Assessing the Role of Environmental Filtering in Structuring Global Dryland Communities

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Tweetable abstract: a test of the environmental filtering hypothesis in global drylands

Summary

1. The environmental filtering hypothesis predicts that the abiotic environment selects species with similar trait values within communities. Testing this hypothesis along multiple – and interacting – gradients of climate and soil variables constitutes a great opportunity to better understand and predict the responses of plant communities to ongoing environmental changes.
2. Based on two key plant traits, maximum plant height and specific leaf area (SLA), we assessed the filtering effects of climate (mean annual temperature and precipitation, precipitation seasonality), soil characteristics (soil pH, sand content and total phosphorus) and all potential interactions on the functional structure and diversity of 124 dryland communities spread over the globe. The functional structure and diversity of dryland communities were quantified using the mean, variance, skewness and kurtosis of plant trait distributions.
3. The models accurately explained the observed variations in functional trait diversity across the 124 communities studied. All models included interactions among factors, i.e. climate – climate (9% of explanatory power), climate – soil (24% of explanatory power) and soil – soil interactions (5% of explanatory power). Precipitation seasonality was the main driver of maximum plant height, and interacted with mean annual temperature and precipitation. Soil pH mediated the filtering effects of climate and sand content on SLA. Our results also

revealed that communities characterized by a low variance can also exhibit low kurtosis values, indicating that functionally contrasting species can co-occur even in communities with narrow ranges of trait values.

4. *Synthesis* We identified the particular set of conditions under which the environmental filtering hypothesis operates in drylands worldwide. Our findings also indicate that species with functionally contrasting strategies can still co-occur locally, even under prevailing environmental filtering. Interactions between sources of environmental stress should be therefore included in global trait-based studies, as this will help to further anticipate where the effects of environmental filtering will impact plant trait diversity under climate change.

Keywords: climate, community assembly, determinants of plant community diversity and structure, functional biogeography, functional diversity, plant height, pH, precipitation seasonality, specific leaf area, trait distribution.

Introduction

Environmental filtering is one of the most pervasive concept in ecology, being central in many studies of plant community assembly, biogeography (e.g. Swenson *et al.* 2012; de Bello *et al.* 2013), and trait-based modelling (see Laughlin & Laughlin 2013 for a review). The environmental filtering hypothesis predicts that the abiotic environment selects species with similar trait values within communities (Keddy 1992; Weiher *et al.* 1998; Grime 2006). The effect of environmental filtering on plant communities has been traditionally assessed along local or regional environmental gradients (e.g. Fonseca *et al*. 2000; Gross *et al.* 2008; de Bello *et al*. 2013; Butterfield & Munson 2016). However, the effect of environmental filtering, *sensu stricto*, is difficult to isolate from that of local biotic interactions along these gradients (Maire *et al*. 2012; Gross *et al.* 2013; Kraft *et al*. 2015). In a recent paper, Kraft *et al.* (2015) called for testing the environmental filtering hypothesis explicitly along marked abiotic gradients. This can be typically achieved using large scale (e.g. continental and global) observational surveys focusing on functional trait diversity (e.g. Coyle *et al.* 2014; Lamanna *et al.* 2014; Simova *et al*. 2015). Although they are still sparse, these studies may inform us on the importance of environmental filtering for shaping in the diversity of plant forms and functions globally.

Multiple sources of abiotic stresses are likely to interact and may determine the outcome of environmental filtering on functional trait diversity at the global scale (e.g. Reich et al. 2006; Simpson & Laughlin 2016). For instance, ongoing climate change involves simultaneous shifts in both temperature and precipitation regimes (IPCC 2013). Large-scale climate gradients such as temperature and precipitation regimes are expected to interact (climate – climate interactions), and impact on plant communities and associated ecosystem processes in complex ways (see Peñuelas *et al*. 2013 for a review). In addition, large-scale climate gradients are prone to interact with local soil conditions (i.e. climate – soil interactions: Ordonez *et al*. 2009; Fridley *et al*. 2011; Liancourt *et al.* 2013). Pervasive climate – soil interactions may explain the large variation in diversity of foliar traits observed between co-occurring species for a given temperature and precipitation level (Wright *et al*. 2004; Freschet *et al.* 2011). Yet, the effect of climate–climate or climate-soil interactions on plant functional trait diversity has been barely quantified (Simpson & Laughlin 2016). Testing the environmental filtering hypothesis along multiple gradients of climate and soil variables, and their interactions, constitutes a great opportunity to better understand and predict the response of plant trait diversity under climate change (Violle *et al*. 2014; Enquist *et al*. 2015).

The environmental filtering hypothesis predicts a shift in the trait values of plant species that confers higher stress tolerance with increased environmental stress (e.g. Grime 2006, see Fig. 1a and b for detailed hypothesis). A second prediction is a reduction in the range of trait values observed within communities, because lower stress tolerant species may be filtered out of the community (Cornwell & Ackerly 2009, Fig. 1c and d). These two predictions implicitly assume that a single, most favorable, functional strategy characterized by a narrow set of suitable trait values, allows plant species to establish and persist under a given level of abiotic stress (Enquist *et al*. 2015). However, the predictions of the environmental filtering hypothesis contrast with the high functional trait diversity that can be observed within plant communities (Wright *et al*. 2004), even in stressful environments (Chesson *et al*. 2004; Freschet *et al*. 2011; Gross et al. 2013).

Dryland ecosystems typically reflect the discrepancy between predictions and *in situ* observations. According to the environmental filtering hypothesis, dryland species should exhibit a stress-tolerant strategy, (sensu Grime 1974), e.g., having thick evergreen leaves [low specific leaf area (SLA)] and short stature (Wright *et al*. 2001; Moles *et al*. 2009). However, stress-tolerant species can often coexist in arid regions with stress-avoidant species with thin and summer-deciduous leaves (Noy-Meier 1973; Grime 1977; Chesson *et al*. 2004), and this coexistence increases trait diversity within dryland plant communities (Gross *et al*. 2013). Understanding the discrepancy between predictions of the environmental filtering hypothesis and the high functional diversity observed in global drylands is crucial. Maintaining a high functional trait diversity can enhance their resistance to aridity (Valencia *et al*. 2015), which is forecasted to increase in drylands worldwide by the end of this century (Huang *et al*. 2016).

We aimed to test the effect of multiple climate and soil drivers on functional trait diversity using a unique data set of 124 arid, semi-arid, and dry-subhumid plant communities spread over all continents, except Antarctica (Appendix S1). The studied environmental drivers included (i) large-scale climate gradients of mean annual temperature (MAT), mean annual precipitation (MAP) and precipitation seasonality (PS); (ii) three soil variables representing the physico-chemical properties of the bedrock, and influencing soil fertility (Maire *et al*. 2015): soil pH, sand content and total phosphorus (TP); (iii) all potential interactions between the environmental drivers, i.e. climate – climate, climate – soil and soil – soil interactions. Functional trait diversity was quantified as the abundance-weighted distributions within communities of specific leaf area (SLA) and maximum plant height (trait distributions hereafter). These two traits capture the global spectrum of plant form and function in terrestrial ecosystems (Diaz *et al.* 2016), and are key determinants of functional diversity and ecosystem functioning in semi-arid plant communities (Gross *et al*. 2013; Le Bagousse-Pinguet *et al*. 2015; Valencia *et al.* 2015). We considered the mean (location), the variance (dispersion), and the skewness and kurtosis (shape) of trait distributions, which are all central to understanding how species assemble within communities, and how plant communities respond to environmental change (Enquist *et al*. 2015).

Following the environmental filtering hypothesis, dryland communities should converge toward shorter statured and conservative plant strategies with increased abiotic stress. This convergence will decrease both their SLA and maximum plant height (lower mean: Fig. 1a and b) and the range of trait values observed (smaller variance, c and d). It will also lead to asymmetric distributions with "optimal" trait values for the shortest and most conservative species occurring within communities (positive skewness, e and f), and decrease the evenness of distributions (high kurtosis, g and h) altogether (i and j).

Material and Methods

STUDY AREA

Based on data availability, we used a subset of 124 sites from the global dryland network presented in Maestre *et al*. (2012a). The 124 study sites are located in 13 countries (Argentina, Australia, Chile, China, Ecuador, Israel, Kenya, Mexico, Morocco, Spain, Tunisia, USA and Venezuela; Appendix S1). Our dataset included representative sites from the major vegetation types found in drylands (excluding hyper arid areas, which usually have little or no perennial vegetation), and differed widely in climate conditions: mean annual temperature and precipitation ranged from -1.8°C to 27.8°C, and from 79 mm to 1177 mm, respectively.

CLIMATE VARIABLES

The climate features of the 124 studied sites included mean annual temperature (MAT), mean annual precipitation (MAP) and precipitation seasonality (PS: coefficient of variation of 12 monthly rainfall totals), all major determinants of ecosystem structure and functioning in drylands worldwide (see Maestre *et al.* 2012b for a review). We selected these large-scale climate gradients because: i) they are important drivers of trait variation both at regional and global scales (e.g., Wright *et al*. 2004; Swenson *et al*. 2012; Moles *et al*. 2014); ii) they are key variables for explaining global variation in dryland ecosystem functioning (Maestre *et al.* 2012a); and (iii), MAT, MAP and PS describe largely independent features of site climate in the studied dataset (bivariate correlations, $r < 0.3$ in all cases, Appendix S2). Standardized climate data for all study sites were obtained from Worldclim (www.worldclim.org), a high resolution (30 arc seconds or ~ 1km at equator) global database (Hijmans *et al*. 2005). We did not include irradiance in our models despite being an important abiotic factor in drylands (Noy-Meier 1973) and a main driver of specific leaf area (Poorter *et al* 2009). We did so because irradiance presented a low coefficient of variation in our dataset (11% in comparison with other climate variables with coefficient of variation above 50%), and was highly correlated with MAT ($r = 0.84$). Temperature seasonality (standard deviation of monthly temperatures * 100) was also not considered due to its correlation with MAT in the studied dataset ($r = 0.59$).

SOIL VARIABLES

We aimed to select only soil variables that are largely independent from any biological activities (plants, microbes) to effectively assess the true abiotic filtering effect of soil variables on functional trait diversity. We considered the physico-chemical properties of the bedrock using the soil sand content, soil pH and total phosphorus (TP), measured for each site in bare soil (i.e. avoiding vegetation patches). The physico-chemical properties widely differed among the 124 sites: soil sand content, soil pH and TP ranged from 28% to 95%, from 5.15 to 9.28, and from

0.05 to 1.45 mg P. g^{-1} soil, respectively. These three physico-chemical properties are considered as primordial master soil variables (Maire *et al*. 2015), play key roles in the availability of water and nutrients in drylands, and are major drivers of the composition and diversity of dryland microbial communities (Delgado-Baquerizo *et al.* 2016). Soil fertility is expected to be higher in less sandy soils (sand content strongly covaries with soil organic matter and silt content but not with clay content, data not shown), in soils with pH between 7.5 and 8.5 (soil enzymatic activities of N, P and C cycles peak between this range, Delgado-Baquerizo *et al*. 2015), and with high phosphorus content (Jenny 1941). Soil water retention is then expected to be highest in less sandy soils. These variables were measured in five soil samples per site as described in Maestre *et al*. (2012a), and were averaged for further statistical analyses. Sand, clay and silt contents were measured in soil samples (0-7.5 cm depth) in open areas devoid of vascular vegetation. Soil pH was measured with a pH meter, in a 1: 2.5 mass: volume soil and water suspension. Total phosphorus was measured using a SKALAR San++ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulphuric acid. Clay and silt contents were not used in our analyses due to their correlation with sand content (r = -0.52 and -0.55, respectively).

OTHER VARIABLES

Changes in the functional trait diversity of plant communities observed along environmental gradients may be partly driven by changes in the local species pools (species richness), historical context and topography. We considered species richness, the latitude and longitude of our study sites, as well as topography (slope angle; it ranged between 0.2° to 27.8° in our dataset) in our analyses to control for all these potential confounding effects. We used the sinus and cosinus of the longitude to avoid any bias due to intrinsic circularity of longitude in the statistical models (i.e., Longitude (sin) and Longitude (cos) hereafter, respectively).

