



Trait-Mediated Plant Responses to Environmental Aridity: Linking Functional Characteristics with Ecological Distribution

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ABSTRACT

Plant functional strategies are significantly affected by environmental aridity, but interactions between this and elevation, vegetation condition, climate and soil properties often make it hard to assess the influence of aridity alone. In this study, the relationships among aridity, plant functional characteristics and ecological distribution were investigated based on a comprehensive observational data set for a wide range of plant records throughout China. Functional traits comprised leaf area, plant height, seed size and cone size, and ecological positioning by latitude, longitude, elevation and environmental conditions. Nonparametric comparisons, correlation analysis, generalized additive models, multivariable regression and principal component analysis were used to evaluate trait variation across quartiles of the Aridity Index. All four traits showed significant differences among the aridity classes, and leaf area and plant height were most strongly affected. Aridity had weaker relationships than elevation, which had mostly negative associations with functional traits; NDVI and soil pH were also important. The multivariate Principal Component Analysis (PCA) showed that a principal component axis was dominant, accounting for 56.3% of the total variation and significantly associated with aridity and ecological position. In general, plant functional responses to aridity were observed, but were heavily influenced by other environmental gradients. The results emphasize the need for trait-based integrated approaches in elucidating environmental filtering, functional adaptation, and ecological distribution in the face of increasing climate stress.

Keywords: environmental aridity; plant functional traits; ecological distribution; elevation gradient; principal component analysis

1. Introduction

Environmental aridity is an emerging ecological filter that affects plant performance, community assembly, and species distribution for terrestrial ecosystems. The functional strategies plants use to survive as they become water-limited under environmental stress are becoming more pronounced in many regions due to rising temperatures, changing precipitation patterns and higher moisture requirements in the atmosphere. Not all plants react to these stresses exactly the same, due to variation in morphology, physiology, resource acquisition and stress tolerance among species. Functional traits are thus suitable tools to describe the response of plant characteristics to environmental gradients and their contribution to ecological distribution. It has become easier to investigate such links over large datasets and broad spatial and climatic scales, as large trait databases and comparative ecological studies have been developed (Kattge et al., 2020; Li & Prentice, 2024).

Plant functional traits combine carbon gain, water use, resource conservation, growth and reproduction-related ecological strategies. Structural properties like leaf area, plant height, seed size and others reflect important aspects of plant ecological differentiation. The traits of leaves are often sensitive to environmental stress and may change in a predictable pattern, though there may be inter-species or biome variation (Cui et al., 2020). Climatic variation in leaf traits explains direct climatic impacts as well as multi-dimensional shifts in functional traits, rather than just a single dimension (Dong et al., 2020). Likewise, plant size and architectural characteristics are closely tied to environmental tolerances and resource availability both above- and below-ground, connecting organismal form to environmental tolerance and resource availability (Tumber-Dávila et al., 2022).

There are several pathways by which aridity affects vegetation. A combination of low soil moisture, high vapor pressure deficit, and higher evaporative demand may affect the regulation of stomatal aperture, hydraulic safety, growth, and biomass partitioning. It is important to understand the various components of drought stress because they can act separately from soil water limitation, and to interpret trait responses accordingly (Grossiord et al., 2020; Watson et al., 2023). Associations between stem and leaf traits can control water loss and determine the limits of aridity tolerance for species (López et al., 2021). The persistence of plants along aridity gradients is also affected by functional characteristics of the underground part of the plant affecting water acquisition, storage and nutrient capture (Klímešová et al., 2023). The multi-dimensional responses suggest that interpretation of aridity should not be made without considering other environmental factors.

The distribution and viability of current plant functional strategies could be further altered by climate change. Successful trait combinations in the present could be increasingly at risk due to climatic shifts outside of historical bounds (Andrew et al., 2022). Furthermore, environmental drivers may indirectly influence plant trait expression through other environmental factors, such as nutrient availability and other resource limitations (Guo et al., 2022). Climatic and edaphic factors have been shown to capture large-scale patterns of plant trait variation across the globe, highlighting the critical need to consider both climate and soil when assessing ecological responses (Joswig et al., 2022). This is particularly true for heterogeneous areas where there are interactions between elevation, soil characteristics, vegetation productivity, and aridity. Another prominent environmental gradient that affects functional diversity and trait composition is elevation. Elevation-related changes in temperature, moisture, atmosphere, and soils may cause significant changes in plant strategies and species composition (Qian et al., 2022). In dryland systems, these coupled environmental stresses could foster co-ordinated trait networks, instead of individual trait responses, indicative of an integrated adaptation to multiple resource limitations (Wang et al., 2023). Knowing such co-ordination is important because the actual ecological distribution of most species depends on a combination of characteristics, which interact with climatic and geographic factors, rather than a single characteristic.

