Climate, topography and soil factors interact to drive community trait distributions in global drylands

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Abstract

The skewness and kurtosis of community trait distributions (CTDs) can provide important insights on the mechanisms driving community assembly and species coexistence. However, they have not been considered yet when describing global patterns in CTDs. We aimed to do so by evaluating how environmental variables (mean annual temperature [MAT] and precipitation [MAP], precipitation seasonality [PS], slope angle and sand content) and their interactions affected the mean, variance, skewness, kurtosis of the plant CTDs in global drylands. We gathered specific leaf area and maximum plant height data from 130 dryland communities from all continents except Antarctica. Over 90% of the studied communities had skewed CTDs for SLA and height or had kurtosis values differing from those of normal distributions. Higher MAT and/or lower MAP led to a shift toward plant communities over-represented by “conservative” strategies, and a decrease in functional diversity. However, considering interactions among environmental drivers increased the explanatory power of our models by 20%. Sand content strongly altered the responses of height to changes in MAT and MAP (climate × topo-edaphic interactions). Increasing PS reversed the effects of MAT and MAP (climate × climate interactions) on the four moments of CTDs for SLA, particularly in dry-subhumid regions. Our results indicate that the increase in PS forecasted by climate change models will reduce the functional diversity of dry-subhumid communities. They also indicate that ignoring interactions among environmental drivers can lead to misleading conclusions when evaluating global patterns in CTDs, and thus may dramatically undermine our ability to predict the impact of global environmental change on plant communities and associated ecosystem functioning.

Keywords: arid systems, functional biogeography, maximum plant height, precipitation regimes, sand content, slope, specific leaf area, temperature.
COMMUNITY TRAIT DISTRIBUTIONS (CTDs) ARE THE FREQUENCY PATTERNS OF TRAIT VALUES WEIGHTED BY THE SPECIES ABUNDANCE OBSERVED IN COMMUNITIES (VIOLLE ET AL. 2007). THEY CAN BE USED TO MAKE ACCURATE PREDICTION OF PLANT SPECIES DISTRIBUTIONS (FRENETTE-DUSSAULT ET AL. 2013), TO ASSESS PLANT COMMUNITY RESPONSES TO ENVIRONMENTAL GRADIENTS (SOUNDZILOVSKAIA ET AL. 2013), AND TO QUANTIFY ECOSYSTEM STABILITY UNDER VARYING ENVIRONMENTAL CONDITIONS (VALENCIA ET AL. 2015). THEREFORE, EVALUATING PATTERNS OF CTDs ALONG BIogeOGRAPHIC GRADIENTS IS A POWERFUL TOOL TO PREDICT THE IMPACT OF CLIMATE CHANGE ON COMMUNITIES AND ECOSYSTEMS (VIOLLE ET AL. 2014, ENQUIST ET AL. 2015), PARTICULARLY AT THE GLOBAL SCALE (PARMESAN ET AL. 2013).


dominant species, and the community-weighted variance (or related indices, e.g., Freschet et al. 2011, Swenson et al. 2012), which measures the general extent of functional diversity in a community. While the mean and variance of CTDs suffice to characterize normal distributions, CTDs are often non-normal and sometimes even multimodal (Fonseca et al. 2000, Enquist et al. 2015). In such cases, the skewness and kurtosis of CTDs complement the information provided by the mean and variance by providing insights on the mechanisms determining community assembly and species coexistence (Schamp et al. 2008, Kraft et al. 2008, Enquist et al. 2015; Fig. 1). Swenson and Weiser (2010) found that the skewness and kurtosis of CTDs from Eastern North American trees were highly sensitive to temperature and precipitation. Their results highlight the importance of their investigation in a context of functional biogeography and global environmental change.

Drylands, including arid, semi-arid and dry-subhumid ecosystems, cover ~41% of Earth’s land surface and support over 38% of the total global population (Safirel and Adeel 2005), and are particularly sensitive to climate change (see Maestre et al., 2012a for a review). Despite their importance, no study so far has simultaneously considered the interactive effects of climate, topography and soil factors on the four moments of the traits distributions in global drylands. We aimed to do so by assessing specific leaf area (SLA) and maximum plant height of perennial vegetation in 130 dryland communities worldwide, which encompass the major abiotic features and vegetation types found in drylands globally (Appendix S1). Specific leaf area is a key trait indexing leaf-level carbon gain strategies (leaf “economics”; Wright et al. 2004). Maximum plant height reflects a trade-off for biophysical constraints in determining water fluxes within the plant (Enquist 2002), and is related to competitive ability (Westoby 1998). Specific leaf area and maximum plant height reflect two important independent axes of plant ecological strategy (Westoby 1998), and are sensitive to both climatic (e.g., Wright et al. 2004) and edaphic (e.g., Fonseca et al. 2000) variables. In
drylands, these traits can help to explain species coexistence and the dominance of particular plant strategies (e.g. stress-tolerant vs. stress avoidant: Fonseca et al. 2000, Frenette-Dussault et al. 2012, Gross et al. 2013). Along a regional aridity gradient, changes in CTDs of the two studied traits have been shown to impact the strength of biotic interactions (Gross et al. 2013), and the stability of ecosystem multifunctionality (Valencia et al. 2015).

Following the environmental filtering hypothesis (Keddy 1992), we predict that (i) higher environmental stress will lead to a shift toward plant communities over-represented by short species with “conservative” strategies. A decrease in the mean and/or an increase in the skewness for height and SLA with environmental stress will reflect this functional shift. Additionally, we expect (ii) either a decrease in functional diversity due to environmental stress (lower variance and/or higher kurtosis) or an increase in functional diversity due to a decrease in the importance of competitive interactions (higher variance and/or lower kurtosis). Finally, we forecast that (iii) the interactions between climate, topography and soil factors will strongly influence the four moments of CTDs.

