hartley, 1998). Evenness was estimated using the modified Pielou’s index (Jost, 2010), $\frac{\exp(H)}{S}$, where H is Shannon diversity index and S is the number of species in the community. This index ranges between zero and one.

Cover (i.e. sum of the cover of different species) was used as a proxy for density because we did not measure the number of individuals per area. To partially account for this limitation, we separated between the total cover of woody species (‘woody cover’) and that of perennial herbs (‘herbaceous cover’) assuming the latter group may include more individuals for a given cover (more herbs than shrubs could grow in a given level of cover due to their typically smaller size).

The last factor, species pool size (the number of species that could colonize a site as determined by evolutionary and historical processes) could not be independently estimated in our observational dataset. In various studies (e.g. Pärtel *et al.*, 1996; Segre *et al.*, 2014), ‘site richness’ (the number of species found when all sampling units are combined) is used as a *proxy* for species pool size. However, some authors argue that the correlation between species richness at different scales is inevitable, and therefore inclusion of ‘site richness’ as an explanatory variable in our models could lead to an underestimation of the real underlying mechanism (Herben, 2000; Švamberková *et al.*, 2017). To avoid this problem we treated site richness in different manner than the other proximate factors used in our analysis (see details in section ‘estimating the drivers of SAR parameters’ below).

Classification of the functional forms—We tested whether vegetation attributes (spatial aggregation, evenness, herbaceous cover and woody cover) determine the SAR functional form using a classification tree. The analysis was conducted using the R package ‘party’, which allows unbiased recursive partitioning based on conditional inference, thereby reducing the risk of overfitting by retaining only significant nodes (Hothorn *et al.*, 2006). In contrast with other classification approaches (e.g. random forest), this approach creates a single best tree which allows easy interpretation of the parameter values separating each node. In addition to the vegetation attributes, the spatial coordinates (longitude and latitude) were also incorporated into this analysis (as explanatory variables) to avoid the bias caused by spatial autocorrelation (i.e. lack of independence among nearby sites).

(c) Estimating the drivers of SAR parameters

We built a structural equation model (SEM) using the R package ‘piecewiseSEM’, which allows a flexible analysis based on the local estimation method (Lefcheck, 2016). The SEM estimates the causal effects of the ‘proximate factors’ (spatial aggregation, evenness, herbaceous cover and woody cover) as well as the abiotic factors (aridity [1-evaporation/precipitation], mean pH and CV pH) on SAR parameters. A full description of the SEM approach used is found in Appendix S1.

Since parameters of different SAR functional forms cannot be compared, we applied the logarithmic functional form for all sites because this function had the highest explanatory power across sites (the median R^2 for all sites was 0.99), meaning that even in cases where the model was not the ‘best’ in terms of AICc, it could still be used as an *approximation* (See Appendix S2 and Figure S1 for an estimation of the bias caused by our approach). Nonetheless, five sites where the R^2 returned when fitting the logarithmic function was less than 0.90 were excluded from the analysis to reduce the bias of our approach. The logarithmic function includes two coefficients, an ‘intercept’ (b_0 , hereafter termed ‘small-scale richness’ because it estimates the number of species in one sampling unit) and a ‘slope’ (b_1 , hereafter termed ‘accumulation coefficient’ because it represents the effect of increasing the number of sampling units on the species richness).

We treated ‘site richness’ (the number of species found when all sampling units are combined) as a variable that depends on the abiotic factors and is *correlated* with SAR parameters in the SEM. The model assumes that there is a correlation between site richness

and SAR parameters, but does not estimate any causal effect (no partial regression coefficients produced) i.e. there was no assumption about the directionality (causality) of this correlation (See Grace & Bollen, 2005 for a detailed explanation). Similarly, the model includes non-causal correlations among the proximate factors, among the SAR parameters and between the mean and CV of soil pH. The *a priori* ‘full’ model included causal effect of all possible abiotic factors on all proximate factors, as well as causal effect of all factors (abiotic and proximate) on SAR parameters (a ‘direct’ effect of abiotic factors on SAR parameters represents effects that are not mediated by the proximate factors). We applied a model selection approach for identifying the best model among all possible subsets of the full models (i.e. similar models with some causal links removed) based on AICc scores (Grueber *et al.*, 2011). In addition, we conducted complementary analyses where species pool was estimated based on the number of species at the whole site (900m²) rather than on the sampled area (180m²) using a subset of sites where this data was available (see Appendix S3 for details)

We transformed several variables to meet the assumption of normality for the SEM: accumulation coefficient and aggregation were log transformed while herbaceous and woody cover were logit transformed. In addition, all variables were standardized (to mean of zero and standard deviation of one) to allow comparison of SEM coefficients (see Figure S2 for bivariate scatter plots and distribution of all variables).