TRAIT DISTRIBUTIONS

Trait distributions were quantified for each of the 124 sites, by using two independent datasets: (i) a detailed dataset containing the cover of each perennial plant species measured in 80 quadrats of 2.25 m² within each site, where the sum of the cover for each species is used as a proxy of species abundance at site (Maestre *et al*. 2012a); and (ii) data for SLA and maximum plant height, retrieved from the TRY database (Kattge *et al*. 2011). The 124 sites were selected because trait data were available for: (1) all the perennial species that together accounted for a cumulative relative abundance >80%, and (2) the four most dominant species to avoid any breaks in the trait distributions. We used averaged values when multiple trait data were available for a given species in the TRY database. Trait data were available for 316 and 526 species out of 622 species, for SLA and maximum plant height respectively. Specific Leaf Area is a key trait indexing leaf-level carbon gain strategies (Wright *et al*. 2004). Plant height reflects a trade-off for biophysical constraints in determining water fluxes within the plant (Diaz *et al*. 2016), and is related to its competitive ability (e.g. Schamp *et al*. 2008). Specific leaf area and height load heavily along two important independent axes of plant ecological strategies (Diaz *et al*. 2016). Maximum plant height and SLA were log-transformed before analysis to amplify the probability of detecting functional community patterns (Majekova *et al*. 2016).

We calculated the mean, variance, skewness and kurtosis (all weighted by the relative abundance of species) of the 124 trait distributions for SLA and maximum plant height separately:

$$Mean_j = \sum_i^n piTi \qquad \text{(Eqn 1);}$$

$$Variance_j = \sum_i^n pi(Ti - Mean_j)^2 \qquad \text{(Eqn 2);}$$

$$Skewness_j = \sum_i^n \frac{pi(Ti - Mean_j)^3}{Variance_j^{\frac{3}{2}}} \qquad \text{(Eqn 3);}$$

$$Kurtosis_j = \sum_i^n \frac{pi(Ti - Mean_j)^4}{Variance_j^2} \qquad \text{(Eqn 4);}$$

where p_i and T_i are the relative abundance and the trait value of the species *i* respectively, *n* is the total number of species in a community with available trait values. For each community, the sum of relative abundance equal to 100%, i.e. $\sum_i^n p_i = 1$.

The skewness and the kurtosis are unitless, and inform on the shape of the trait distribution. The skewness represents the asymmetry of the distributions. Highly negative or positive values of skewness occur when trait distributions are strongly right-or left-skewed, with a few species that have extreme trait values compared to the bulk of the distribution. Skewed distributions typically result from phenomena such as environmental changes or asymmetric competition (Schamp *et al*. 2008; Enquist *et al*. 2015). Kurtosis represents the relative peakiness of the trait distribution and the heaviness of its tails. Low kurtosis reflects the evenness in abundance of trait values occurring within the community, i.e., a high functional diversity (Enquist *et al*. 2015).

STATISTICAL ANALYSES

We built four competing models using multiple linear regressions to assess the effect of climate, soil variables and their interactions on each moment of the trait distributions for SLA and plant height separately. We included in the first model species richness, geography, topography and climate variables as predictors (model "CLIMATE"). The second model included species richness, geography, topography, and soil variables as predictors (model "SOIL"). The third model included all predictors of these models (model "CLIMATE + SOIL"). Finally, the fourth model includes all predictors of the model "CLIMATE + SOIL" plus all possible two-way interactions between MAT, MAP, PS, sand content, pH and TP (model "CLIMATE + SOIL + INTERACTIONS"). The variance inflation factors among the predictors used were far below 10 in all cases, hence multicollinearity was low (Appendix S2). Note that we also considered quadratic terms for all predictors since functional structure and trait diversity do not necessarily change linearly along strong gradients (e.g. Gross *et al*. 2013; Le Bagousse-Pinguet *et al*. 2015; Valencia *et al*. 2015).

We used a model selection procedure, based on minimizing the corrected Akaike information criterion (AICc), to select the best predictors of trait distributions. In a first step, we performed model simplification using a backward regression procedure. We subsequently removed non-significant quadratic and interaction terms that did not impact model predictive ability (r^2), and further kept all models with lower AICc (ΔAICc < 10). Then, a model selection procedure based on AICc selection (ΔAICc < 2) was applied on the resulting full models to select the best predictors most supported by the data. This procedure was performed using the function *dredge* in the R package *MuMIn* (Barton 2013). Species richness, geography and topography were always maintained during the model selection procedure. Model averaging was performed based on AICc thresholds (ΔAICc < 2; Burhnam & Anderson 2002) when multiple models were selected. Model residuals were inspected for constant variance and normality. All predictors were standardized before analyses using the Z-score to interpret parameter estimates on a comparable scale. Response variables were log-transformed when necessary before analysis to meet the assumptions of the tests used.

We evaluated the relative effect of each predictor on the four moments of the trait distributions. We used an analogue of the variance decomposition analysis based on Z-scores. Since predictors were all Z-scored prior analyses, the relative effect of each predictor can be simply calculated as the ratio between its parameter estimate and the sum of all parameter estimates, and expressed in %. Then, the obtained relative effects of predictors are grouped into five identifiable variance fractions: i) climate – climate interactions, ii) climate, iii) climate – soil interactions, iv) soil, v) soil – soil interactions, vi) species richness, vii) geography (latitude, longitude (sin), longitude (cos), slope), and viii) unexplained variance.

We also used the parameter estimates of interacting predictors to illustrate how climate – climate, climate – soil and soil – soil interactions impact the moments of the trait distributions. We fixed one of the two interacting predictors at either low or high value, and examined the effect of the other predictor on the four moments of trait distributions, while the parameter estimates of all other predictors were fixed to their mean value (i.e. 0 since all predictors were Z-scored). All statistical analyses were performed using the R statistical software 2.15.1 (R Core Team 2012).

Results

The predictive power of our models was high, but gradually decreased when explaining higher moments of trait distributions for maximum plant height (Fig. 2) and specific leaf area (Fig. 3). For plant height, the predictive power of the models was higher for the mean (Fig. 2: adjusted $r^2 = 0.817$) and variance (0.587), compared to skewness (0.275) and kurtosis (0.262). For specific leaf area, the predictive power of the models on trait distributions was the highest for the mean (Fig. 3: adjusted $r^2 = 0.638$), and also reached more than 40% for the variance (0.415) and skewness (0.408).

Models including climate – climate, climate – soil and soil – soil interactions explained more variance than the additive models for the four moments of both plant height and specific leaf area (Appendices S3, S4 and S5). These results highlight the importance of considering interactions between multiple sources of abiotic stress when assessing functional trait diversity at global scale. Climate – climate interactions explained up to 9% of the model variance for maximum plant height (Fig. 2), and up to 7% for SLA (Fig. 3). For instance, increasing precipitation seasonality significantly interacted with mean annual temperature and precipitation (Fig. 2). Under low seasonality, higher aridity (i.e. an increase in MAT together with a decrease in MAP) increased mean plant height (Fig. 4a), weakly impacted the variance (c), and decreased the skewness (e) and kurtosis (g). Under low seasonality, these results indicated a weak effect of increased aridity on functional trait diversity. In contrast, we observed a strong filtering effect of aridity under high precipitation seasonality (Fig. 4, right panels). Under high seasonality, aridity decreased the mean (Fig. 4b) and variance for plant height (d), and increased the skewness (f). Note that kurtosis of plant height also strongly decreased in the harshest conditions (Fig. 4h: low MAP and high MAT), suggesting for the local co-occurrence of functionally contrasting strategies.

Climate – soil interactions explained up to 15% for maximum plant height, and up to 24% for SLA. The effects of climate on trait distributions were significantly modulated by soil pH, and notably for SLA (Fig. 3). In acidic conditions, the mean SLA increased, and the skewness decreased with lower MAP and higher MAT (Fig. 5a and g). The variance of SLA decreased in the most arid sites while its kurtosis increased (Fig. 5d and j), indicating a decline in functional trait diversity. Communities developing under basic soil conditions were dominated by more stress-tolerant species exhibiting low SLA values with increasing aridity (Fig. 5c: low mean SLA; 5i: high skewness). A higher SLA variance and a lower kurtosis were also observed in most arid sites (Fig. 5f and l). These results indicate an increase in functional trait diversity with environmental stress.

Finally, soil – soil interactions explained a smaller, but significant fraction of the variation in functional trait diversity observed (up to 5%, Fig. 3), mostly due to the interaction between sand content and soil pH for SLA (Fig. 6). Both the lowest and the highest mean SLA occurred at low sand content (Fig. 6a). The lowest mean SLA occurred under basic soil conditions (soil pH ~ 8), whereas the highest mean SLA was observed under acidic conditions (pH ~ 5.5). Also, the variance of SLA strongly increased with soil pH in sandy soils (high sand content), but it was not sensitive to soil pH at low sand content (Fig. 6b). Finally, we also observed lowest values in the kurtosis of SLA for pH ~ 7 (Fig. 6d), indicating that trait diversity was the highest under neural conditions.

Discussion

Interactions between multiple abiotic stress sources are key for predicting functional trait diversity at a global scale. By considering the interactions among abiotic drivers, and by controlling for the local species pool, we identified the particular sets of environmental conditions under which the environmental filtering hypothesis operates in drylands worldwide. Shifts in functional trait diversity along abiotic drivers were trait-specific, with a major role of climate-climate interactions in driving the abundance distributions of maximum plant height. Climate – soil and soil – soil interactions had a predominant effect on SLA.

FUNCTIONAL TRAIT DIVERSITY RESPONSES TO CLIMATE AND SOIL CONDITIONS IN DRYLANDS

Precipitation seasonality was a major driver of functional trait diversity for maximum plant height in the drylands studied, and strongly modulated the effects of MAT and MAP on this diversity (Fig. 4). Under high precipitation seasonality, increased MAT and lower MAP not only filtered plant communities toward the dominance of shorter species (Fig. 4b: lower mean), but also narrowed the range of trait values (Fig. 4d: lower variance). Therefore, intense drought periods in the most arid part of the studied gradient filtered plant communities toward a narrow set of suitable trait values allowing them to cope with the strong abiotic constraint, supporting for the environmental filtering hypothesis (Keddy 1992; Weiher *et al*. 1998; Grime 2006). The observed reduction in plant height in the harshest conditions of our climate gradients (i.e., high precipitation seasonality and temperature, and low annual precipitation) supports the hypotheses of height limitation due to hydraulic constraints (e.g. Koch *et al*. 2004). Although a loss of hydraulic conductivity following embolisms can also be common for shorter plant species, tall plants show low recovery capacity after the loss of hydraulic functions (Koch *et al*. 2004).

Soil pH was an important driver explaining functional trait diversity for SLA, but its effect was modulated by the climate drivers and the sand content (Figs. 3, 5, 6). A negative correlation between soil pH and mean SLA has been documented at the global scale (Maire *et al*. 2015), but we found that this is true only under low sand content conditions in drylands (Fig. 6a). When SLA decreases, leaf nitrogen content (per area) can increase, favoring leaf photosynthesis for a given water use (Maire *et al*. 2015). Our results would accord with the theory and observations that predict the dominance of species with high leaf nitrogen strategy to increase water use efficiency (Wright *et al*. 2003). This leaf nitrogen strategy is viable only when plant nitrogen uptake is less expensive (in terms of energy cost) than water uptake and transport from soil to leaves (Prentice *et al* 2014). In arid ecosystems, this may occur under high soil fertility conditions, i.e., under intermediate/high soil pH, low sandy soils (Fig. 6a), and warm temperatures favoring soil organic matter decomposition (Fig. 5b and c).

We also observed an increase in SLA variance with soil pH (Fig. 3). Over evolutionary time scale, soil pH has also been recognized as creating an environmental backdrop under which species diversity is shaped (Laliberté *et al*. 2014). As such, we expect the size of the calcicolous trait pool to be larger in drylands, where the regional soil pH, which can be different from the local soil pH, is on average alkaline (Hengl *et al*. 2014). This may favor the highest functional diversity observed in our alkaline sites, especially under warm climate conditions where a larger set of species may benefit from higher soil fertility and faster growing conditions (Fig. 6b). On the other hand, when climate is cold, soil organic matter decomposition slows down and soil fertility decreases, while residual negative impact of high soil pH (e.g. salinity) may increase the environmental stress and act as a strong filter (decreasing SLA variance).