MATERIALS AND METHODS

Study sites and environmental variables

Field data for this study were obtained from 130 sites located in 13 countries (Argentina, Australia, Chile, China, Ecuador, Israel, Kenya, Mexico, Morocco, Spain, Tunisia, USA and Venezuela; Fig S1). These sites are a subset of the global network of sites from Maestre et al. (2012b) that cover a wide range of the environmental conditions found in global drylands (excluding hyper arid areas, which usually have little or no perennial vegetation). Mean annual temperature (MAT) and mean annual precipitation (MAP) of the studied sites varied between -1.8°C to 27.8°C, and from 79 mm to 1177 mm, respectively. Slope values ranged
between 0.2° and 28°. The sites studied include a wide variation in soil types, with more than 25 different categories from the FAO’s classification (FAO 1998).

Site climate was summarised using three variables: mean annual temperature (MAT), mean annual precipitation (MAP) and precipitation seasonality (PS: coefficient of variation of 12 monthly rainfall totals). We selected these variables because: i) their measurement is unambiguous; ii) 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); iii) they are key variables for explaining global variation in dryland ecosystem functioning (Maestre et al. 2012b); and (iv), MAT, MAP and PS describe largely independent features of site climate in the studied dataset (bivariate correlations, r < 0.36 in all cases, Appendix S2). Temperature seasonality (standard deviation * 100) was not considered due to its correlation with MAT in the studied dataset (r = 0.59). 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).

Topo-edaphic variables (i.e. soil properties and topography) at each site were summarised using slope angle and soil sand content. These variables are particularly interesting in the context of this study because they can largely affect moments of CTDs such as community-weighted mean and variance (Dubuis et al. 2013), and because they play key roles in controlling infiltration, water and nutrient availabilities and run-on/run-off processes in drylands (e.g., Gómez-Plaza et al. 2001). Sand, clay and silt contents were measured in soil samples (0-7.5 cm depth) from under the canopy of the dominant perennial plants, and in open areas devoid of vascular vegetation, corresponding to the main microsites present at each site (see Maestre et al. 2012b for details). Soil pH was measured with a pH meter, in a 1:2.5 mass: volume soil and water suspension. Site-level estimates for all variables were obtained by using the average of the mean values observed in bare ground and vegetated...
areas, weighted by their respective area at each site (Maestre et al. 2012b). We did not consider soil pH in further analyses due to its correlation with MAP and sand content ($r = -0.62$ and -0.53, respectively). Similarly, clay and silt contents were not used in our analyses due to their correlation with sand content ($r = -0.52$ and -0.55, respectively). Slope at each site was quantified by direct measurements in situ with a clinometer.

**Community trait distributions**

Community trait distributions were estimated by merging two independent datasets. The cover of each perennial plant species measured in situ was used as a proxy of species abundance. SLA and maximum plant height were retrieved from the TRY database (Kattge et al. 2011). Site selection was based on the availability of trait data. A site was selected when SLA and plant height data were available for all the perennial species that accounted together for at least 60% of the total perennial vegetation cover (Appendix S3). In total, 130 sites were selected, providing SLA and maximum plant height data for 347 and 512 species, respectively. We also repeated our analyses using a subset of 95 sites for which SLA and plant height data were available for all the perennial species that accounted together for at least 80% of the total perennial vegetation cover at each site, a threshold recommended when estimating CTDs (Pakeman and Quested 2007). Results from this subset of data were consistent with those based on the dataset used with the 60% threshold (Appendix S4), and thus will not be presented in the main text.

For each of the 130 studied sites, community-weighted mean, community-weighted variance, community-weighted skewness and community-weighted kurtosis were computed using the R functions of Bernard-Verdier et al. (2012). In the case of non-normal CTDs, differences in the degree of skewness highlight a shift in the dominance of species with trait values toward one of the extreme of the trait range in a given community (Fig. 1). This pattern may arise from abiotic filtering selecting for a particular set of extreme trait values (Keddy...
1992), from biotic filtering such as asymmetric light competition among species (Schamp et al. 2008), the importance of rare species in local co-existence or time lags in community responses to rapid environmental changes (Enquist et al. 2015). Kurtosis highlights the level of trait differentiation between co-occurring species (similar to the trait spacing in Kraft et al. 2008). High kurtosis is characteristic of peaked CTDs, and reflects the occurrence of strong environmental filtering. Low kurtosis is characteristic of flat CTDs, reflecting multiple community assembly processes, or the occurrence of stabilizing niche differences among interacting species (Chesson 2000). Very low kurtosis is characteristic of bimodal CTDs. Bimodal CTDs arise from multiple optimal trait values reflecting either the co-existence of contrasting functional strategies (Gross et al. 2013), or the co-occurrence of past and present optimal trait values in response to recent environmental changes (Enquist et al. 2015).

Statistical analyses

We first built separate linear regression models for each moment of CTDs (mean, variance, skewness and kurtosis) for SLA and height using the five selected environmental variables as predictors (MAT, MAP, PS, slope and sand content) without interactions. Correlation among the predictors used, and thus multicollinearity, was low ($r < 0.39$ and Variance Inflation Factor [VIF] <1.25 in all cases, Appendix S2). Latitude and longitude were also included in all models to account for potential effects of spatial autocorrelation between sites (Maestre et al. 2012b). Correlation between geographical and studied environmental variables was also low ($r < 0.33$ and VIF < 1.44 in all cases, Appendix S2). Then, we ran a second set of analyses where all possible two-way interactions between MAT, MAP, PS, slope and sand content were included in the models. For each trait and moment, we used a backward-forward stepwise regression procedure to select the models that minimized the second-order Akaike information criterion (AICc).
We evaluated the relative importance of the predictors considered and their interactions as drivers of the variation found for each trait and moment using a variance decomposition analysis based on the best model selected (see Dubuis et al. 2013 for a similar approach). First, the variance decomposition was used to highlight the percentage of variance explained by the interactions among predictors. Thus, the following five identifiable variance fractions were disentangled: i) latitude and longitude, ii) MAT, MAP and PS, iii) slope and sand content, iv) interactions among predictors and v) unexplained variance. Second, the variance decomposition was used to highlight the percentage of variance explained by climate (and their interactions), topo-edaphic (and their interactions) and climate × topo-edaphic interactions. Thus, the following seven identifiable fractions of variance were disentangled: i) latitude and longitude, ii) climatic variables, iii) climate × climate interactions, iv) local topo-edaphic variables (slope and sand content), v) topo-edaphic × topo-edaphic interactions, vi) climate × topo-edaphic interactions and vii) unexplained variance.