To avoid problems of spatial autocorrelation we used Moran Eigenvectors Maps that were built using the R package ‘adespatial’ (Dray *et al.*, 2012). The inclusion of these eigenvectors enables the reduction of potential bias in parameter estimation caused by unmeasured factors related to spatial autocorrelation such as disturbances, historical land-use or soil characteristics. For reducing these confounding effects as much as possible (i.e. applying the most conservative approach), we included all the 10 positive eigenvectors in all the relationships included in the SEM (more details on the SEM are found in Appendix S1).

Results

All the functional forms evaluated were found in the drylands studied (Figure 2). The logarithmic function was the most common (85 sites [50%]) followed by Michaelis-Menten (56 sites [33%]) and power-law (30 sites [17%]) functions. Evenness was the only variable that predicted SAR functional form in the classification tree, although its predictive power was relatively modest, i.e. none of the terminal nodes created by the tree was comprised from only one functional form (Figure 3). Power-law relationships were found mostly under low evenness (< 0.31), logarithmic relationships were common at all evenness levels but peaked under intermediate levels (0.31 - 0.42) and the Michaelis-Menten relationships increased in frequency with increasing evenness, being most dominant under the highest level (> 0.42). These results were robust to exclusion of six sites with high uncertainty regarding the best model describing their functional form (Figure S3).

The graphical representation of the SEM (Figure 4, see Table S1 for detailed results) shows the main drivers of small-scale richness (b_0 , ‘SAR intercept’) and accumulation coefficient (b_1 , ‘SAR slope’). As expected, evenness increased small-scale richness but decreased the

accumulation coefficient. The effects of aggregation were opposite, as it decreased small-scale richness but increased the accumulation coefficient. Herbaceous and woody cover had positive effects on the accumulation coefficient but did not affect small-scale richness. Surprisingly, all proximate factors were independent of both aridity and pH. Additionally, aridity had a negative effect on small-scale richness (independent of all proximate factors as indicated by a 'direct arrow' in Figure 4) but did not affect the accumulation coefficient; therefore its effect on site richness was smaller than its effect on small-scale richness. There was also small positive effect of mean pH on small-scale richness and a small positive effect of the CV of pH on the accumulation coefficient. Interestingly, there was a strong correlation between site richness and the accumulation coefficient ($r = 0.93$, $p < 0.001$), a weaker correlation between site richness and small-scale richness ($r = 0.42$, $p < 0.001$) and a non-significant correlation between small-scale richness and the accumulation coefficient ($r = 0.08$, $p = 0.32$). These correlations remained almost unchanged in alternative SEMs where we used other proxies for species pool (Appendix S3, Tables S2, S3)

Discussion

In this study we used species area relationship (SAR) for characterizing the diversity of perennial plants in drylands worldwide. We found that the SAR functional form is mainly determined by evenness, and that the SAR parameters are determined by contrasting effects of evenness and aggregation. In addition, we found that aridity decreases small-scale richness (b_0 , the intercept of the SAR), but does not affect the accumulation coefficient (b_1 , the slope of the SAR).

Debates regarding SAR functional forms date back to the beginning of the 20th century (reviewed in Connor & McCoy, 1979; Dengler, 2009; Tjørve *et al.*, 2018). For years, the most common approach for describing SAR was based on the power-law function (Drakare *et al.*, 2006; Dengler, 2009). At the beginning of the 21st century, ecologists still disagreed on whether SAR should reach an asymptote or not based on both theoretical and empirical considerations (Lomolino, 2000; Williamson *et al.*, 2002). Since then, theoretical models have aimed to reconcile this debate by showing that the functional form of SAR largely depends on evenness, aggregation, density and species pool (Tjørve *et al.*, 2008; Chase & Knight, 2013). While we expected that functional form will be determined by complex interactions among these factors, we found that the best classification tree of the drivers of functional form incorporated only evenness. As expected from the models, Power-law relationships were found mostly under low evenness, logarithmic relationships peaked under intermediate evenness and the asymptotic Michaelis-Menten function increased in frequency with increasing evenness. Still, evenness cannot fully predict the SAR functional form, suggesting that there are additional important drivers that were not captured by our predictors.