THE ENVIRONMENTAL FILTERING HYPOTHESIS IN GLOBAL DRYLANDS

It is imperative to consider pervasive interactions between environmental drivers in order to identify the circumstances under which environmental filtering will impact functional trait diversity (Simpson & Laughlin 2016). Previous large-scale studies reported that higher abiotic stress does not necessarily filter plant communities toward a narrower range of trait values (Coyle *et al*. 2014; Simova *et al*. 2015). Our study reveals the environmental conditions under which functional trait diversity may decrease in global dryland in response to abiotic filtering processes: e.g., under the combining effect of high precipitation seasonality, high MAT and low MAP (Fig 4: right panels), or under high MAT and low MAP in acidic conditions (Fig. 5: left panels).

Importantly, our study also shows that abiotic stress should not necessarily imply a reduction in functional trait diversity. For instance, higher MAT and lower MAP did not affect the functional trait diversity of height in the studied drylands when precipitation seasonality was low (Fig. 4c). We even observed an increase in functional trait diversity (variance) for SLA with higher MAT and lower MAP in basic soil conditions (Fig. 5e and f). Our results support the view that multiple sets of trait values can allow functionally contrasting species to cross the filtering effect imposed by an abiotic stress, where they can equally perform in term of abundance in a given community (e.g. Gross *et al*. 2013). In dry and hot conditions, high trait variance can reflect the co-occurrence of stress-avoidant vs. stress tolerant species within communities for a given level of stress (Poorter *et al*. 2009; Gross *et al*. 2013), the occurrence of positive interactions (e.g. Butterfield & Briggs 2011; Butterfield & Munson 2016), or spatial / temporal storage effects (Chesson 2000; Chesson *et al*. 2004).

Our approach focusing on the four moments of trait distributions also reveals the existence of additional mechanisms that can promote the local co-occurrence of functionally contrasting species within communities. We showed that variance and kurtosis varied independently along environmental stress gradients. For instance, we observed an increased evenness in the abundance of trait values for maximum plant height under high MAT and low MAP (i.e. low kurtosis value, Fig. 4g and h), while variance slightly or strongly decreased under low and high precipitation seasonality, respectively (Fig. 4c and d). Also, we observed that kurtosis was minimized for neutral pH, a signal that was not observed with the variance (Fig. 6b and d). Our results indicated that functionally contrasting species can still co-occur even under prevailing environmental filtering, i.e., even when the abiotic environment selects for narrower ranges of trait values within communities (see also Cornwell & Ackerly 2009 and Gross *et al*. 2013 for similar evidences along local environmental gradients).

Finally, it is worth noting that we observed an overall decrease in the predictive power of our statistical models using the higher moments for maximum plant height (Fig. 2) and specific leaf area (Fig. 3). The predictive power of our models was very high for the mean of trait distributions, intermediate for the variance, and low for the shape parameters (skewness and kurtosis). These results may arise from a higher sensitivity of the skewness and the kurtosis to sampling effort. When considering frequency distribution, skewness and kurtosis might be very sensitive to the local species richness, making their estimation potentially difficult in species-poor communities. However, we focused on abundance-weighted skewness and kurtosis using an extensive field survey. This should circumvent such a methodological limitation because: (i) the shape of the distribution is driven by the abundance of traits within the community; (ii) the sampling effort for species relative abundance is standardized across communities; and (iii) skewness and kurtosis were largely independent from local species richness in our dataset (Figs. 2 and 3). Instead, the observed decrease in the predictive power of our models when using the higher moments likely reflects a decrease in the abiotic determinism of the moments of trait distributions. The mean and the variance of trait distributions reflect the functional type and diversity of plant communities (Mouillot *et al*.

2011); in turn, this reflects the effect of the abiotic environment in sorting species with a given set of traits values. By contrast, the shape parameters reflect the intrinsic structure of plant communities and how the abundance and trait diversity are assembled and distributed locally (see Gross *et al*. 2009 for an experimental test on how biotic interactions can shape trait abundance distribution). Skewness and kurtosis are then likely encompassing not only abiotic factors, but also the biotic processes involved in shaping plant diversity (Schamp *et al*. 2008; Gross *et al*. 2009; Butterfield & Munson 2016). Hence, this work provides strong evidence that these parameters are crucial for improving our predictions of the effects of climate change on plant communities and associated ecosystem functions (Enquist *et al*. 2015).

CONCLUSIONS

Our study, which is based on the four moments of trait distributions and that considers interactions between multiple abiotic stress drivers, plays an important role in depicting the complex effects of environmental filtering on plant functional trait diversity in global drylands. This approach would certainly gain predictive power by integrating intraspecific trait variability that can strongly impact plant community assembly (e.g. Le Bagousse-Pinguet *et al*. 2014, 2015; Siefert *et al*. 2015), and particularly by considering complex shapes of individual-level trait distributions (Laughlin *et al*. 2015). We show that interactions between climate and soil variables highlight the importance of environmental filtering and are fundamental in the understanding of trait diversity patterns. Identifying the combinations of environmental factors leading to lower functional diversity is of primary importance to better understand and predict how global environmental change will impact plant communities in drylands.

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Author Contribution

Y.L.B.P., N.G., V.M., F.T.M. and P.L. developed the conceptual and methodological foundation of this study. Y.L.B.P. and N.G. conducted statistical analyses. F.T.M designed the field study and coordinated field data acquisition. Y.L.B.P., N.G., C.R.T., J.K., E.V and F.T.M.

provided plant trait data. Y.L.B.P., N.G. and P.L. wrote the first draft, and all authors substantially contributed to the subsequent drafts.

Data Accessibility

All data associated with this manuscript are available from figshare: https://figshare.com/s/25987d7f8d8fda8206cc (Le Bagousse-Pinguet *et al*. 2017), as well as in Appendix S6.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1 Map of the 124 sampled sites in global drylands.

Appendix S2 Correlations among predictors included in the statistical models.

Appendix S3 Akaike Information Criterion of the best selected models for the trait-abundance distributions of maximum plant height and specific leaf area (SLA).

Appendix S4 Results of multiple regression models for the trait-abundance distributions of maximum plant height.

Appendix S5 Results of multiple regression models for the trait-abundance distributions of specific leaf area (SLA).

Appendix S6 All data associated with this manuscrip

Figures

Fig. 1. Schematic representation of shifts in trait distributions for maximum plant height and specific leaf area (SLA), following the environmental filtering concept. We represent the shifts in mean (a,b), variance (c,d), skewness (d,e), kurtosis (f,g), and all moments together (h,i) of the trait distributions under low and high abiotic stress.

Fig. 2. Effects of multiple sources of environmental stress and their interactions on the trait distributions for maximum plant height. Results are presented for the mean, variance, skewness and kurtosis of trait distributions. We show the averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals and the relative importance of each factor, expressed as the percentage of explained variance. The adj.r^2 of the averaged models and the *p*-value of each predictor are given as: (.), $p < 0.1$; *, $p < 0.05$; ** $p > 0.01$; *** $p < 0.001$.

MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality; TP: total phosphorus.

Fig. 3. Effects of multiple sources of environmental stress and their interactions on the trait distributions for specific leaf area (SLA). Rest of legend as in Fig. 2.

MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality; TP: total phosphorus.

Fig. 4. Predicted trait distributions (black dots) from the interactions between mean annual temperature (MAT) and precipitation seasonality, and between mean annual precipitation (MAP) and precipitation seasonality for maximum plant height in a 3D plot. We represented the effects of interactions using the standardized parameter estimates of MAT and MAP (Fig.

2). Predictions were calculated for low and high precipitation seasonality ($CV_{seasonality} = 12$ and $CV_{seasonality} = 124$, respectively). All other standardized parameter estimates were fixed at their mean value. The colours of the predicted planes change from blue (low values of the moments) to red (high values).

Fig. 5. Predicted trait distributions (black dots) from the interactions between mean annual temperature (MAT) and pH, and between mean annual precipitation (MAP) and pH for specific leaf area (SLA) in a 3D plot. We represented the effects of interactions using the standardized parameter estimates of MAT and MAP (Fig. 3). Predictions were calculated for acidic, slightly basic and basic conditions (pH = 5.5, pH = 7.8, pH = 9.3, respectively). All other standardized parameter estimates were fixed at their mean value. The colours of the predicted planes change from blue (low values of the moments) to red (high values).

Fig. 6. Predicted trait distributions (black dots) from the interactions between pH and sand content for specific leaf area (SLA) in a 3D plot. We represented the effects of interactions using the standardized parameter estimates of pH and sand content (Fig. 3). All other standardized parameter estimates were fixed at their mean value. The colours of the predicted planes change from blue (low values of the moments) to red (high values).

Figures

Fig. 1.

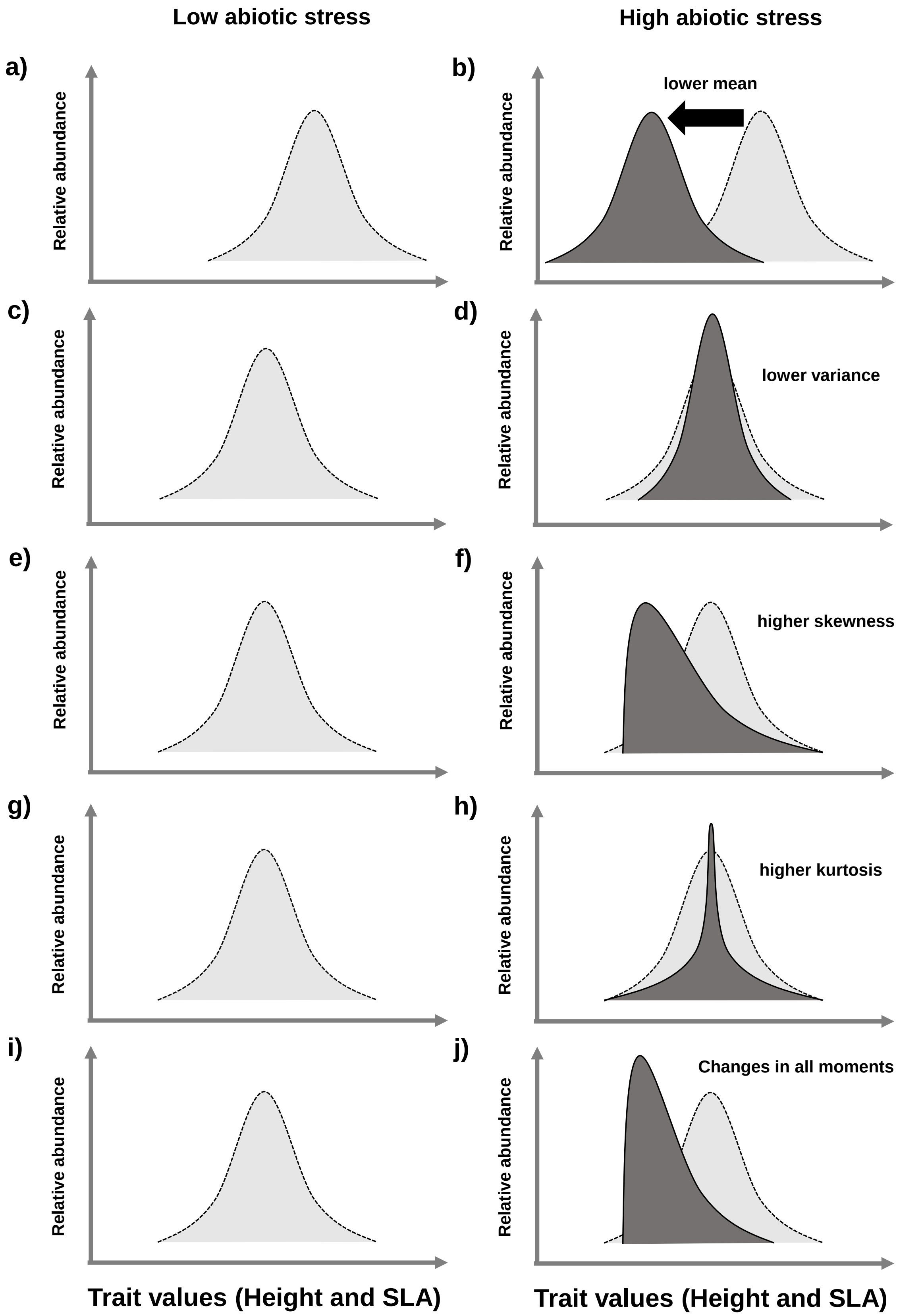

Low abiotic stress
High abiotic stress
a)
b)
lower mean
c)
d)
lower variance
e)
f)
higher skewness
g)
h)
higher kurtosis
i)
j)
Changes in all moments
Relative abundance
Trait values (Height and SLA)
Trait values (Height and SLA)

Fig. 2.