Finally, we conducted a sensitivity analysis of the selected models to illustrate how climate × climate and climate × topo-edaphic interactions drive variations in CTDs in the studied drylands. For doing so, we used the parameter estimates of the climatic and topo-edaphic variables obtained from the best models (based on AICc). Other variables included in these best models were treated as constants and fixed to their mean. Predicted values were obtained by fixing one of the two interacting predictors both at the lowest and highest values observed in the dataset.

All statistical analyses were performed using the R statistical software 2.15.1 (R Core Team 2012). All response variables (community-weighted moments) were log-transformed, and all the predictors (climatic and topo-edaphic variables) were standardized and normalized (z-score) before analyses.
RESULTS

Most of the CTDs did not follow a normal distribution, highlighting the relevance of the use of skewness and kurtosis in evaluating change in CTDs (Appendix S5). Among the 130 studied communities, over 90% of the CTDs for SLA and height were skewed (skewness < -1 or > 1) or had kurtosis values differing from those of normal distributions (kurtosis < -1 or > 1). Furthermore, more than 53% of the CTDs for SLA and height were highly skewed (skewness < -2 or > 2) or had a kurtosis highly departing from that characterizing normal distributions (kurtosis < -2 or > 2).

Additive effects of climate soil and topographic factors on CTDs

When interactions among predictors were not included in the models, the predictive power of the models was relatively modest, and decreased for skewness and kurtosis (Table 1). Climatic variables were always significant predictors for all moments and traits evaluated (Table 1), explaining up to 27% of the total variance for SLA (Fig. 2a: variance) and up to 18% for height (Fig. 2b: mean). Topo-edaphic variables explained less than 4% of the total variance in all cases (Table 1).

Higher MAT simultaneously decreased the mean and variance for SLA and increased kurtosis (Table 1), reflecting a shift from flat and wide spread or even bimodal distributions, dominated by high SLA values, to narrow and peaked trait distributions dominated by low SLA. In contrast, higher MAP increased the mean and decreased the skewness for SLA, apparently leading to skewed distributions dominated by high SLA values. Higher MAP was also associated with increased variance for SLA, reflecting wide spread distributions. Finally, higher sand content was also associated with trait distributions dominated by low mean SLA (Table 1), with flat, wide spread or even bimodal distribution (low kurtosis).

Higher MAT and slope angle values increased the mean and kurtosis for height (Table 1), reflecting changes in trait distributions toward peaked CTDs dominated by tall species.
contrast, higher MAP led to skewed and peaked trait distributions for height (high skewness and kurtosis), i.e., communities over-represented by relatively small species. Both mean and variance for height decreased with increases in PS, indicating changes toward narrow trait distributions dominated by small species.

Interactive effect of climate, soil and topographic factors on CTDs

Including interactions among predictors substantially increased the predictive power of the models (Table 1). Interactions between MAT and PS, and between MAP and PS (Table 1), explained a large part of the variation in SLA (Fig. 2c: climate × climate interactions). At low values of PS, MAT and MAP increased the mean and variance for SLA, and decreased its skewness (Fig. 3a, c and e). This reflected changes in CTDs toward left-skewed and widespread distributions dominated by species with high SLA values. In contrast, large PS values strongly dampened, and even reversed the effect of MAT and MAP (Fig. 3b, d and f). Narrow distributions (low variance) dominated by species with low SLA values (low mean and right-skewed) occurred under higher MAT and MAP conditions.

Interactions between MAT and sand content, and between MAP and sand content, explained a large part of variation for height (Table 1, Fig. 2d: climate × topo-edaphic interactions). These results indicate that sand content mediates the effect of climate on CTDs. For instance, CTDs were primarily dominated by short species (Fig 4a and e) but were bimodal (Fig. 4g) at low levels of sand content under high MAT and low MAP. At high level of sand contents, and under similar MAT and MAP conditions, CTDs were dominated by the tallest species (Fig. 4b), and were unimodal (Fig 4h).

DISCUSSION

Community trait distributions (CTDs) in global drylands are highly sensitive to climatic variables such as MAT and MAP. Following our first two hypotheses, environmental stress...
(i.e. higher MAT and/or lower MAP values) leads to plant communities over-represented by “conservative” strategies and a decrease in functional diversity. However, climate × climate interactions largely explain variations in CTDs of global drylands, and topo-edaphic variables mediate the effect of climate on the four moments (climate × topo-edaphic interactions), consistently with our third hypothesis. Precipitation seasonality reverses the effects of mean temperature and precipitation on CTDs for SLA. Similarly, soil parameters such as sand content determine the effect of MAT and MAP on plant community height. Importantly, the CTDs of most of the studied communities strongly departed from normal distributions, which highlight the need for detailed analyses of skewness and kurtosis.

Additive effects of climate, soil and topographic factors on CTDs

The effects of climate on the mean of the CTDs for SLA and maximum plant height are consistent with other global studies conducted at the species level (e.g., Wright et al. 2004, Reich et al. 2007, Moles et al. 2014). Higher MAT decreased the mean SLA and increased the height of communities (Soudzilovskaia et al. 2013, Moles et al. 2014), reflecting a decrease in abundance of herbaceous perennial vegetation relative to the abundance of shrubs with evergreen leaves in warmer drylands. Such functional shifts have been documented in the Chihuahuan Desert, and have been attributed to recent climate warming (Brown et al. 1997). Interestingly, functional shifts toward higher abundances of evergreen shrubs have also been observed in response to experimental climate warming in colder biomes (e.g., Walker et al. 2006).