Trait-based ecology has gained in popularity, there is still a degree of uncertainty about the relative importance of aridity alone as it relates to the functional characteristics of an organism versus elevation, vegetation condition, and soil properties. Discrimination of univariate trait responses from coordinated multivariate functional strategies and the association of these patterns with ecological positioning along environmental gradients is also needed. These problems provide a way to better understand how environmental filtering, functional adaptation, and the possible redistribution of plant strategies are influenced by future climate change.

Objectives:

- Measure differences in plant functional traits along an environmental aridity gradient.

- Identify the relationships between aridity, elevation, climatic factors, vegetation condition and soil factors with functional trait variability.
- Determine if there is a relationship between coordinated functional trait patterns and geographic and elevational ecological distribution.

2. Materials and Methods

2.1 Study Design and Data Source

The design used in this research was secondary data and observational. The dataset “Elevational patterns and thresholds of plant functional traits across China's biomes” (Zheng, 2026) was used for data acquisition. The total number of plant records used for analysis was 20,774, representing about 176 families and 2,052 genera from a wide geographical and elevational distribution in China. It incorporates taxonomic information, plant functional traits, spatial features, topography, climate data, vegetation indices, soil data, and an Aridity Index, thus offering a suitable platform for assessing trait–environment relationships (Zheng, 2026).

2.2 Study Variables

Aridity was captured by the Aridity Index (AI) as the main variable for environmental aridity and treated as a continuous variable. Leaf area, plant height, seed size and cone size were all considered plant functional characteristics. Ecological distribution was assessed by latitude, longitude, elevation, and with environmental conditions at the occurrence records. The other environmental factors were bioclimatic temperature and precipitation factors, and also Normalized Difference Vegetation Index (NDVI), soil nitrogen, soil phosphorus, soil potassium, total organic carbon and soil pH. The variables were used in this study to see if there is a specific aridity association for functional trait variation, while controlling for other environmental influences.

2.3 Data Preparation and Quality Control

Before performing statistical analysis the data set was screened for blank record, duplicate variables, invariant variable, missing observation, and implausible value. Only one instance of duplicate Aridity Index columns was found, but the invariant site variable was not duplicated since there was no analytical variation with it. Due to significant differences in missingness across functional traits, a trait-specific complete-case approach was used in the analysis of missing data. Seed size and cone size were thus not always available and were limited to the analyses where they were available at all, while leaf area and plant height were given more weighting in the primary analyses due to the greater completeness of data. Where appropriate, continuous variables were standardized for multivariate modelling.

2.4 Descriptive and Comparative Analysis

Descriptive statistics were performed for the Aridity Index, functional traits, elevation, climatic factors and major soil characteristics. Data distribution was used to decide whether to use mean and standard deviation or median and interquartile range with minimum and maximum values for summarizing variables. Functional trait distributions were graphically analyzed by the use of histograms, density plots and boxplots. Aridity Index was also segmented into ordered quantile-based groups, representing contrasting positions along the gradient of aridity, for comparative analysis. Statistically significant overall comparisons were followed by appropriate post hoc tests.

2.5 Trait–Aridity Relationship Analysis

Spearman rank correlation was used to initially assess correlations between aridity and individual traits. Each functional trait was then regressed against the Aridity Index, and the resulting models were used to predict functional traits. Generalized additive models (GAMs) were also employed to look for nonlinear trends and/or threshold responses along the aridity gradient, as plant responses to environmental gradients may be nonlinear. The direction and magnitude of trait–aridity associations were reported using effect estimates, 95% confidence intervals and statistical significance.

2.6 Multivariable Environmental Modelling

To assess if the relationships between aridity and functional traits remained after controlling for other environmental factors, we used multivariable regression models. Climatic, soil, vegetation, geographic and elevational variables were selected as covariates. To prevent multicollinearity, the predictor variables were checked for multicollinearity using the pairwise correlation and variance inflation factors before developing the models. No two predictors were highly correlated. Environmental predictors were compared with respect to the relative contribution of their effects on plant functional variation using standardized regression coefficients.