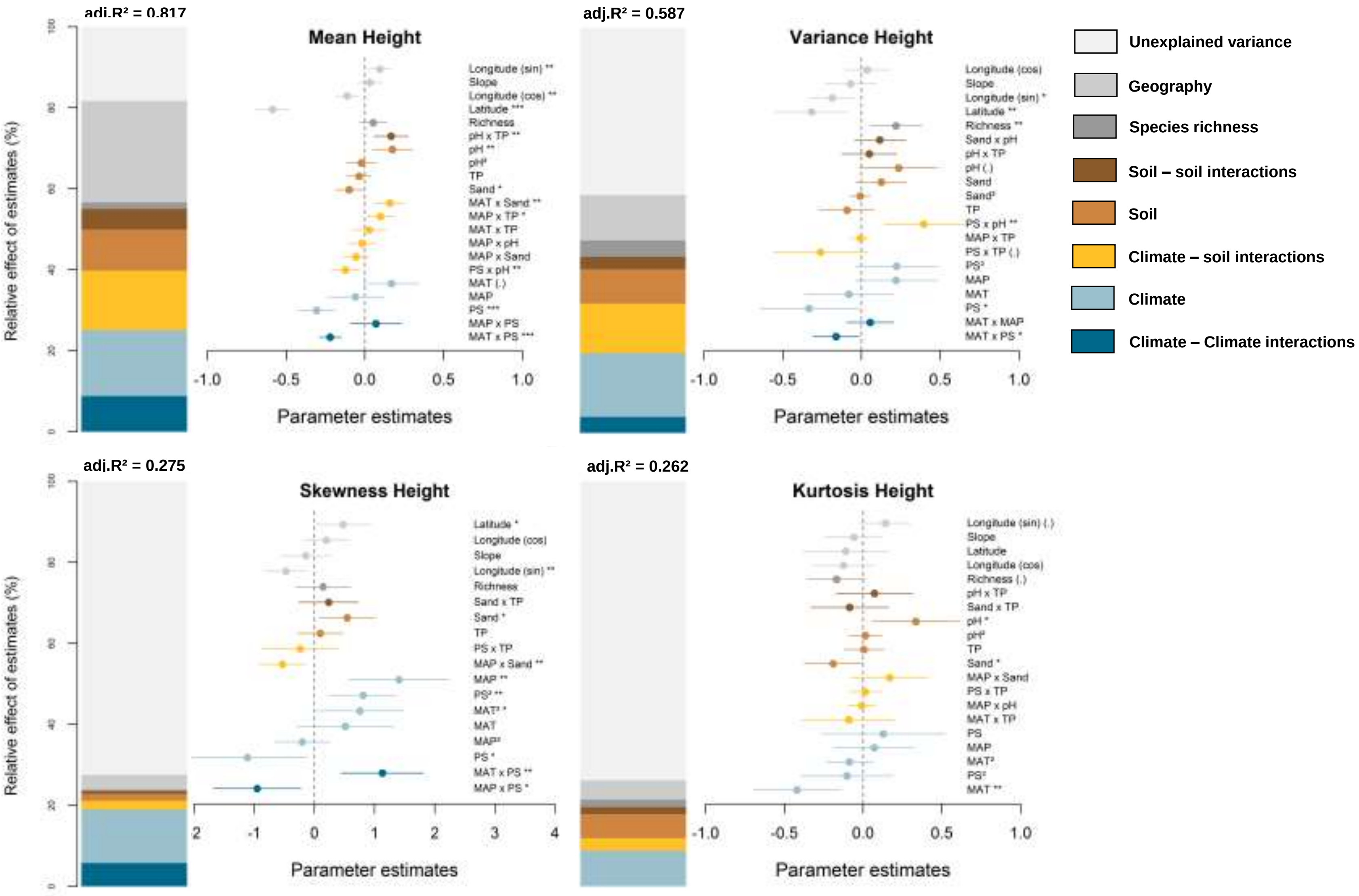

adj.R² = 0.817
Mean Height
Longitude (sin) **
Slope
Longitude (cos) **
Latitude ***
Richness
pH x TP **
pH **
pH²
TP
Sand *
MAT x Sand **
MAP x TP *
MAT x TP
MAP x pH
MAP x Sand
PS x pH **
MAT (.)
MAP
PS ***
MAP x PS
MAT x PS ***
Relative effect of estimates (%)
-1.0 -0.5 0.0 0.5 1.0
Parameter estimates
adj.R² = 0.587
Variance Height
Longitude (cos)
Slope
Longitude (sin) *
Latitude **
Richness **
Sand x pH
pH x TP
pH (.)
Sand
Sand²
TP
PS x pH **
MAP x TP
PS x TP (.)
PS²
MAP
MAT
PS *
MAT x MAP
MAT x PS *
-1.0 -0.5 0.0 0.5 1.0
Parameter estimates
Unexplained variance
Geography
Species richness
Soil – soil interactions
Soil
Climate – soil interactions
Climate
Climate – Climate interactions
adj.R² = 0.275
Skewness Height
Latitude *
Longitude (cos)
Slope
Longitude (sin) **
Richness
Sand x TP
Sand *
TP
PS x TP
MAP x Sand **
MAP **
PS² **
MAT² *
MAT
MAP²
PS *
MAT x PS **
MAP x PS *
Relative effect of estimates (%)
2 -1 0 1 2 3 4
Parameter estimates
adj.R² = 0.262
Kurtosis Height
Longitude (sin) (.)
Slope
Latitude
Longitude (cos)
Richness (.)
pH x TP
Sand x TP
pH *
pH²
TP
Sand *
MAP x Sand
PS x TP
MAP x pH
MAT x TP
PS
MAP
MAT²
PS²
MAT **
-1.0 -0.5 0.0 0.5 1.0
Parameter estimates

Fig. 3.

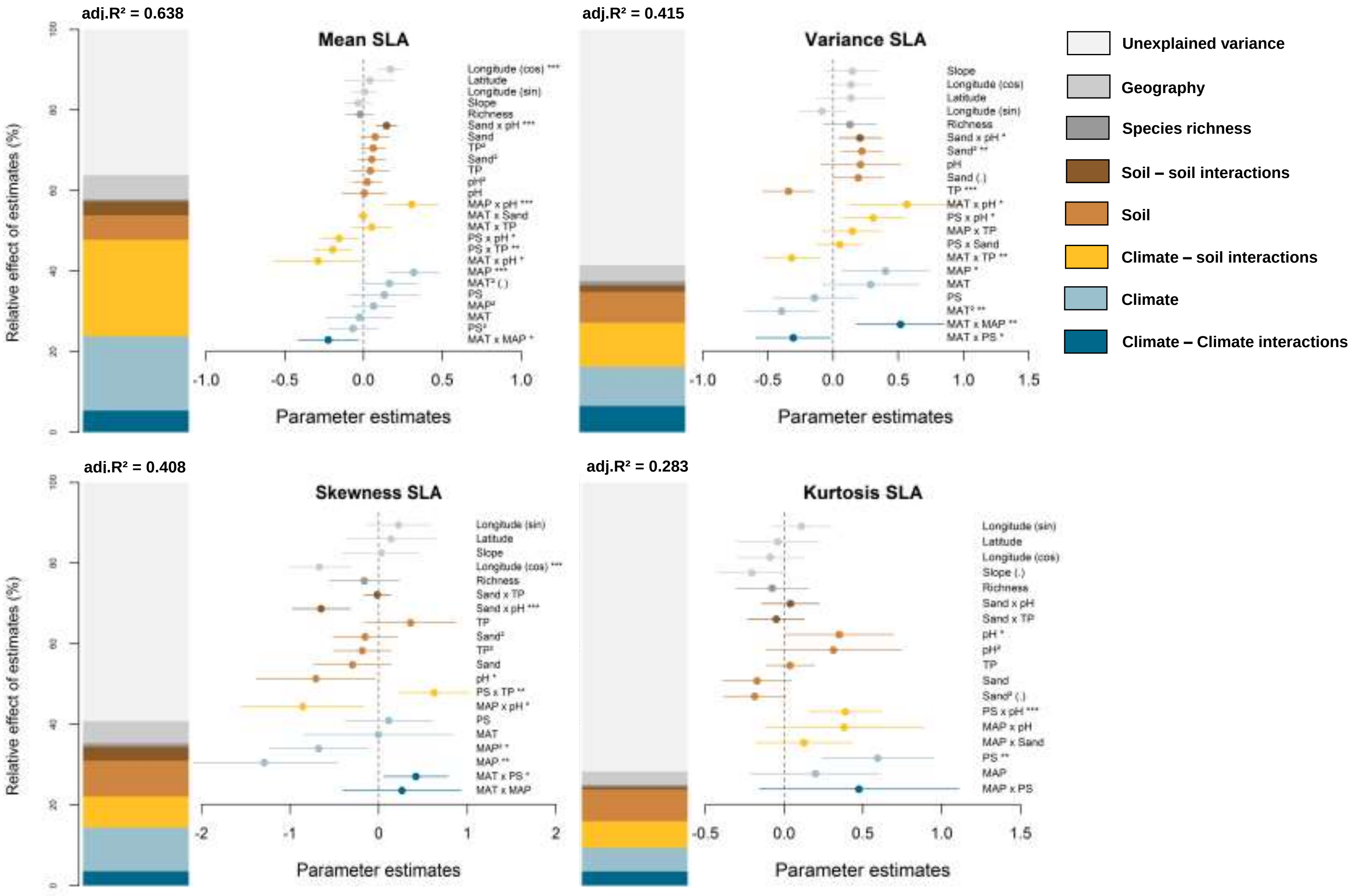

adj.R² = 0.638
Mean SLA
Longitude (cos) ***
Latitude
Longitude (sin)
Slope
Richness
Sand x pH ***
Sand
TP²
Sand²
TP
pH²
pH
MAP x pH ***
MAT x Sand
MAT x TP
PS x pH *
PS x TP **
MAT x pH *
MAP ***
MAT² (.)
PS
MAP²
MAT
PS²
MAT x MAP *
Parameter estimates
Relative effect of estimates (%)
adj.R² = 0.415
Variance SLA
Slope
Longitude (cos)
Latitude
Longitude (sin)
Richness
Sand x pH *
Sand² **
pH
Sand (.)
TP ***
MAT x pH *
PS x pH *
MAP x TP
PS x Sand
MAT x TP **
MAP *
MAT
PS
MAT² **
MAT x MAP **
MAT x PS *
Parameter estimates
Unexplained variance
Geography
Species richness
Soil – soil interactions
Soil
Climate – soil interactions
Climate
Climate – Climate interactions
adj.R² = 0.408
Skewness SLA
Longitude (sin)
Latitude
Slope
Longitude (cos) ***
Richness
Sand x TP
Sand x pH ***
TP
Sand²
TP²
Sand
pH *
PS x TP **
MAP x pH *
PS
MAT
MAP² *
MAP **
MAT x PS *
MAT x MAP
Parameter estimates
Relative effect of estimates (%)
adj.R² = 0.283
Kurtosis SLA
Longitude (sin)
Latitude
Longitude (cos)
Slope (.)
Richness
Sand x pH
Sand x TP
pH *
pH²
TP
Sand
Sand² (.)
PS x pH ***
MAP x pH
MAP x Sand
PS **
MAP
MAP x PS
Parameter estimates

Fig. 4.