Higher MAP led to communities with increased average SLA values. Communities occurring in the wettest part of the precipitation range studied (i.e. sub-humid drylands) are dominated by species with exploitative strategies, with potential for relatively quick returns on investments of nutrient and dry mass in leaves (Fonseca et al. 2000, Wright et al. 2004). Soil characteristics and topography had much lower explanatory power than climatic
variables as predictors of variations in SLA and maximum height, and only slightly drove variations in the distributions of both traits. Soil texture is an important abiotic filtering that selects for particular set of trait values (e.g., Keddy 1992), i.e. slow-growing perennial vegetation (or evergreen habit). Such a functional shift likely occurs because high sand content is typically found in sites with low nitrogen contents within the sites studied (Maestre et al. 2012b, Delgado-Baquerizo et al. 2013).

Skewness and kurtosis of CTDs were highly sensitive to climate, soil and topography. Higher MAT led to peaked or narrow distributions for SLA and height, reflecting a loss of functional diversity due to the strong effect of abiotic filtering (Keddy 1992). In contrast, flat and even bimodal distributions for SLA occurred for communities in cooler conditions, reflecting an increase in the importance of competitive interactions (Gross et al. 2013).

Higher MAP increased the over-representation of short species with relatively high SLA, co-occurring with rare tall species with low SLA (i.e. a shift toward right-skewed distributions for height and left-skewed distributions for SLA). This over-representation in high SLA may reflect a direct response to a more favorable environment. Alternatively, it may also reflect the occurrence of positive interactions between tall stress-tolerant and exploitative stress-intolerant species. Gross et al. (2013) found that, at low aridity levels, conservative tall species can facilitate the persistence of short fast-growing species that do not tolerate water stress in Mediterranean shrublands.

Interactive effects of climate, soil and topographic factors on CTDs

Considering interactions among environmental drivers strongly increased the explanatory power of our models. Thus, our findings highlight the importance of considering these interactions when assessing large-scale patterns of CTDs. Until now, both climate × climate and climate × topo-edaphic interactions have received very little attention when exploring the drivers of variations in functional traits at both species and community levels (see Reich et al.
2007 for climate × climate interactions, Ordonez et al. 2009 for climate × topo-edaphic interactions). While considering effects of environmental variables as additive (without interactions) can allow capturing general biological trends of large-scale patterns of CTDs (e.g., Freschet et al. 2011, Swenson and Weiser 2010, Swenson et al. 2012), conclusions drawn from such analyses could be misleading, and may dramatically undermine our ability to predict the impact of global environmental change on plant community structure and associated ecosystem functioning.

The importance to consider interactions between environmental drivers is clearly illustrated by the effect of precipitation seasonality, which reversed the effects of MAT and MAP on SLA (Fig. 3). Climate warming is expected to spatially and temporally alter precipitation regimes, and to trigger complex interactive influences on diversity (see Peñuelas et al. 2013 for review). Our results indicate that an increase in PS can particularly affect drylands with warm and relatively wet climate, such as the dry-subhumid regions of our dataset (e.g., Ecuador and Venezuela). Under low seasonality, dry-subhumid ecosystems are dominated by communities with relatively fast-growing and water stress-intolerant vegetation (high SLA), and harbor a high functional diversity. Increasing seasonality can strongly affect the functional structure of these communities by increasing the dominance of slow-growing species and thus reducing their functional diversity. This finding is particularly important because dry-subhumid regions are facing altered seasonal climatic patterns due to ongoing climate change which will likely increase the degree of drought stress they will experience in the future (IPCC 2013).

Sand content altered the height responses to changes in MAT and MAP, highlighting the importance to also consider edaphic factors to forecast the effect of climate change on plant communities (Fridley et al. 2011, Liancourt et al. 2013). Small and tall species tend to co-occur within communities under high MAT and low MAP conditions (bimodal trait
distributions for height). Bimodal distributions for height reflect the structure of perennial dryland vegetation characterized by patches of tall shrubs co-occurring with small species (e.g., Australian woodlands; Eldridge 1999). However, an increase in sand content can alter the functional structure of those communities by selecting for tall species only (unimodal trait distributions for height). The support of taller and denser perennial vegetation on coarse (sandy) soils than on finer-textured soils is a commonly observed pattern in arid and semi-arid climates, generally referred as “inverse texture effect” (Noy Meier 1973).

Finally, it is interesting to notice that latitude and longitude explained a large part of the variation found in our data, and drove the overall decrease in explanatory power for the higher moments of the trait distribution. While our dataset did not allow us to explore the role of these geographic variables (they were not correlated with the studied environmental variables), their predictive power on CTDs is intriguing, and calls for further studies to identify their biological meaning. Latitude and longitude are increasingly used to assess patterns in functional biogeography (e.g., Swenson et al. 2012), and they likely reflect non-considered sources of variations associated to geography in our study. They may encompass differences in species pool, solar irradiance, soil variables not measured here or land-use patterns and history, which are all likely to affect CTDs.

Conclusions

Our study illustrates how trait-based approaches that consider the four moments of the CTDs, reveals the signature of ecological processes at large scales. It has ramifications for improving our predictions on the effect of climate change on plant communities (Violle et al. 2014) and on ecosystem functions (Enquist et al. 2015). This approach would certainly gain predictive power by integrating intraspecific trait variations, and particularly by considering complex shapes of individual-level trait distributions (Laughlin et al. 2015).
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LITERATURE CITED


Food and Agriculture Organization (FAO), World Reference Base for Soil Resources (FAO, Rome, 1998).


TABLE 1. Best-fitting regression models with and without interactions among predictors. Models are presented for each moment and each trait separately. The best models are selected according to AICc values (Appendix S5). Shaded cells indicate variables that were selected in a particular model. Latitude and longitude were introduced to avoid spatial auto-correlations. Slope directions are indicated when significant.

LL: latitude / longitude, MAT: mean temperature, MAP: mean precipitation, PS: precipitation seasonality, SL: slope, and SC: sand content

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FIGURE LEGENDS

FIG. 1. Formulas (after Enquist et al. 2015), shapes and ecological implications of the four moments of community trait distributions.