2.7 Multivariate Functional Trait Analysis

Principal Component Analysis (PCA) was used to find the major dimensions of coordinated variation in

plant functional characteristics. Prior to PCA, functional variables were standardized and only observations with all variables in the models were kept. The principal-component loadings, scores, eigenvalues and percentage variance explained were assessed. PCA scores were then correlated with Aridity Index and elevation to assess if there were systematic environmental gradients in multidimensional functional strategies.

2.8 Functional Traits and Ecological Distribution

Ecological distribution sections were evaluated against plant functional characteristic with the use of latitude, longitude, elevation and environmental occurrence conditions. Trait values and PCA-derived functional scores were studied along geographic and elevation gradients under the two models, regression and generalized additivity model. The plant-record coordinates were also plotted to visualize geographic occurrence patterns. Ecological distribution was inferred as the geographic and environmental location of species occurrences in the data rather than species occupancy or abundance because the data was not standardized as to species abundance or presence/absence and many species had limited occurrence records.

2.9 Integrated Trait–Environment Analysis

A path analysis model to analyze eco-environmental relationships among environmental conditions, aridity, functional characteristics and eco-positioning was designed and integrated together. Standardized direct and indirect effects were calculated to determine if there were functional traits that statistically related changes in environmental aridity with changes in ecological occurrence patterns. These relationships were not causal and were therefore considered as possible mediation pathways, not as causal mechanisms, as the data were not experimental.

2.10 Statistical Criteria

Two-tailed tests of all statistical comparisons were conducted, and a p-value < 0.05 was considered statistically significant. If two or more comparisons were performed, the proper correction was used. Where possible, effect sizes and 95% confidence intervals were reported. All graphics were created using publication-quality resolution with well-defined measurement scales, legends, and axes.

2.11 Ethical Considerations

For this study, no human participants, experimental animals, or manipulation of plant populations were involved, and no new ecological data was collected. So, there was no need for institutional ethical approval. The dataset “Elevational patterns and thresholds of plant functional traits across China's biomes” was only used for scientific secondary analysis following the data use and attribution conditions it had provided, and the data source was mentioned appropriately.

3. Results

3.1 Dataset Characteristics and Environmental Coverage

The final data set consisted of 20,774 plant records from 176 families, 2,052 genera and some 17,049 different genus–species combinations at 3,904 geographic coordinate locations. Elevation ranged from 10 to 5,800 m, with a mean of $2,098.49 \pm 1,155.26$ m. The Aridity Index (AI) varied from 0.000 to 4.757, with a median of 0.739. There was a wide range in plant functional traits along the environmental gradient, as outlined in Table 1. The most complete data were obtained for leaf area (18,455 observations), then plant height (16,725 observations) and followed by cone size (12,417 observations). There were 3,373 observations for seed size.

Table 1. Descriptive characteristics of environmental variables and plant functional traits

Variable	N	Mean	SD	Median	IQR	Minimum	Maximum
Aridity Index	20,774	0.782	0.417	0.739	0.493–1.162	0.000	4.757
Elevation (m)	20,774	2,098.49	1,155.26	1,900.00	1,150–3,000	10	5,800
Leaf area	18,455	0.886	0.830	1.040	0.367–1.483	–2.783	3.989
Plant height	16,725	0.010	0.675	–0.046	–0.456–0.477	–2.398	1.875
Seed size	3,373	–0.520	0.486	–0.561	–0.921– –0.155	–2.000	1.000
Cone size	12,417	–0.075	0.462	–0.097	–0.398–0.204	–2.301	1.829

NDVI	20,774	0.541	0.233	0.648	0.384–0.715	–0.300	0.862
Annual mean temperature, Bio1 (°C)	20,774	11.547	6.996	15.178	6.879–16.200	–12.740	24.196
Annual precipitation, Bio12 (mm)	20,774	916.12	477.31	814.70	572.24–1,322.00	0.00	3,243.02

Note: Functional-trait values are reported on the transformed scale provided in the source dataset.

3.2 Functional Trait Variation Across the Aridity Gradient

To evaluate trait differentiation along the aridity gradient, AI values were divided into four empirical quartiles: Q1, 0.000–0.4933; Q2, 0.4934–0.7385; Q3, 0.7386–1.1624; and Q4, 1.1632–4.7568. As indicated in Table 2, significant differences were found between the AI quartiles for all four functional traits.