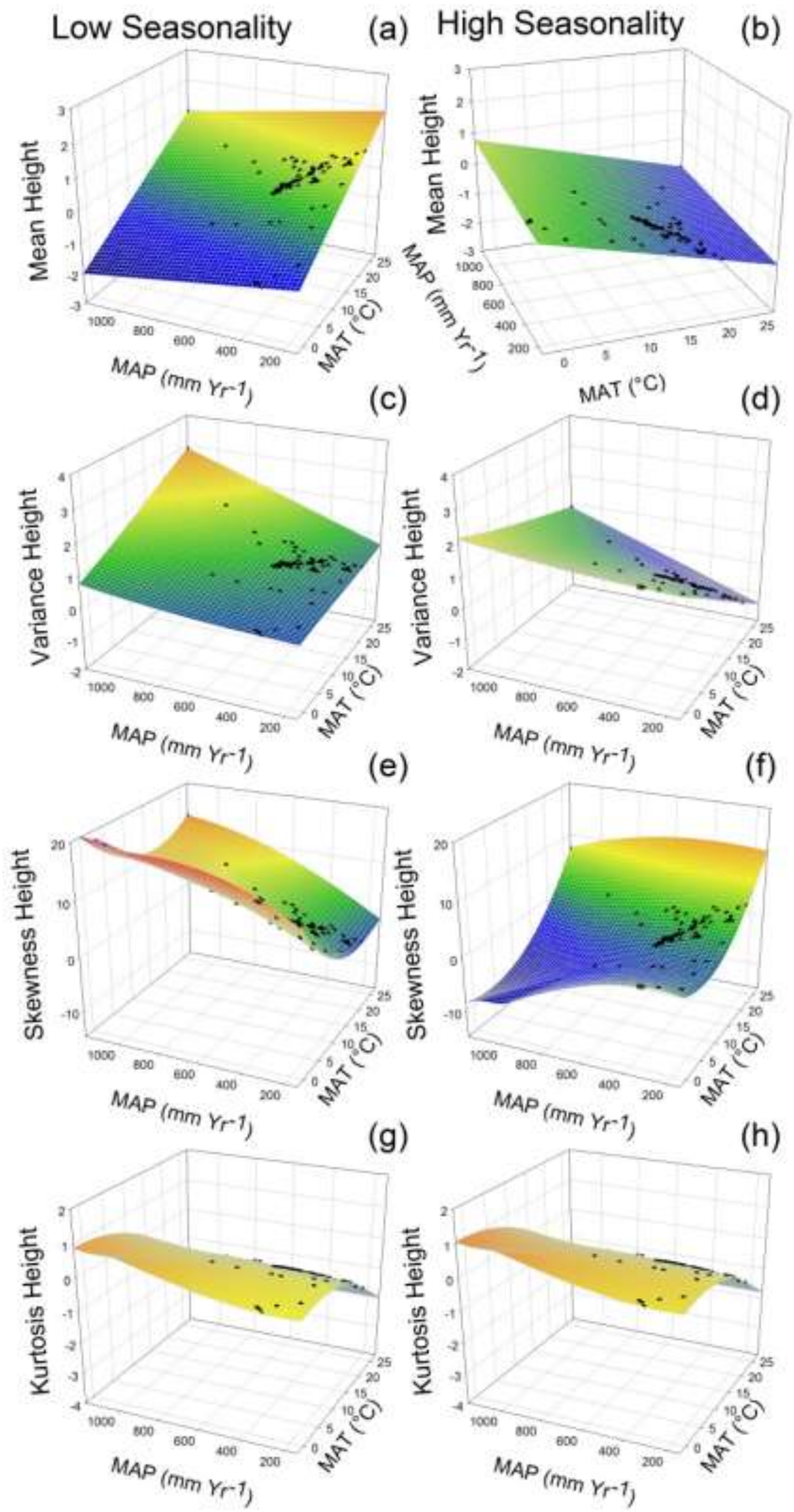

Low Seasonality
(a)
High Seasonality
(b)
Mean Height
MAP (mm Yr-1)
MAT (°C)
(c)
(d)
Variance Height
(e)
(f)
Skewness Height
(g)
(h)
Kurtosis Height

Fig. 5

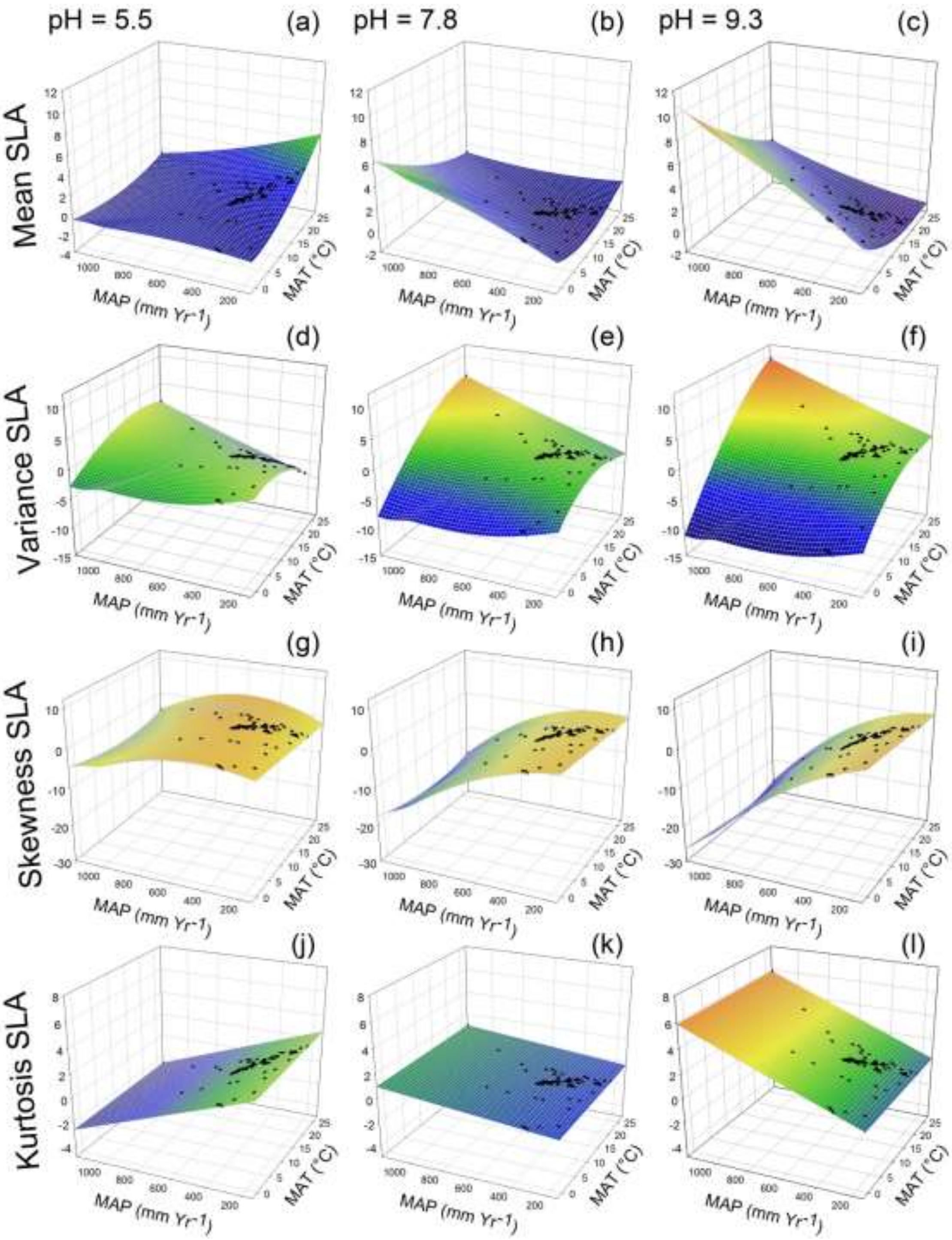
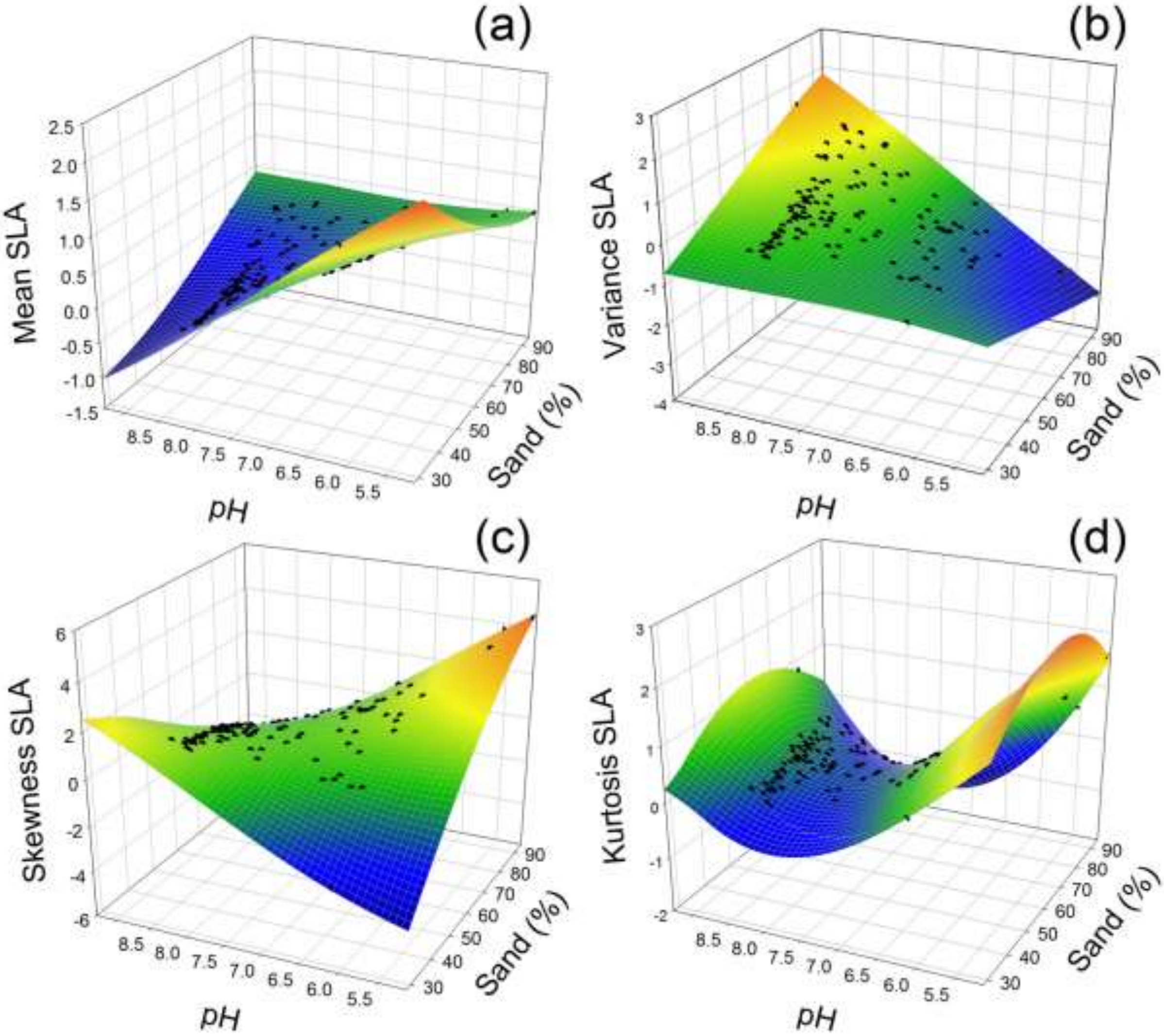
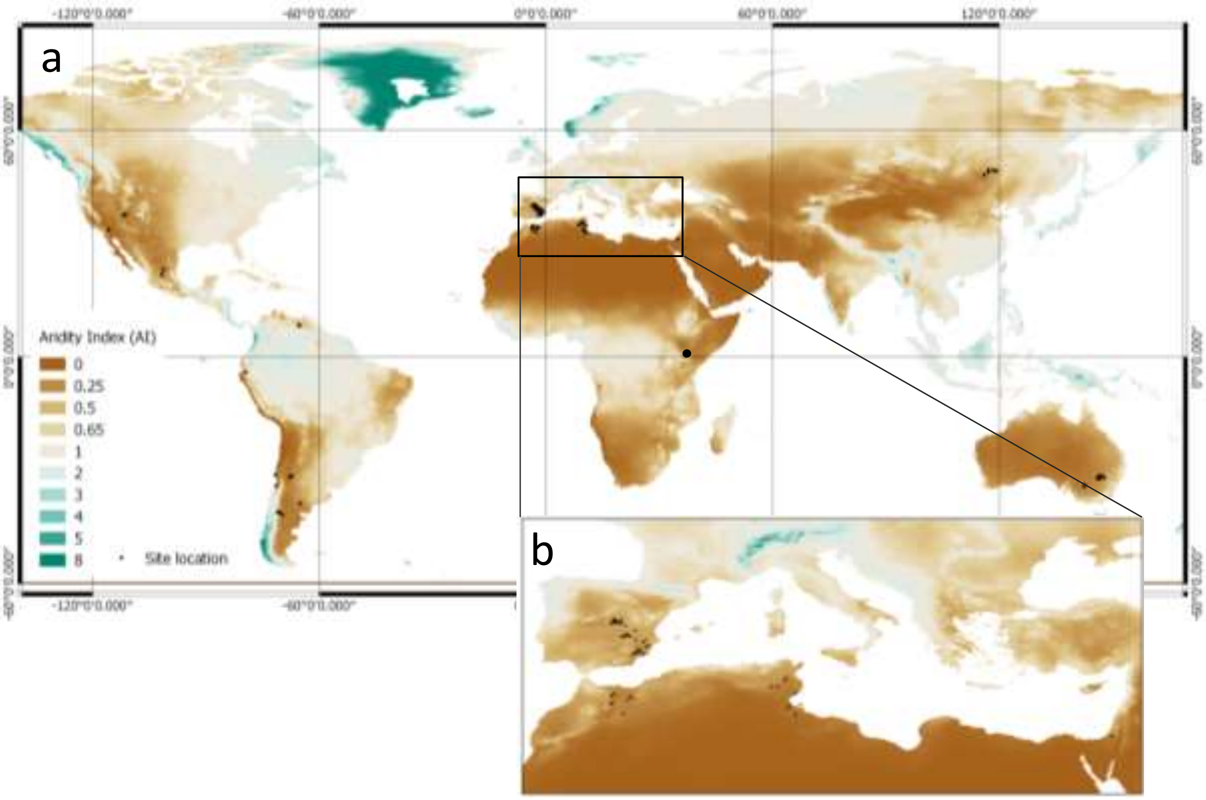