FIG. 2. Percentage of variance explained for each group of predictors (i.e. climate and topo-edaphic variables) and two-way interactions (a, b), and for each group of predictors and their interactions separately (c, d). Grey portions represent the unexplained variances. The proportions were calculated using a variance decomposition analysis based on the best model selected for each trait and moment (Table 1, Appendices S4 and S6).

FIG. 3. Predicted values (black dots) and planes representing the interactions between mean temperature (MAT) and precipitation seasonality, and between mean precipitation (MAP) and precipitation seasonality on the mean (a, b), variance (c, d) and skewness (e, f) for specific leaf area (SLA). The interactions were selected by the best fitting models (Table 1, Appendices S4 and S6). Effects of interactions are presented at low (CV seasonality = 12: a, c and e) and high seasonality (CV seasonality = 124: b,d and f). The colours of the predicted planes change from blue (low values of the moments) to red (high values).

FIG. 4. Predicted values (black dots) and planes representing the interactions between mean temperature (MAT) and sand content and between mean precipitation (MAP) and sand content on the mean (a, b), variance (c, d), skewness (e, f) and kurtosis (g, h) for height. The interactions were selected by the best fitting models (Table 1, Appendices S4 and S6). Effects of interactions are presented at low (sand content = 27.66%: a, c, e and g) and high sand content (sand content = 94.54%: b,d, f and h). The colours of the predicted planes change from blue (low values of the moments) to red (high values of the moments).
### FIGURES

#### FIG. 1.

<table>
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<th>Formula</th>
<th>Shape</th>
<th>Ecology</th>
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<td><strong>Mean</strong>&lt;br&gt;[ CWM_{ij} = \sum_{k=1}^{n} A_{kj} \times z_{k} ] with CWM = community-weighted mean&lt;br&gt;[ A_{kj} = \text{relative abundance of species } k \text{ in plot } j ]&lt;br&gt;[ z_{k} = \text{mean trait value of species } k ]&lt;br&gt;[ n = \text{number of sampled species in a plot } j ]</td>
<td><img src="image1.png" alt="Shape" /></td>
<td>- Trait values of the most dominant species in a community (normal distributions)</td>
</tr>
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<td><strong>Variance</strong>&lt;br&gt;[ CWV_{ij} = \sum_{k=1}^{n} A_{kj} \times (z_{k} - CWM_{ij})^2 ] with CWV = community-weighted variance</td>
<td><img src="image2.png" alt="Shape" /></td>
<td>- General extent of functional diversity in a community</td>
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<tr>
<td><strong>Skewness</strong>&lt;br&gt;[ CWS_{ij} = \frac{\sum_{k=1}^{n} A_{kj} \times (z_{k} - CWM_{ij})^3}{CWV_{ij}^{3/2}} ] with CWS = community-weighted skewness</td>
<td><img src="image3.png" alt="Shape" /></td>
<td>- Change in the dominance of species with trait values toward one of the extreme of the trait range&lt;br&gt;- Abiotic filtering: selection for a particular set of extreme values&lt;br&gt;- Time lags in community responses to rapid environmental changes&lt;br&gt;- Biotic filtering: asymmetric light competition&lt;br&gt;- Importance of rare species in local co-existence</td>
</tr>
<tr>
<td><strong>Kurtosis</strong>&lt;br&gt;[ CWK_{ij} = \frac{\sum_{k=1}^{n} A_{kj} \times (z_{k} - CWM_{ij})^4}{CWV_{ij}^{2}} - 3 ] with CWK = community-weighted kurtosis</td>
<td><img src="image4.png" alt="Shape" /></td>
<td>- Level of trait differenciation between co-occurring species&lt;br&gt;- Abiotic filtering: selection for a particular set of trait values (leptokurtic)&lt;br&gt;- Co-occurrence of past and present optimal trait values in response to rapid environmental changes (bimodal)&lt;br&gt;- Co-occurrence of multiple community assembly process in a community&lt;br&gt;- Co-existence of contrasting functional strategies due to competition or to cope with the abiotic constraint (platykurtic / bimodal)</td>
</tr>
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</table>
FIG. 3.

Low Seasonality

(a) Log Mean SLA
(b) Log Mean SLA
(c) Log Variance SLA
(d) Log Variance SLA
(e) Skewness SLA
(f) Skewness SLA
FIG. 4.

Low Sand Content

(a)

High Sand Content

(b)

(c)

(d)

(e)

(f)

(g)

(h)

Log Mean H

Log Variance H

Skewness H

Log Kurtosis H

Low Sand Content

High Sand Content

Log Mean H

Log Variance H

Skewness H

Log Kurtosis H

MAP (mm Yr\(^{-1}\))

MAT (°C)

MAP (mm Yr\(^{-1}\))

MAT (°C)

MAP (mm Yr\(^{-1}\))

MAT (°C)

MAP (mm Yr\(^{-1}\))

MAT (°C)

MAP (mm Yr\(^{-1}\))

MAT (°C)
APPENDICES

APPENDIX S1. Map showing the sampling effort for a) the 130 studied dryland communities and b) the Mediterranean basin.
**APPENDIX S2.** Correlation matrices among the four moments (mean, variance, skewness and kurtosis) and among environmental predictors (climate and edaphic conditions). Correlations with Pearson coefficients higher than 0.50 (absolute value) are indicated in bold. We also present the results of the variance inflation factor (VIF) to evaluate the risk of multicollinearity.

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We also present the results of the variance inflation factor (VIF) to evaluate the risk of multicollinearity.
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**APPENDIX S3.** Species number (Sp.nb) and abundance of perennial vegetation for which trait data were available in each of the 130 sites. Data are shown for both Specific Leaf Area and maximum plant height.

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NOT PEER-REVIEWED
**APPENDIX S4.** Results of analyses using community abundances above 80% (n = 95 communities). a) Best-fitting regression models in absence of interactions among predictors. Models are presented for each moment and each trait separately. The best models are selected according to AICc values. Shaded cells indicate variables that were selected in a particular model. Latitude and longitude were introduced to avoid spatial auto-correlations. Slope directions are indicated when significant. b) Proportion of variance explained for each group of predictors (i.e. climate and topo-edaphic variables) and two-way interactions (a. and b), and for each group of predictors and their interactions separately (c and d). Grey portions represent the unexplained variances. The proportions were calculated using a variance decomposition analysis based on the best model selected for each trait and each moment.