Power-law SARs have been often documented in tropical forests, which are characterized by a large species pool (Drakare *et al.*, 2006). In contrast, a study in the Sonoran desert found power-law relationships relatively rare and interpreted this pattern as a result of smaller species pool in these systems (Stiles & Scheiner 2007). Our results are in accordance with that study, as only 17% of the SARs we studied were characterized by a power law.

Nonetheless, our study, as well as Stiles & Scheiner (2007), focuses on SAR type IIIB while most previous studies focus on other SAR types with a nested design (Drakare *et al.*, 2006). Hence, it remained to be tested whether the differences in SAR functional form reflect ecological differences between drylands and other systems or merely the differences in the sampling design used among studies.

In most communities (c. 96%) the different functional forms were very distinguishable ($AIC_c > 7$). However, despite these detectable differences, we found that the logarithmic function could be used as approximation for almost all SARs due to its high explanatory power ($R^2 > 0.90$ for 97% of the sites). Nonetheless, this function leads to underestimation of the number of species in a given sampling unit (b_0 , the estimate of sampling unit richness, is on average 1.3 lower than the real values, Figure S1). The logarithmic approximation thus leads to a conservative bias (underestimation of c.18%) of the regression coefficients of 'small-scale richness' in the SEM (see Appendix S2 and Figure S1 for a detailed investigation of the bias).

We predicted that small-scale richness and the accumulation coefficient (SAR parameters) will be affected by four proximate factors namely, woody cover, herbaceous cover, evenness and spatial aggregation (following He & Legendre, 2002; Tjorve *et al.*, 2008; Chase & Knight, 2013). In accordance, we found that aggregation decreased small-scale richness but increased the accumulation coefficient while the effect of evenness was opposite. We also found a positive effect of woody and herbaceous cover on the accumulation coefficients, which contrasts the theoretical expectation that the effect of density should be stronger in small scales (Chase & Knight, 2013).

We found that both aridity and soil pH affected small scale richness. However, these effects were 'direct', i.e. not mediated by any proximate factors (they did not affect cover, aggregation and evenness). A possible explanation for these results is small species pool in more arid and acidic sites (due to combination of historical and evolutionary processes). Importantly, if the effects of aridity and pH on SAR were mediated by species pool size, we would expect that aridity will also decrease the accumulation coefficient, since the effects of species pool increase with area (Chase & Knight, 2013). However, no effects of aridity and pH on the accumulation coefficient or site-scale species richness were found. Hence, we speculate that the 'direct' effects of aridity and pH are related to other drivers that were not captured by our indicators, especially density that was approximated by cover.

Environmental heterogeneity is considered a main driver of SARs (Scheiner *et al.*, 2011). We used the CV in pH (hereafter CVpH) as an indicator for heterogeneity (this variable is by no means the only source of heterogeneity). We assumed that higher heterogeneity (as an ultimate factor) will increase the spatial aggregation (species will be aggregated into different microsites representing different niches) thereby increasing the accumulation coefficient. However, we did not find any effect of CVpH on aggregation. Instead, we found a 'direct' effect of CVpH the accumulation coefficient. Since any ultimate factor should be mediated by one of the proximate factors, this result suggests that our indicator for spatial aggregation does not capture aggregation in the most relevant scale by which CVpH affect species distribution.

Aggregation is scale dependent. Therefore, any index describing aggregation at one scale (often the sampling unit scale) inevitably underestimates the effect of aggregation at all scales (Hui *et al.*, 2010). Furthermore, since species vary in size, it is impossible to select a spatial scale adequate for all species simultaneously. Although our study design allowed us to assess aggregation and to show that it is a main driver of SAR parameters, we probably underestimated the aggregation of some large woody species where each individual is larger than the sampling unit (1.5 x 1.5 m). Nevertheless, this bias is relatively modest since the proportion of species larger than the sampling unit was very low in almost all sites (Mean = 3%, Median = 0%, see Appendix S4 and Figure S4 for details)

It is possible that the effect of density was also underestimated in our study because we used cover as its proxy. A previous study of SAR along an aridity gradient found that aridity affected small-scale, but not large-scale, richness, and therefore their authors hypothesized that cover mediates the effects of aridity on SAR (De Bello *et al.*, 2007). Our results did not support this hypothesis because we found an effect of cover on the accumulation coefficient but not on small-scale richness. Still, theoretical models suggest that *density* rather than *cover* is the underlying driver of small-scale richness (Chase & Knight, 2013). Hence, it is possible that cover is not a good indicator of density, thereby leading to an underestimation of density effects.