pH = 5.5
(a)
pH = 7.8
(b)
pH = 9.3
(c)
Mean SLA
(d)
(e)
(f)
Variance SLA
(g)
(h)
(i)
Skewness SLA
(j)
(k)
(l)
Kurtosis SLA
MAP (mm Yr-1)
MAT (°C)

Fig. 6.


(a)
Mean SLA
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
8.5
8.0
7.5
7.0
6.5
6.0
5.5
pH
30
40
50
60
70
80
90
Sand (%)
(b)
Variance SLA
3
2
1
0
-1
-2
-3
-4
8.5
8.0
7.5
7.0
6.5
6.0
5.5
pH
30
40
50
60
70
80
90
Sand (%)
(c)
Skewness SLA
6
4
2
0
-2
-4
-6
8.5
8.0
7.5
7.0
6.5
6.0
5.5
pH
30
40
50
60
70
80
90
Sand (%)
(d)
Kurtosis SLA
3
2
1
0
-1
-2
8.5
8.0
7.5
7.0
6.5
6.0
5.5
pH
30
40
50
60
70
80
90
Sand (%)

Appendices

Appendix S1. Map of the 124 drylands sampled (black dots).



Appendix S2. Pearson correlation coefficients among predictors included in the statistical models. We also present the results of the variance inflation factor (VIF) to evaluate the risk of multicollinearity. Multicollinearity occurs when VIF values exceed 10.

MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality, TP: total phosphorus.

Longitude (sin)	Longitude (cos)	Slope	Richness	MAT	MAP	PS	Sand	pH	TP	
0.08	-0.21	0.47	-0.04	-0.20	-0.05	0.12	-0.32	0.56	0.01	Latitude
	-0.35	0.23	-0.05	0.06	0.00	-0.03	-0.10	0.09	-0.06	Longitude (sin)
		-0.21	0.17	-0.22	-0.02	0.04	0.07	-0.16	0.09	Longitude (cos)
			0.20	-0.13	0.13	0.03	-0.40	0.28	-0.18	Slope
				-0.14	0.10	-0.45	-0.22	-0.11	-0.16	Richness
					0.27	-0.21	0.05	0.02	-0.32	MAT
						0.02	-0.06	-0.50	-0.16	MAP
							0.12	-0.21	0.36	PS
								-0.26	-0.03	Sand
									0.05	pH

Models	r^2	VIF
Latitude ~ Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + MAP + PS + Sand + pH + TP	0.55	2.22
Longitude (sin) ~ Latitude + Longitude (cos) + Slope + Richness + MAT + MAP + PS + Sand + pH + TP	0.08	1.09
Longitude (cos) ~ Latitude + Longitude (sin) + Slope + Richness + MAT + MAP + PS + Sand + pH + TP	0.20	1.24
Slope ~ Latitude + Longitude (sin) + Longitude (cos) + Richness + MAT + MAP + PS + Sand + pH + TP	0.44	1.77
Richness~ Latitude + Longitude (sin) + Longitude (cos) + Slope + MAT + MAP + PS + Sand + pH + TP	0.37	1.60
MAT ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAP + PS + Sand + pH + TP	0.37	1.59
MAP ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + PS + Sand + pH + TP	0.49	1.96
PS ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + MAP + Sand + pH + TP	0.48	1.92
Sand ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + MAP + PS + pH + TP	0.19	1.23
pH ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + MAP + PS + Sand + TP	0.70	3.30
TP ~ Latitude + Longitude (sin) + Longitude (cos) + Slope + Richness + MAT + MAP + PS + Sand + pH	0.27	1.37

Appendix S3. Akaike Information Criterion (AICc and ΔAICc) of the best selected models for the trait distributions of maximum plant height and specific leaf area (SLA). We present the best selected models for the mean, variance, skewness and kurtosis. The model "CLIMATE" included species richness, geography, topography and climate variables (MAT, MAP, precipitation seasonality). The model "SOIL" included species richness, geography, topography and soil variables (sand, pH, total phosphorus). The model "CLIMATE+SOIL" included all predictors of these models. The model "CLIMATE+SOIL+INTERACTIONS" included all predictors of the model "CLIMATE+SOIL", and all possible two-way interactions between MAT, MAP, precipitation seasonality, sand content, pH and total phosphorus.

MAT: mean annual temperature, MAP: mean annual precipitation.

Maximum plant height												
Models	Mean			Variance			Skewness			Kurtosis		
	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2
CLIMATE	139.7	49.84	0.7	269.7	12.53	0.499	511.6	16.41	0.103	312.7	12.53	0.155
SOIL	170.6	80.74	0.603	269.6	12.43	0.499	520.3	25.11	0.007	313.3	13.13	0.151
CLIMATE + SOIL	135.9	46.04	0.716	265.1	7.93	0.522	510.9	15.71	0.147	307.8	7.63	0.196
CLIMATE + SOIL + INTERACTIONS	89.86	0	0.817	257.17	0	0.587	495.19	0	0.275	300.17	0	0.262
Specific leaf area (SLA)												
Models	Mean			Variance			Skewness			Kurtosis		
	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2	AICc	ΔAICc	adj. R^2
CLIMATE	165.4	69.48	0.266	326.3	10.66	0.272	512.6	21.36	0.205	339.9	7.52	0.195
SOIL	172.5	76.58	0.206	338.2	22.56	0.189	516.5	25.26	0.197	345.6	13.22	0.175
CLIMATE + SOIL	156.6	60.68	0.332	319.4	3.76	0.326	512.6	21.36	0.205	338	5.62	0.224
CLIMATE + SOIL + INTERACTIONS	95.92	0	0.638	315.64	0	0.415	491.24	0	0.408	332.38	0	0.283

Appendix S4. Results of multiple regression models for the trait distributions of maximum plant height. We tested the effects species richness, geography, topography, climate variables, soil variables and all pair-wise interactions on the mean, variance, skewness and kurtosis of trait distributions (model "CLIMATE + SOIL + INTERACTIONS" in Appendix S3). We provided Model r^2, adj r^2, AICc and weight for the selected models (ΔAICc ≤ 2).

MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality, TP: total phosphorus

Height	Geo / Topo	Rich	MAT		MAP		PS		pH		Sand		TP		MAT X MAP	MAT X PS	MAP X PS	MAT X pH	MAT X Sand	MAT X TP	MAP X pH	MAP X Sand	MAP X TP	PS X pH	PS X Sand	PS X TP	pH X Sand	pH X TP	Sand X TP	r^2	adj. r^2	AICc	ΔAICc	Weight
			x	x^2	x	x^2	x	x^2	x	x^2	x	x^2	x	x^2																				
Mean																														0.85	0.82	89.86	0.00	0.26
																														0.85	0.82	90.48	0.61	0.19
																														0.84	0.82	90.49	0.63	0.19
																														0.85	0.81	90.69	0.83	0.17
																														0.84	0.82	91.67	1.81	0.10
																														0.85	0.82	91.85	1.99	0.09
Variance																														0.65	0.59	257.17	0.00	0.19
																														0.63	0.58	257.61	0.44	0.15
																														0.64	0.59	257.92	0.75	0.13
																														0.66	0.60	258.17	1.00	0.11
																														0.65	0.59	258.56	1.40	0.09
																														0.65	0.59	258.61	1.44	0.09
																														0.64	0.58	258.82	1.65	0.08
																														0.65	0.59	258.89	1.72	0.08
																														0.63	0.58	258.97	1.80	0.08
Skewness																														0.41	0.30	495.19	0.00	0.42
																														0.35	0.26	496.10	0.90	0.27
																														0.35	0.26	497.04	1.85	0.17
																														0.37	0.27	497.19	2.00	0.15
Kurtosis																														0.33	0.26	300.17	0.00	0.22
																														0.38	0.29	301.39	1.22	0.12
																														0.33	0.26	301.41	1.25	0.12
																														0.31	0.24	301.79	1.62	0.10
																														0.33	0.26	301.90	1.74	0.09
																														0.31	0.24	302.01	1.85	0.09
																														0.31	0.24	302.05	1.88	0.09
																														0.36	0.28	302.14	1.97	0.08
																														0.39	0.29	302.14	1.97	0.08

Appendix S5. Results of multiple regression models for the trait distributions of specific leaf area (SLA). We tested the effects of species richness, geography, topography, climate variables, soil variables and all pair-wise interactions on the mean, variance, skewness and kurtosis of trait distributions (model "CLIMATE + SOIL + INTERACTIONS" in Appendix S3). We provided Model r^2, adj r^2, AICc and weight for the selected models ($\Delta AICc \leq 2$).

MAT: mean annual temperature; MAP: mean annual precipitation; PS: precipitation seasonality, TP: total phosphorus

SLA	Geo / Topo	Rich	MAT		MAP		PS		pH		Sand		TP		MAT X MAP	MAT X PS	MAP X PS	MAT X pH	MAT X Sand	MAT X TP	MAP X pH	MAP X Sand	MAP X TP	PS X pH	PS X Sand	PS X TP	pH X Sand	pH X TP	Sand X TP	r²	adj. r²	AICc	ΔAICc	Weight
			x	x²	x	x²	x	x²	x	x²	x	x²	x	x²																				
Mean																														0.70	0.64	95.92	0.00	0.07
																														0.71	0.65	95.99	0.07	0.07
																														0.71	0.65	95.99	0.07	0.07
																														0.70	0.64	96.11	0.18	0.06
																														0.70	0.64	96.17	0.25	0.06
																														0.70	0.64	96.19	0.26	0.06
																														0.69	0.63	96.25	0.33	0.06
																														0.72	0.65	96.53	0.61	0.05
																														0.72	0.65	96.66	0.73	0.05
																														0.71	0.64	96.87	0.94	0.04
																														0.71	0.65	97.04	1.12	0.04
																														0.71	0.64	97.07	1.14	0.04
																														0.70	0.64	97.16	1.23	0.04
																														0.71	0.64	97.21	1.28	0.04
																														0.67	0.62	97.22	1.30	0.04
																														0.71	0.64	97.23	1.31	0.04
																														0.68	0.63	97.24	1.31	0.04
																														0.72	0.65	97.33	1.41	0.03
																														0.70	0.64	97.37	1.45	0.03
																														0.70	0.64	97.77	1.85	0.03
																														0.66	0.61	97.78	1.85	0.03
																														0.70	0.64	97.80	1.88	0.03
Variance																														0.51	0.42	315.64	0.00	0.43
																														0.52	0.42	316.06	0.42	0.34
																														0.50	0.40	316.88	1.24	0.23
Skewness																														0.50	0.41	491.24	0.00	0.22
																														0.49	0.40	491.74	0.51	0.17
																														0.49	0.40	491.76	0.52	0.17
																														0.50	0.41	492.25	1.01	0.14
																														0.51	0.41	492.71	1.48	0.11
																														0.50	0.41	492.86	1.63	0.10
																														0.49	0.40	493.10	1.86	0.09
Kurtosis																														0.38	0.29	332.38	0.00	0.22
																														0.39	0.30	333.25	0.87	0.14
																														0.36	0.28	333.28	0.90	0.14
																														0.32	0.25	333.81	1.43	0.11
																														0.39	0.29	333.93	1.55	0.10
																														0.34	0.27	334.08	1.70	0.10
																														0.40	0.30	334.12	1.74	0.09
																														0.37	0.28	334.35	1.97	0.08

Appendix S6. Data used in the study.