**LL:** latitude and longitude. **MAT:** mean annual temperature. **MAP:** mean annual precipitation. **PS:** precipitation seasonality, **SL:** slope angle, **SC:** sand content.

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APPENDIX S5. Boxplots representing the ranges of data for community-weighted mean, variance, skewness and kurtosis for both specific leaf area (SLA) and maximum plant height.

The grey boxes represent the envelope of the 50% central region.
APPENDIX S6. Best models selected from the multiple regressions including geographical, climatic and edaphic variables as predictors (Table 1) and with interactions among predictors (Table 2). Models are presented for each moment separately for a) specific leaf area and b) height.

\( P \) values of each best multiple regression model are indicated as follows: ns = \( P > 0.05 \). * = \( P < 0.05 \). ** = \( P < 0.01 \). *** = \( P < 0.001 \).

### a) Specific Leaf Area (SLA)

#### Mean

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|----------|
| (Intercept)   | 4.12110  | 0.04091    | 100.734 | < 2e-16 *** |
| Latitude      | -0.19960 | 0.04637    | -4.305  | 3.36e-05 *** |
| Longitude     | -0.29176 | 0.04420    | -6.601  | 1.07e-09 *** |
| mean_temp     | -0.23849 | 0.04434    | -5.378  | 3.60e-07 *** |
| mean_precipitation | 0.12558 | 0.04637 | 2.708  | 0.00772 ** |
| sand          | -0.11461 | 0.04542    | -2.524  | 0.01288 * |

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.4665 on 124 degrees of freedom
Multiple R-squared: 0.4197. Adjusted R-squared: 0.3963
F-statistic: 17.94 on 5 and 124 DF. p-value: 2.354e-13

#### Mean + interactions

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|----------|
| (Intercept)   | 4.10656  | 0.03550    | 115.665 | < 2e-16 *** |
| Latitude      | -0.05148 | 0.05004    | -1.029  | 0.30572  |
| Longitude     | -0.51606 | 0.06409    | -8.052  | 7.63e-13 *** |
| mean_temp     | 0.22597  | 0.09042    | 2.499   | 0.01384 * |
| mean_precipitation | 0.48790 | 0.08786 | 5.553  | 1.78e-07 *** |
| prec_season   | -0.28308 | 0.06637    | -4.265  | 4.07e-05 *** |
| slope         | -0.04601 | 0.04333    | -1.062  | 0.29052  |
| sand          | 0.00305  | 0.04905    | 0.062   | 0.95052  |
| mean_temp:prec_season | -0.30009 | 0.05387 | -5.570  | 1.65e-07 *** |
| mean_temp:slope | 0.08965 | 0.07880 | 1.138   | 0.25753  |
| mean_precipitation:prec_season | -0.41290 | 0.09583 | -4.309  | 3.44e-05 *** |
| mean_precipitation:sand | -0.10807 | 0.03072 | -3.518  | 0.00062 *** |
| prec_season:slope | 0.11759 | 0.06453 | 1.822   | 0.07098 . |

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.3826 on 117 degrees of freedom
Multiple R-squared: 0.6317. Adjusted R-squared: 0.5943
F-statistic: 16.72 on 12 and 117 DF. p-value: < 2.2e-16

#### Variance

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|----------|
| (Intercept)   | 6.4252   | 0.1006     | 63.879  | < 2e-16 *** |
| Latitude      | -0.2657  | 0.1068     | -2.488  | 0.01415 * |
| Longitude     | -0.3195  | 0.1192     | -2.681  | 0.00834 ** |
| mean_temp     | -0.5618  | 0.1101     | -5.101  | 1.23e-06 *** |
### Variance + interactions

**Coefficients:**

|                        | Estimate | Std. Error | t value | Pr(>|t|) |
|------------------------|----------|------------|---------|----------|
| (Intercept)            | 6.40009  | 0.09812    | 65.226  | < 2e-16  *** |
| Latitude               | -0.16409 | 0.10793    | -1.520  | 0.13108  |
| Longitude              | -0.92322 | 0.15883    | -5.813  | 5.26e-08 *** |
| mean_temp              | 0.45439  | 0.20821    | 2.182   | 0.031049 * |
| mean_precipitation     | 0.72447  | 0.20473    | 3.539   | 0.000575 *** |
| prec_season            | -0.98249 | 0.15751    | -6.238  | 7.03e-09 *** |
| slope                  | -0.12570 | 0.11105    | -1.132  | 0.259963 |
| mean_temp:mean_precipitation | -0.18363 | 0.09010    | -2.038  | 0.043760 * |
| mean_temp:prec_season  | -0.77997 | 0.14247    | -5.475  | 2.48e-07 *** |
| mean_precipitation:prec_season | -0.34769 | 0.20356    | -1.708  | 0.090235 . |
| mean_precipitation:slope | 0.20269  | 0.12397    | 1.635   | 0.104700 |

**Signif. codes:** 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**Residual standard error:** 1.147 on 124 degrees of freedom

**Multiple R-squared:** 0.2765. Adjusted R-squared: 0.2473

**F-statistic:** 9.476 on 5 and 124 DF. p-value: 1.131e-07

### Skewness

**Coefficients:**

|                        | Estimate | Std. Error | t value | Pr(>|t|) |
|------------------------|----------|------------|---------|----------|
| (Intercept)            | 2.78190  | 0.01619    | 171.799 | < 2e-16  *** |
| Latitude               | 0.01688  | 0.01694    | 0.996   | 0.32096  |
| Longitude              | 0.05538  | 0.01732    | 3.197   | 0.00176 ** |
| mean_temp              | 0.02871  | 0.01753    | 1.638   | 0.10390  |
| mean_precipitation     | -0.05958 | 0.01788    | -3.333  | 0.00113 ** |