The change in Leaf area was the most pronounced between the lowest quartile in AI and the other quartiles. Median leaf area increased from 0.538 in Q1 to 1.215 in Q4, with a significant overall difference, $H = 1,308.44$, $p < 0.001$. The corresponding effect size was $\varepsilon^2 = 0.071$. After correcting the differences, the results of the pairwise comparisons revealed that Q1 was significantly different from all the other quartiles, while Q3 was not significantly different from Q4. This is shown in Figure 1 as an abrupt rise and a subsequent leveling off at higher values of AI.

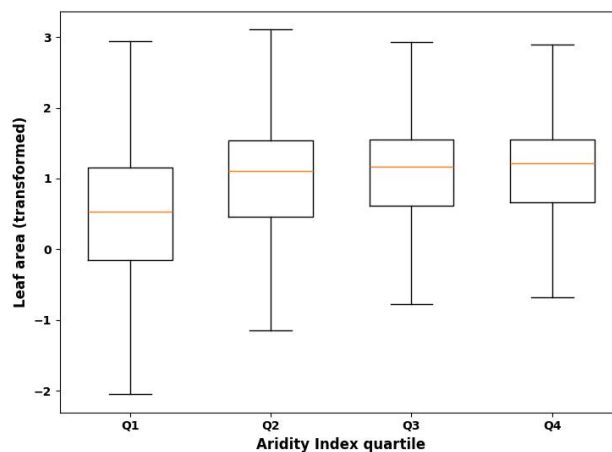


Figure 1. Distribution of transformed leaf area across quartiles of the Aridity Index

Height of plants was similar. Median plant height increased from –0.347 in Q1 to approximately 0.10–0.13 in Q3 and Q4, with $H = 1,259.37$ and $p < 0.001$. The highest effect size of the four traits was for the phenotype "effect size" of $\varepsilon^2 = 0.075$. There was a significant difference between Q1 and all of the higher quartiles while there was no significant difference between Q3 and Q4. This distribution is plotted in Figure 2.

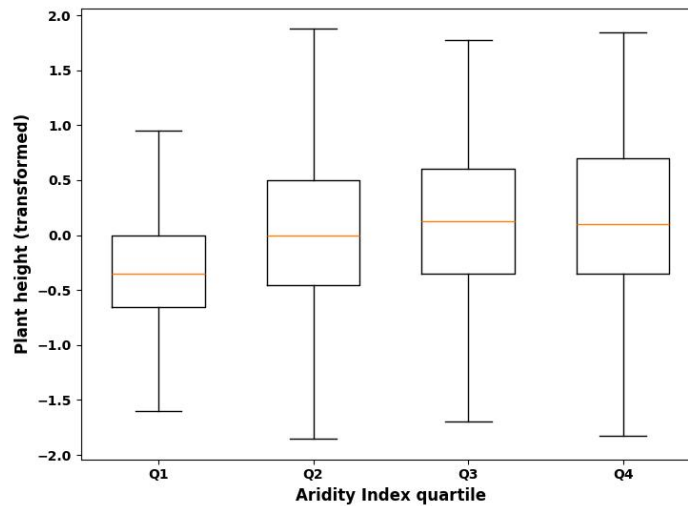


Figure 2. Distribution of transformed plant height across quartiles of the Aridity Index

Seed size also showed significant differences between AI quartiles ($H = 89.12$, $p < 0.001$; $\varepsilon^2 = 0.026$) but to a lesser extent. Median seed size increased from -0.699 in Q1 to -0.415 in Q4. The size of the cone exhibited the smallest, but statistically significant differentiation among the quartiles, $H = 39.94$, $p < 0.001$, $\varepsilon^2 = 0.003$. For both traits of reproduction, there was a large proportion of the detectable difference between Q1 and the higher AI groups.