Lat: Latitude, Long_sin: sinus Longitude; Long_cos: cosinus Longitude; MAT: mean annual temperature (°C), MAP: mean annual precipitation (mm), PS: precipitation seasonality; Sand: sand content (%); TP: total phosphorus (mgP.$^{g-1}$ soil); Var: variance; Skew: Skewness; Kurt: Kurtosis; H: maximum plant height (cm), SLA: Specific Leaf Area (cm².g^{-1})

Country	Lat	Long_sin	Long_cos	Slope	MAT	MAP	PS	Sand	pH	TP	Richness	Mean_H	Var_H	Skew_H	Kurt_H	Mean_SLA	Var_SLA	Skew_SLA	Kurt_SLA
Argentina	-41.81	-0.53	0.85	1.1	7	217	51	72.86	6.83	0.90	7	3.71	0.28	-0.76	1.51	4.06	0.12	0.68	-0.01
Argentina	-41.24	-0.97	0.26	0.6	8	375	70	90.25	6.88	0.51	10	3.87	0.18	-1.28	2.96	4.29	0.16	0.48	-0.97
Argentina	-41.11	-0.98	-0.20	5.7	7	568	69	79.42	6.60	1.13	10	3.53	0.16	-0.53	-0.04	4.64	0.46	-0.08	-1.47
Argentina	-41.00	-0.93	-0.37	1.1	7	685	66	67.18	6.33	1.45	9	3.79	0.07	-2.71	9.51	4.71	0.17	-1.51	0.96
Argentina	-41.03	-0.99	0.16	0.6	8	416	72	77.67	6.77	0.72	9	3.90	0.29	-1.36	3.14	4.13	0.29	0.87	0.77
Argentina	-38.76	-0.78	-0.62	0.5	15	320	33	83.53	7.70	0.46	9	4.85	0.68	-0.17	0.24	4.26	0.16	1.38	2.61
Argentina	-31.49	0.97	-0.26	1.0	19	267	84	84.69	8.66	0.38	5	5.34	0.86	-1.51	0.50	3.62	1.42	-1.23	0.27
Argentina	-31.72	0.96	0.29	1.5	18	179	84	81.75	9.28	0.62	5	5.48	0.54	-2.38	4.00	3.57	0.81	-1.74	2.35
Australia	-34.22	-0.92	-0.38	0.5	17	317	13	74.20	7.01	0.13	12	5.17	2.47	0.40	-1.72	3.72	0.75	-0.16	-1.82
Australia	-34.20	-0.93	-0.38	0.5	17	318	13	76.47	7.19	0.18	16	5.78	1.86	-0.74	-1.10	3.66	0.28	-0.43	-0.07
Australia	-34.25	-0.90	-0.44	0.5	17	312	14	74.00	6.81	0.16	16	5.73	2.27	-0.36	-1.64	3.38	0.48	0.43	-1.26
Australia	-34.02	-0.91	-0.42	0.5	17	308	13	70.63	8.04	0.18	12	5.86	1.95	-0.71	-0.72	3.20	0.37	1.42	1.20
Australia	-34.11	-0.92	-0.39	0.5	17	315	13	72.99	6.89	0.17	12	5.53	2.69	-0.14	-1.88	3.33	0.61	0.72	-1.22
Australia	-34.20	-0.87	-0.50	0.5	17	310	14	55.22	7.47	0.15	13	5.86	2.85	-0.67	-1.46	3.21	0.42	0.81	-0.80
Australia	-33.96	-0.89	-0.46	0.5	17	312	13	82.71	7.27	0.16	10	6.05	1.55	-1.40	0.82	3.48	0.33	-0.25	-0.99

Australia	-33.97	-0.96	-0.27	0.5	17	311	13	72.36	7.99	0.17	13	6.04	1.27	-1.63	0.92	3.23	0.31	0.94	-0.24
Australia	-34.11	-0.93	-0.37	0.5	17	317	13	69.40	7.08	0.18	15	5.29	2.21	-0.05	-1.63	3.62	0.38	-0.28	-0.99
Australia	-33.96	-0.89	-0.46	0.5	17	312	13	77.56	6.85	0.15	11	6.65	1.48	-2.23	3.19	2.91	0.24	2.60	5.65
Australia	-33.93	-0.97	-0.25	0.5	17	312	12	76.17	7.81	0.23	14	6.26	1.75	-1.32	0.07	3.19	0.30	0.51	-1.21
Australia	-33.94	-0.96	-0.27	0.5	17	312	12	72.70	7.20	0.15	15	6.25	1.82	-1.37	0.48	3.20	0.43	1.00	-0.32
Australia	-32.16	0.98	0.19	5.0	18	405	19	75.75	6.20	0.23	21	5.38	0.72	-1.14	1.44	4.03	0.10	3.22	11.80
Australia	-31.56	0.97	-0.22	4.0	18	448	24	63.97	6.27	0.28	31	5.48	1.49	-0.64	-0.22	3.73	0.33	-0.14	0.61
Australia	-31.32	0.69	-0.73	2.0	19	476	26	47.93	6.62	0.30	18	6.18	0.80	-1.22	3.27	4.05	0.06	2.37	15.28
Australia	-31.30	0.68	-0.73	3.5	19	477	26	49.38	6.59	0.41	29	5.06	2.19	-0.12	-1.51	4.11	0.25	1.99	3.38
Australia	-31.86	-0.05	-1.00	3.0	18	508	25	28.11	6.12	0.68	17	4.87	1.76	0.71	-0.65	4.81	0.77	-0.98	-0.05
Australia	-32.12	0.84	-0.55	0.2	18	450	19	47.55	6.39	0.34	17	5.55	1.26	-1.01	0.44	4.08	0.07	-1.87	15.81
Chile	-34.11	-0.79	-0.61	14.6	17	442	108	63.16	6.97	0.23	3	5.38	0.38	0.96	2.21	4.72	0.03	-1.10	2.36
Chile	-31.20	-0.62	-0.78	12.0	14	177	114	62.97	6.76	0.27	2	4.70	0.08	-0.78	0.32	4.83	0.01	0.95	-1.09
Chile	-31.20	-0.62	-0.78	11.9	14	177	114	69.31	6.33	0.28	2	4.67	0.10	-0.36	0.96	4.83	0.01	0.97	-1.07
China	49.26	-0.20	0.98	5.0	-1	344	113	56.60	6.53	0.67	11	3.91	0.17	-2.12	3.28	5.03	0.04	-1.94	2.09
China	49.49	-0.83	0.56	6.0	-1	329	116	82.71	6.53	0.43	14	3.49	0.35	-0.24	-1.31	4.72	0.06	0.91	-0.63
China	49.53	-0.86	-0.51	8.0	-2	314	120	69.57	6.52	0.74	12	3.59	0.09	-0.56	-0.31	3.97	0.28	0.94	-0.72
China	49.03	-0.69	-0.73	8.0	0	273	124	72.45	6.93	0.65	9	3.38	0.23	-0.71	0.33	4.16	0.29	0.19	-1.49
China	48.22	0.22	-0.98	6.0	2	194	105	72.61	6.86	0.43	10	3.41	0.67	0.00	-1.14	4.17	0.30	0.23	-1.44
Ecuador	-4.01	0.81	-0.59	17.4	21	847	82	47.00	6.74	0.53	4	4.86	0.08	-1.66	1.02	5.01	0.73	-2.41	4.10
Israel	31.36	-0.26	-0.97	8.0	19	288	104	55.14	8.22	0.63	5	3.09	0.19	1.04	0.53	3.03	0.03	4.06	14.56
Israel	31.36	-0.26	-0.97	8.1	19	288	104	56.53	7.97	0.68	6	3.25	0.16	0.57	-0.68	3.02	0.02	5.17	24.84
Israel	31.36	-0.26	-0.97	9.0	19	288	104	60.54	8.53	0.68	6	3.13	0.14	1.39	1.95	3.02	0.02	5.47	28.90
Israel	31.36	-0.26	-0.97	9.2	19	288	104	62.29	8.45	0.67	5	3.08	0.09	2.22	6.76	3.01	0.01	8.83	79.16
Israel	31.36	-0.26	-0.97	9.3	19	288	104	60.03	8.27	0.75	6	3.08	0.12	2.96	10.57	3.02	0.03	5.40	28.29
Israel	31.36	-0.26	-0.97	7.9	19	288	104	40.72	8.39	0.51	6	3.08	0.28	0.95	-0.21	3.07	0.05	2.77	5.67
Kenya	0.35	-0.72	0.69	2.0	18	652	56	48.26	6.27	0.41	8	4.42	0.51	-0.15	-0.83	4.53	0.45	0.04	-1.81

Mexico	23.20	-0.68	0.74	2.0	17	345	63	57.49	7.99	0.64	8	3.49	0.54	0.58	-1.08	4.67	0.42	-1.27	0.03
Mexico	21.77	-0.91	0.41	5.5	16	598	82	58.53	6.73	0.15	5	3.11	0.23	1.11	-0.41	4.83	0.25	-2.19	3.84
Mexico	21.77	-0.91	0.42	7.5	16	598	82	51.55	6.97	0.13	5	3.21	0.41	1.12	-0.55	4.87	0.29	-2.67	5.24
Morocco	34.16	-0.70	-0.72	5.3	15	294	47	58.93	8.35	0.58	9	4.23	0.63	-2.80	6.41	3.44	0.12	2.71	5.57
Morocco	34.43	-0.81	-0.58	5.8	15	321	50	52.89	8.33	0.67	10	4.45	0.12	-8.49	80.74	3.44	0.15	2.81	5.95
Morocco	34.47	0.48	-0.88	4.0	16	401	55	42.80	8.43	0.53	6	4.46	0.07	-7.09	57.21	3.37	0.06	4.91	22.21
Morocco	34.44	0.44	-0.90	14.3	15	399	53	54.25	8.36	0.38	7	4.40	0.23	-4.88	22.63	3.37	0.06	4.83	21.79
Morocco	34.31	-0.91	-0.42	7.0	14	377	48	51.51	8.38	0.60	9	4.32	0.55	-3.92	13.87	3.40	0.10	3.80	12.98
Morocco	33.87	0.47	-0.88	7.3	15	307	45	66.28	8.39	0.37	7	4.12	1.19	-2.60	4.80	3.50	0.21	2.05	2.25
Morocco	33.93	0.41	-0.91	10.8	16	289	46	72.62	8.64	0.26	2	4.31	0.45	-3.17	8.04	3.41	0.10	3.17	8.04
Morocco	33.07	-0.40	-0.92	5.8	15	310	46	67.52	8.35	0.31	5	4.42	0.23	-6.53	42.71	3.36	0.05	5.55	29.09
Morocco	34.63	0.27	-0.96	20.0	16	339	56	55.55	8.49	0.30	8	4.30	0.18	-2.52	8.18	3.65	0.40	1.45	0.26
Morocco	34.63	0.32	-0.95	16.5	15	385	54	42.78	8.35	0.44	6	4.31	0.17	-3.52	17.03	3.86	0.46	0.48	-1.76
Spain	39.05	-0.79	-0.61	4.5	14	415	34	39.30	8.26	0.28	12	4.46	0.67	-1.94	4.17	3.58	0.18	1.35	0.50
Spain	39.05	-0.79	-0.61	4.5	14	415	34	45.53	8.37	0.33	9	4.32	0.36	-3.20	8.77	3.44	0.14	2.69	5.42
Spain	40.33	0.28	-0.96	20.8	14	439	39	44.28	8.26	0.41	7	4.62	0.26	0.54	-0.97	4.02	0.37	0.07	-1.61
Spain	40.32	0.28	-0.96	18.8	14	436	38	48.10	8.35	0.45	10	4.32	0.11	-2.13	6.25	3.87	0.47	0.43	-1.79
Spain	40.25	0.11	-0.99	20.5	14	418	37	63.74	7.75	0.14	13	4.26	0.22	-1.94	2.16	3.91	0.50	0.36	-1.84
Spain	37.80	-0.96	0.26	21.0	17	339	43	49.85	8.11	0.42	24	4.23	0.41	-0.58	0.70	3.72	0.32	0.97	-0.70
Spain	37.80	-0.96	0.26	15.8	16	353	43	50.12	8.20	0.29	20	4.01	0.37	-0.71	-1.04	3.92	0.42	0.31	-1.71
Spain	40.27	0.36	-0.93	14.0	14	436	38	58.37	7.40	0.34	15	4.67	0.43	-0.74	0.74	3.89	0.26	0.31	-1.13
Spain	40.27	0.36	-0.93	15.8	14	436	38	60.20	7.41	0.19	7	4.31	0.13	-2.20	4.35	3.79	0.42	0.64	-1.56
Spain	40.14	-0.01	-1.00	27.5	14	417	36	58.15	8.12	0.13	8	4.37	0.13	-3.19	8.81	3.66	0.37	1.19	-0.55
Spain	40.07	-0.24	-0.97	18.8	13	462	32	62.24	7.78	0.42	29	4.59	1.61	0.54	0.10	3.79	0.30	0.72	-0.77
Spain	40.07	-0.24	-0.97	21.5	13	465	32	48.76	7.76	0.43	20	4.14	0.37	-1.45	1.29	3.71	0.35	0.97	-0.84
Spain	40.21	0.27	-0.96	14.8	14	432	37	56.05	8.07	0.31	16	4.32	0.48	-1.06	1.43	3.66	0.26	1.13	-0.28
Spain	40.21	0.27	-0.96	22.0	14	432	37	54.11	8.26	0.34	13	4.43	0.09	-4.31	19.78	3.38	0.07	4.42	17.91
Spain	39.99	0.46	-0.89	14.5	15	412	38	63.76	8.20	0.32	7	4.70	0.25	0.10	-0.20	3.79	0.29	0.72	-0.85
Spain	39.99	0.46	-0.89	10.3	15	412	38	47.64	8.15	0.49	5	4.47	0.04	-6.79	45.36	3.34	0.03	6.71	43.68
Spain	39.99	0.46	-0.89	16.5	15	409	37	61.78	7.76	0.19	7	4.19	0.28	-1.39	0.24	3.84	0.49	0.65	-1.51