**Signif. codes:** 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**Residual standard error:** 1.015 on 119 degrees of freedom

**Multiple R-squared:** 0.4557. Adjusted R-squared: 0.41

**F-statistic:** 9.964 on 10 and 119 DF. p-value: 5.501e-05

### Skewness+ interactions

**Coefficients:**

|                        | Estimate | Std. Error | t value | Pr(>|t|) |
|------------------------|----------|------------|---------|----------|
| (Intercept)            | 2.800172 | 0.018195   | 153.894 | < 2e-16  *** |
| Latitude               | -0.020416| 0.022741   | -0.898  | 0.37116  |
| Longitude              | 0.130593 | 0.029579   | 4.415   | 2.28e-05 *** |
| mean_temp              | -0.064494| 0.035615   | -1.810  | 0.07295  |
| mean_precipitation     | -0.135138| 0.041304   | -3.272  | 0.00141 ** |
| prec_season            | 0.061300 | 0.028120   | 2.180   | 0.03128 * |
| slope                  | 0.034268 | 0.020595   | 1.664   | 0.09884 . |
| sand                   | 0.007016 | 0.022150   | 0.317   | 0.75199  |
| mean_temp:prec_season  | 0.079503 | 0.025505   | 3.117   | 0.00230 ** |
| mean_precipitation:prec_season | 0.104395| 0.047522   | 2.197   | 0.03002 * |
| mean_precipitation:slope | -0.033637| 0.022842  | -1.473  | 0.14357  |
| prec_season:slope      | -0.036113| 0.032406   | -1.114  | 0.26742  |
| prec_season:sand       | 0.048707 | 0.023901   | 2.038   | 0.04384 * |
| slope:sand             | 0.043777 | 0.025423   | 1.722   | 0.08774 . |

**Signif. codes:** 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 0.1729 on 116 degrees of freedom
Multiple R-squared: 0.342. Adjusted R-squared: 0.2683
F-statistic: 4.639 on 13 and 116 DF. p-value: 2.21e-06

Kurtosis

Coefficients:

| Estimate       | Std. Error | t value | Pr(>|t|) |
|----------------|------------|---------|---------|
| (Intercept)    | 1.8873     | 0.1111  | 16.991  | <2e-16 ***|
| Latitude       | -0.1645    | 0.1260  | -1.305  | 0.1944 |
| Longitude      | 0.2749     | 0.1271  | 2.163   | 0.0325 *|
| mean_temp      | 0.2854     | 0.1170  | 2.439   | 0.0161 *|
| prec_season    | 0.2260     | 0.1252  | 1.805   | 0.0736 .|
| sand           | -0.2585    | 0.1205  | -2.145  | 0.0339 *|

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.266 on 124 degrees of freedom
Multiple R-squared: 0.1281. Adjusted R-squared: 0.0 9293
F-statistic: 3.643 on 5 and 124 DF. p-value: 0.004137

Kurtosis + interactions

Coefficients:

| Estimate       | Std. Error | t value | Pr(>|t|) |
|----------------|------------|---------|---------|
| (Intercept)    | 1.936173   | 0.107946| 17.937  | < 2e-16 ***|
| Latitude       | -0.231775  | 0.137831| -1.682  | 0.095228 .|
| Longitude      | 0.521882   | 0.140738| 3.708   | 0.000103 ***|
| mean_temp      | 0.622793   | 0.155102| 4.015   | 0.0000103 ***|
| prec_season    | 0.074760   | 0.127431| 0.587   | 0.558520 |
| slope          | -0.003104  | 0.133272| -0.023  | 0.981459 |
| sand           | -0.231873  | 0.128036| -1.811  | 0.072622 .|
| mean_temp:slope| 0.605646   | 0.223593| 2.709   | 0.007734 **|
| prec_season:slope|-0.623508 | 0.187514| -3.325  | 0.001170 **|

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.215 on 121 degrees of freedom
Multiple R-squared: 0.2167. Adjusted R-squared: 0.1 649
F-statistic: 4.185 on 8 and 121 DF. p-value: 0.0001894

B) Height

Mean

Coefficients:

| Estimate       | Std. Error | t value | Pr(>|t|) |
|----------------|------------|---------|---------|
| (Intercept)    | 4.63717    | 0.03943 | 117.606 | < 2e-16 ***|
| Latitude       | -0.51669   | 0.04585 | -11.268 | < 2e-16 ***|
| Longitude      | 0.23301    | 0.04595 | 5.071   | 1.41e-06 ***|
| mean_temp      | 0.09862    | 0.04129 | 2.388   | 0.0184 *|
| prec_season    | -0.35912   | 0.04437 | -8.094  | 4.54e-13 ***|
| slope          | 0.10326    | 0.04533 | 2.278   | 0.0244 *|

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.4496 on 124 degrees of freedom
Multiple R-squared: 0.7297. Adjusted R-squared: 0.7 188
F-statistic: 66.94 on 5 and 124 DF. p-value: < 2.2e-16

Mean + interactions

Coefficients:

| Estimate       | Std. Error | t value | Pr(>|t|) |
|----------------|------------|---------|---------|
| (Intercept)    | 4.52395    | 0.03533 | 128.042 | < 2e-16 ***|
| Latitude       | -0.46556   | 0.04678 | -9.953  | < 2e-16 ***|
| Longitude      | 0.12123    | 0.06113 | 1.983   | 0.049744 *|
### Variance

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|---------|
| (Intercept)   | 7.5762   | 0.1361     | 55.652  | < 2e-16 *** |
| Latitude      | -1.0569  | 0.1444     | -7.320  | 2.65e-11 *** |
| Longitude     | 0.6818   | 0.1557     | 4.380   | 2.48e-05 *** |
| mean_temp     | 0.2267   | 0.1426     | 1.590   | 0.114 |
| prec_season   | -1.0158  | 0.1530     | -6.641  | 8.56e-10 *** |