Table 2. Functional trait variation across Aridity Index quartiles

Trait	Q1, median [IQR]	Q2, median [IQR]	Q3, median [IQR]	Q4, median [IQR]	Kruskal–Wallis H	p- value	ε^2
Leaf area	0.538 [−0.154, 1.154]	1.102 [0.463, 1.538]	1.165 [0.615, 1.546]	1.215 [0.662, 1.556]	1,308.44	<0.001	0.071
Plant height	−0.347 [−0.658, 0.000]	0.000 [−0.456, 0.503]	0.130 [−0.347, 0.602]	0.097 [−0.347, 0.699]	1,259.37	<0.001	0.075
Seed size	−0.699 [−1.000, −0.409]	−0.523 [−0.921, −0.097]	−0.523 [−0.824, −0.046]	−0.415 [−0.824, −0.125]	89.12	<0.001	0.026
Cone size	−0.155 [−0.432, 0.176]	−0.097 [−0.372, 0.230]	−0.125 [−0.347, 0.217]	−0.097 [−0.347, 0.217]	39.94	<0.001	0.003

3.3 Associations Between Functional Traits, Aridity, and Ecological Position

Spearman correlation analysis showed significant correlations between functional traits and AI, elevation, latitude and longitude, as shown in Table 3. Among other values, there was a significant positive correlation between plant height and AI ($\rho = 0.242$), followed by leaf area ($\rho = 0.224$), seed size ($\rho = 0.145$) and cone size ($\rho = 0.042$). Correlations with AI were all significant at the $p < 0.001$ level.

Elevation was more strongly associated with functional traits than was AI. The elevation was negatively correlated with plant height at $\rho = -0.405$, while leaf area and seed size were negatively correlated at $\rho = -0.356$ and $\rho = -0.304$, respectively. The negative elevation relationship was weaker for cone size ($\rho = -0.105$). In addition, there were trends of decreasing functional traits with increasing latitude, while all four traits were positively correlated with increasing longitude.

Table 3. Spearman correlations between functional traits and environmental/geographic gradients

Trait	Aridity Index, ρ	Elevation, ρ	Latitude, ρ	Longitude, ρ
Leaf area	0.224***	−0.356***	−0.305***	0.216***
Plant height	0.242***	−0.405***	−0.310***	0.233***
Seed size	0.145***	−0.304***	−0.212***	0.182***
Cone size	0.042***	−0.105***	−0.089***	0.052***

*Note: ** $p < 0.001$.

The results of the generalized additive modelling also revealed important nonlinear associations between AI and all four functional traits. The amount of variation accounted for by the AI smooth was ~8.1% for leaf area, ~7.7% for plant height, ~3.2% for seed size, and ~0.5% for cone size, and each overall smooth term was significant at $p < 0.001$. These results showed significantly greater structuring of vegetative traits by aridity than of cone size.

3.4 Independent Environmental Drivers of Functional Traits

There was some degree of multicollinearity between annual precipitation and AI, with a variance inflation factor for Bio12 of more than 25 when both variables were included in one model. Bio12 was therefore omitted from the multivariable models and all remaining VIFs were less than 4.1.

Summaries of the adjusted models are presented in Table 4. Elevation continued to be the strongest negative predictor of all four functional traits. Its standardized coefficient was $\beta = -0.327$ for leaf area, $\beta = -0.397$ for plant height, $\beta = -0.245$ for seed size, and $\beta = -0.103$ for cone size, with all effects significant at $p < 0.001$.

NDVI was independent positively related to leaf area with $\beta = 0.210$, plant height with $\beta = 0.169$, seed size with $\beta = 0.094$ and cone size with $\beta = 0.067$. There were negative correlations between soil pH and all four traits.

The influence of AI was greatly diminished after adjusting for elevation and other environmental covariates. AI was a small positive predictor of plant height ($\beta = 0.030$, $p = 0.010$) but not a significant independent predictor of leaf area, seed size or cone size. The adjusted model accounted for 21.6% of the variation in plant height, 19.1% of leaf area, 9.8% of seed size and 1.5% of cone size.

Table 4. Standardized coefficients from multivariable environmental models

Trait	N	R ²	AI β , p	Elevation β , p	pH β , p	NDVI β , p
Leaf area	16,345	0.191	-0.021, 0.052	-0.327, <0.001	-0.114, <0.001	0.210, <0.001
Plant height	14,817	0.216	0.030, 0.010	-0.397, <0.001	-0.098, <0.001	0.169, <0.001
Seed size	2,958	0.098	-0.029, 0.276	-0.245, <0.001	-0.088, <0.001	0.094, 0.008
Cone size	11,092	0.015	-0.019, 0.183	-0.103, <0.001	-0.046, <0.001	0.067, <0.001

Note: Models additionally adjusted for annual mean temperature, soil nitrogen, soil phosphorus, and total organic carbon. Standardized β coefficients are reported.