Interestingly, our study documented a very strong correlation between site richness and the accumulation coefficient, as well as a weaker correlation between site richness and small-scale richness. These results indicate that variations in species richness at the site level are more related to differences in accumulation coefficient than to small-scale richness. We are not sure what is the mechanism behind this interesting pattern but we speculate that it could be related to the large spatial heterogeneity that characterizes drylands (Noy-Meir, 1985). Another interesting finding that is yet to be explained is the lack of correlation between the SAR parameters, small-scale richness and accumulation rate. More theoretical models investigating the expected correlation between SAR parameters (from the logarithmic model) are required for a better interpretation of this pattern.

The correlation between SAR parameters and site level species richness could be interpreted as an evidence for species pool size being the most important factor determining SAR, in accordance with the theoretical prediction (Chase & Knight, 2013). Yet this type of reasoning has been criticized by some authors suggesting that correlation between site-richness and smaller scale richness is inevitable and does not necessarily reflect any species pool effect (Herben, 2000; Švamberková *et al.*, 2017). Hopefully future experimental studies manipulating species pool would allow separating the causal effects of species pool size and unavoidable correlations that could not be separated using observational data.

Conclusions

Our findings support untested theoretical predictions (He & Legendre, 2002; Tjorve *et al.*, 2008; Chase & Knight, 2013) and question the automatic use of power law functions to describe SARs (see also Stiles & Scheiner, 2007; Smith, 2010). Importantly, the link between SAR functional form and evenness has important implications for management

since SAR is a common tool for characterizing biodiversity in conservation science (Smith, 2010). While it is reasonable to expect a nearly asymptotic behavior (when enough sampling units are sampled) in even communities, this expectation is unlikely in uneven communities that would require extrapolation methods (e.g. Walther & Moore, 2005). The strong effects of evenness and spatial aggregation on SAR highlight the importance of understanding their main ultimate drivers (e.g. competition, heterogeneity, dispersal). Hence, we propose that future theoretical and empirical studies should focus on the mechanisms behind spatial aggregation and evenness that determine biodiversity patterns in several scales instead of focusing on species number in a given (arbitrary) scale.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Three examples of 'species-area relationships' (SARs) characterized by different functional forms. (*power-law relationship* - 'Morata_CCA' [Spain], *logarithmic relationship* - 'Site A' [China], *Michaelis-Menten relationship* - 'Aspe' [Spain]). The black lines are the SAR (the mean number of species based on all combinations of sampling units), while the gray areas represent their 95% confidence intervals. The colored lines represent the trend line of the best fitted functional form ($AIC_c > 200$ in all sites). The upper panels show the SAR in a linear space. In this scale all functions are concave. The lower panels show the same SAR (from the same sites) on a semi-logarithmic space (the x-axis is logarithmic). In this scale power-law function is convex, logarithmic function is linear and Michaelis-Menten function is concave.

Figure 2.

Pie charts describing the proportion of SAR functional forms in drylands from across the globe (sites are aggregated by country). Red – Power-law function, blue – logarithmic function, green – Michaelis-Menten function. Circle size represents the number of sites per country. N=171

Figure 3.

A classification tree predicting the functional form of the species-area relationship based on evenness index (other factors were found to be non-significant). The bars in each terminal node represent the portion of sites classified to each functional form (P - Power-law, L - Logarithmic, M - Michaelis-Menten). N=171

Figure 4.

Results of the structural equation model (SEM) of factors determining ‘small-scale richness’ and ‘accumulation coefficient’ (i.e. the intercept [b_0] and the ‘slope’ [b_1] of the species-area relationship assuming a logarithmic relationship). Rectangles represent observed variables; unidirectional arrows represent significant ($P < 0.05$) positive (solid lines) and negative causal effects (dashed lines). The numbers above the unidirectional arrows are standardized regression coefficients (effect size). The bidirectional grey arrows represent significant positive (solid line) and negative (dashed line) correlations (the numbers near the lines are Pearson correlation coefficients). Line width is proportional to the strength of the causal regression correlation coefficients. The model is in agreement with the data (local estimation, Fisher.C = 56, df = 44, p-value = 0.11). All the parameters of the model are summarized in Table S1. N=166