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Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.552 on 125 degrees of freedom
Multiple R-squared: 0.5994. Adjusted R-squared: 0.5866
F-statistic: 46.76 on 4 and 125 DF. p-value: < 2.2e-16

### Variance + interactions

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|---------|
| (Intercept)   | 7.4304   | 0.1440     | 51.569  | < 2e-16 *** |
| Latitude      | -0.8386  | 0.1890     | -4.436  | 2.09e-05 *** |
| Longitude     | 0.5063   | 0.1775     | 2.852   | 0.00514 ** |
| mean_temp     | -0.0118  | 0.1993     | -0.59   | 0.55696 |
| mean_precipitation | 0.0317   | 0.0075     | 4.234   | 4.41e-05 *** |
| prec_season   | -1.3011  | 0.2103     | -6.184  | 9.39e-10 *** |
| slope         | -0.1050  | 0.1426     | -0.728  | 0.47387 |
| sand          | 0.1877   | 0.1913     | 0.981   | 0.32854 |
| mean_temp:mean_precipitation | 0.2928   | 0.1475     | 1.982   | 0.04978 * |
| mean_temp:slope | -0.6193  | 0.2927     | -2.115  | 0.03651 * |
| mean_precipitation:prec_season | 0.0495   | 0.3451     | 0.0694  | 0.94594 |
| mean_precipitation:sand | -0.3196  | 0.1240     | 2.576   | 0.01124 * |
| prec_season:slope | 0.7231   | 0.2442     | 2.961   | 0.00371 ** |

---

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.448 on 117 degrees of freedom
Multiple R-squared: 0.6736. Adjusted R-squared: 0.6401
F-statistic: 20.12 on 12 and 117 DF. p-value: < 2.2e-16

### Skewness

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------|----------|------------|---------|---------|
| (Intercept)   | 3.8123   | 0.0068     | 553.777 | < 2e-16 *** |
| Latitude      | 0.0060   | 0.0076     | 0.797   | 0.4267 |
| Longitude     | 0.0004   | 0.0074     | 0.064   | 0.9489 |
| mean_precipitation | 0.0317   | 0.0074     | 4.234   | 4.41e-05 *** |

---

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.448 on 117 degrees of freedom
Multiple R-squared: 0.6736. Adjusted R-squared: 0.6401
F-statistic: 20.12 on 12 and 117 DF. p-value: < 2.2e-16
| Variable                          | Estimate  | Std. Error  | t value | Pr(>|t|)   |
|----------------------------------|-----------|-------------|---------|-----------|
| (Intercept)                      | 3.803854  | 0.007449    | 510.658 | < 2e-16 *** |
| Latitude                         | 0.022997  | 0.009935    | 2.315   | 0.022421 * |
| Longitude                        | 0.024273  | 0.012168    | 2.019   | 0.057170   |
| mean_temp                       | -0.052191 | 0.017888    | -2.918  | 0.004249 **|
| mean_precipitation               | 0.049405  | 0.018612    | 2.654   | 0.009079 **|
| prec_season                      | 0.012271  | 0.012507    | 0.981   | 0.328598   |
| slope                            | -0.006265 | 0.008376    | -0.752  | 0.452408   |
| mean_temp:mean_precipitation    | 0.021378  | 0.007940    | 2.692   | 0.008163 **|
| mean_temp:prec_season            | 0.040736  | 0.010857    | 3.752   | 0.000278 **|
| mean_temp:slope                 | -0.027401 | 0.014976    | -1.830  | 0.069924   |
| mean_precipitation:prec_season   | -0.033039 | 0.019377    | -1.705  | 0.089096   |
| mean_precipitation:slope        | -0.034237 | 0.013392    | -2.557  | 0.011884 * |
| mean_precipitation:sand         | -0.026067 | 0.009597    | -2.716  | 0.007634 **|
| slope:sand                      | -0.016495 | 0.010879    | -1.516  | 0.132241   |

**Kurtosis**

| Variable                          | Estimate  | Std. Error  | t value | Pr(>|t|)   |
|----------------------------------|-----------|-------------|---------|-----------|
| (Intercept)                      | 2.0452    | 0.1022      | 20.012  | < 2e-16 ***|
| Latitude                         | 0.3887    | 0.1069      | 3.635   | 0.000405 ***|
| Longitude                        | -0.2122   | 0.1093      | -1.942  | 0.054432   |
| mean_temp                       | 0.2376    | 0.1106      | 2.148   | 0.033655 * |
| mean_precipitation               | 0.4508    | 0.1128      | 3.996   | 0.000109 ***|

**Kurtosis + interactions**

| Variable                          | Estimate  | Std. Error  | t value | Pr(>|t|)   |
|----------------------------------|-----------|-------------|---------|-----------|
| (Intercept)                      | 2.00532   | 0.10966     | 18.286  | < 2e-16 ***|
| Latitude                         | 0.37655   | 0.13528     | 2.783   | 0.00627  **|
| Longitude                        | -0.42288  | 0.23284     | -1.816  | 0.07190   |
| mean_temp                       | 0.26573   | 0.17372     | 1.530   | 0.12879   |
| mean_precipitation               | 0.25221   | 0.13617     | 1.852   | 0.06652   |
| prec Season                      | -0.01365  | 0.12354     | -0.110  | 0.91220   |
| slope                            | -0.06738  | 0.13876     | -0.486  | 0.62816   |
| mean_temp:mean_precipitation    | 0.31956   | 0.12267     | 2.605   | 0.01038 * |
| mean_temp:prec Season            | 0.45421   | 0.15848     | 2.866   | 0.00493  **|
| mean_temp:sand                  | 0.21389   | 0.12607     | 1.697   | 0.09245   |
| mean_precipitation:slope        | -0.49243  | 0.20046     | -2.456  | 0.01550   |
| mean_precipitation:sand         | -0.41305  | 0.16228     | -2.545  | 0.01222   |
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.118 on 117 degrees of freedom
Multiple R-squared: 0.3968. Adjusted R-squared: 0.3349
F-statistic: 6.413 on 12 and 117 DF. p-value: 1.184e-08