Spain	37.82	-0.99	-0.10	2.9	15	378	40	46.15	7.58	0.27	20	4.40	0.29	-0.61	1.75	3.88	0.43	0.52	-1.44
Spain	37.82	-0.99	-0.10	1.3	15	378	40	49.95	7.65	0.28	16	4.35	0.15	-3.03	10.12	3.82	0.41	0.53	-1.69
Spain	40.19	0.35	-0.94	17.8	14	429	39	50.19	8.22	0.44	11	4.62	0.17	0.19	2.11	3.58	0.20	1.45	0.82
Spain	40.04	0.07	-1.00	27.8	14	416	36	55.99	7.71	0.09	11	4.34	0.21	-2.49	4.43	3.50	0.22	2.35	3.79
Spain	39.21	-0.59	-0.81	3.5	14	426	34	53.95	8.31	0.54	11	4.63	1.12	0.88	0.49	3.99	0.38	0.23	-1.40
Spain	39.21	-0.59	-0.81	1.8	14	422	34	54.14	8.30	0.42	11	3.99	0.21	-0.77	-0.23	4.40	0.42	-0.99	-0.83
Spain	38.59	-0.93	0.36	14.5	14	454	34	55.73	8.31	0.42	29	4.30	0.30	-0.35	2.60	3.96	0.45	0.27	-1.70
Spain	38.59	-0.93	0.36	18.5	14	444	34	61.14	8.17	0.36	19	4.05	0.51	-1.32	0.31	3.88	0.42	0.40	-1.70
Spain	40.35	-0.26	-0.97	10.3	14	405	33	81.68	7.74	0.28	26	4.41	0.55	0.68	3.19	4.14	0.38	-0.32	-1.58
Spain	40.35	-0.26	-0.97	8.0	14	405	33	72.69	7.58	0.30	26	4.13	0.25	-1.39	2.24	4.23	0.38	-0.68	-1.35
Spain	38.79	-0.99	-0.15	16.3	14	422	34	59.63	8.41	0.53	15	4.12	0.25	0.52	10.92	4.43	0.29	-1.45	0.33
Spain	38.31	-0.69	0.73	18.8	17	353	46	73.76	8.58	0.32	15	3.53	1.37	0.49	-0.91	3.99	3.10	-2.49	4.56
Spain	39.04	-0.77	-0.63	8.3	14	423	34	56.95	8.36	0.28	9	4.92	0.36	-0.64	-1.15	4.25	0.15	0.52	-1.67
Spain	39.01	-0.46	-0.89	6.2	13	468	34	60.88	8.38	0.44	10	4.16	0.16	2.95	15.25	4.70	0.03	-0.56	14.17
Spain	37.72	-0.96	-0.26	0.5	16	341	42	77.34	8.68	0.53	10	3.80	0.75	-1.42	0.53	4.29	0.34	-0.92	-0.87
Spain	40.16	-0.25	-0.97	21.0	13	448	31	49.84	8.41	0.26	29	4.52	0.53	-0.25	-0.68	4.15	0.28	0.03	-0.73
Spain	37.92	-0.99	0.10	2.3	16	344	43	39.89	8.53	0.28	8	4.09	0.18	-1.53	1.51	4.43	0.32	-1.43	0.17
Spain	37.73	-0.98	-0.21	9.1	16	339	42	63.82	8.40	0.43	7	4.05	0.28	-3.59	11.53	4.65	0.07	-4.10	17.11
Spain	38.31	-0.82	0.57	15.4	16	398	40	39.60	8.31	0.57	19	4.34	0.44	0.03	0.27	4.39	0.24	-0.99	-0.24
Spain	40.37	0.24	-0.97	12.8	13	453	37	48.24	8.39	0.34	10	4.21	0.13	0.63	5.43	4.45	0.42	-0.98	-0.72
Spain	37.59	-0.94	0.33	4.3	18	294	48	44.11	8.38	0.90	8	4.22	0.23	-0.83	0.26	5.10	0.12	-1.64	5.29
Spain	39.54	-0.97	-0.23	8.5	12	466	29	54.56	8.45	0.48	20	4.24	0.79	1.02	1.06	4.50	0.15	-0.78	0.76
Spain	38.07	-1.00	0.04	7.8	16	341	42	54.16	8.35	0.21	14	3.86	0.28	-0.62	0.07	4.44	0.22	-0.95	-0.61
Spain	39.13	-0.71	-0.70	11.8	14	420	34	53.15	8.36	0.28	7	4.49	0.29	1.36	1.58	4.33	0.31	-0.83	-0.89
Spain	38.77	-0.85	0.52	10.8	14	457	34	58.76	8.40	0.32	16	4.06	0.31	0.26	2.37	4.57	0.12	-2.05	4.02
Spain	39.00	-0.30	-0.95	3.3	13	467	36	54.04	8.35	0.49	8	3.78	0.44	1.96	8.73	4.48	0.11	-0.78	-0.68
Spain	39.05	-0.54	-0.84	4.8	13	446	35	41.83	8.36	0.32	12	4.23	0.41	2.61	10.43	4.46	0.30	-1.40	0.25
Spain	40.02	-0.26	-0.97	20.0	13	470	31	53.30	8.11	0.21	21	4.19	0.74	0.18	-0.86	4.18	0.29	-0.03	-0.89
Spain	40.26	0.34	-0.94	21.8	14	437	38	56.93	8.44	0.24	11	4.49	0.29	0.25	0.64	4.18	0.37	-0.39	-1.52
Spain	37.63	-0.89	-0.45	16.0	14	405	39	73.09	8.57	0.22	9	3.82	0.45	-1.87	2.51	4.55	0.13	-1.94	2.99

Spain	40.11	0.32	-0.95	18.5	14	441	37	46.64	8.41	0.22	14	4.93	0.24	-0.95	2.26	3.66	0.11	0.10	-1.34
Spain	39.86	-0.56	-0.83	14.8	13	479	31	46.43	8.35	0.26	16	4.08	0.22	-1.01	2.32	4.38	0.21	-0.24	-1.19
Spain	37.89	-0.99	-0.13	21.8	13	468	35	42.62	8.31	0.27	17	3.84	0.19	0.35	3.00	4.49	0.17	-1.27	1.20
Tunisia	35.17	0.68	-0.73	5.0	16	355	27	56.71	8.44	0.34	6	4.24	0.28	-1.63	1.21	3.73	0.37	0.85	-1.17
Tunisia	33.52	-0.52	-0.85	22.0	19	221	60	65.87	8.50	0.20	6	4.10	0.26	-1.59	2.14	3.95	0.69	0.40	-1.71
Tunisia	35.16	0.30	-0.95	4.0	17	274	29	59.81	8.44	0.25	6	4.47	0.05	-6.42	40.75	3.36	0.05	5.34	27.75
Tunisia	32.98	-0.88	-0.48	1.0	20	141	66	81.17	8.48	0.16	4	4.03	0.27	-0.74	-0.66	4.10	0.65	0.12	-1.87
Tunisia	34.69	-0.88	-0.47	3.0	18	193	49	59.20	8.01	0.26	8	4.57	0.14	-1.65	6.20	3.69	0.27	1.22	0.79
Tunisia	33.76	-0.57	-0.82	1.5	20	175	60	69.14	8.09	0.26	8	4.03	0.41	-0.76	-1.31	3.86	0.37	0.33	-1.67
Tunisia	35.63	-0.26	-0.97	2.0	18	314	35	74.52	8.16	0.25	5	4.47	0.03	-0.39	4.83	3.60	0.36	1.89	2.17
Tunisia	35.86	-0.34	-0.94	1.5	17	407	38	54.76	7.96	0.37	6	4.77	0.47	0.70	-0.94	3.97	0.36	0.19	-1.33
USA	37.85	0.98	-0.21	3.0	11	205	32	84.03	8.61	0.15	7	4.47	0.10	-1.78	14.44	4.11	0.26	0.73	-0.56
USA	37.51	0.88	0.48	4.0	10	257	27	82.39	8.31	0.30	6	3.39	0.64	0.54	-1.66	4.73	0.11	-0.27	-1.86
USA	33.75	-0.42	-0.91	1.0	18	203	48	85.98	8.45	0.86	5	4.38	0.35	0.48	-1.04	4.16	0.06	0.43	-1.07
USA	33.75	-0.42	-0.91	1.0	18	193	45	87.83	8.13	0.80	5	4.60	0.13	-1.26	1.37	4.29	0.11	-0.20	-1.87
USA	33.75	-0.43	-0.90	1.5	18	207	47	79.37	8.07	0.68	5	4.47	0.34	0.21	-1.10	4.15	0.07	0.52	-1.10
USA	33.75	-0.42	-0.91	1.0	18	203	48	79.18	7.89	0.77	4	4.43	0.21	-0.57	-1.66	4.05	0.06	1.32	0.24
USA	33.75	-0.41	-0.91	1.5	18	197	47	86.83	8.13	0.50	5	4.17	0.21	0.65	-1.37	4.22	0.05	-0.04	-0.68
USA	33.75	-0.43	-0.90	1.0	18	207	47	76.00	8.44	0.71	5	4.36	0.31	0.48	-0.90	4.27	0.07	-0.12	-1.27
Venezuela	8.43	-0.54	-0.84	3.5	27	1177	79	94.54	5.54	0.05	6	4.16	0.24	1.05	7.26	3.56	0.20	-0.82	-0.74
Venezuela	8.43	-0.54	-0.84	3.5	27	1177	79	92.73	5.15	0.07	7	3.90	0.18	0.82	1.21	3.25	0.24	0.41	-1.68
Venezuela	8.32	-0.71	-0.71	2.9	27	1171	78	88.28	5.61	0.09	3	4.26	0.12	-0.66	3.93	3.67	0.13	-1.90	1.62