3.5 Multivariate Functional Trait Structure

All four functional traits were used to create a complete-case PCA, which contained 2,074 observations. PC1 accounted for 56.3% of the total variance of the traits and had positive loadings from the leaf area, plant height, seed size and cone size, suggesting a common multivariate dimension in the magnitude of functional traits. The first two components explained 78.5% of the variance (first two PCs explained 22.1% each). The largest PC1 loadings were for plant height (0.561) and seed size (0.562), followed by leaf area (0.447) and cone size (0.412). The cone-size loading for PC2 was mainly positive (0.727) with leaf-area loading being mainly negative (-0.619) as shown in Table 5.

Table 5. PCA loadings of the four plant functional traits

Functional trait	PC1	PC2	PC3	PC4
Leaf area	0.447	-0.619	0.611	-0.209
Plant height	0.561	-0.229	-0.410	0.682
Seed size	0.562	0.189	-0.449	-0.669
Cone size	0.412	0.727	0.507	0.211
Variance explained (%)	56.3	22.1	13.0	8.5
Cumulative variance (%)	56.3	78.5	91.5	100.0

Figure 3 is a two-dimensional PCA ordination where there was some overlap between the AI quartiles, yet a clear gradient of observations along PC1. Records with higher AI values were found to be positively correlated with PC1 ($\rho = 0.261$, $p < 0.001$).

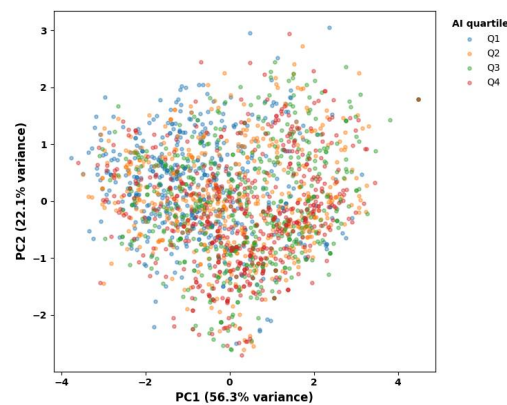


Figure 3. Principal component ordination of leaf area, plant height, seed size, and cone size across Aridity Index quartiles

3.6 Geographic and Elevational Distribution of Functional Strategies

The overall PC1 functional-trait score was clearly related to geographic position and elevation. PC1 was negatively associated with elevation, $\rho = -0.468$, $p < 0.001$, and latitude, $\rho = -0.373$, $p < 0.001$, whereas a positive relationship was observed with longitude, $\rho = 0.287$, $p < 0.001$. Figure 4 shows the geographic patterns in the composition of functional traits in the sampled range, as indicated by the distribution of PC1 scores.

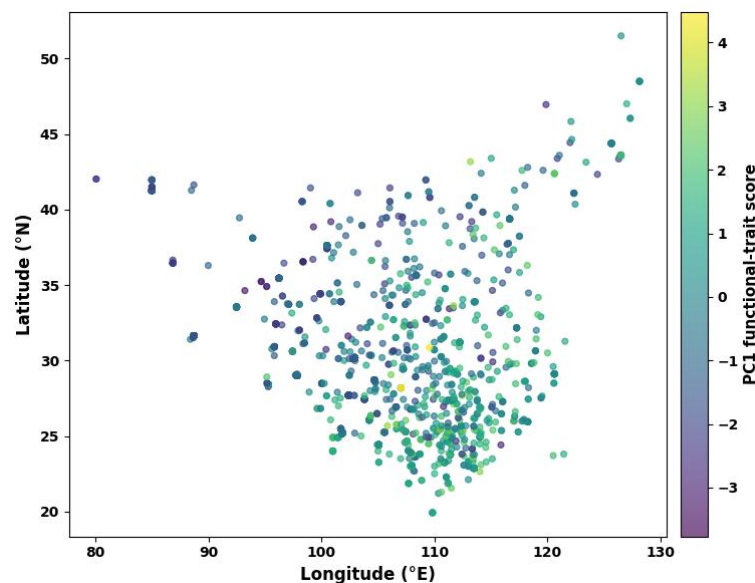


Figure 4. Geographic distribution of the PC1 functional-trait score across plant occurrence coordinates in China

The importance of the elevational relationship was especially evident. As illustrated in Figure 5, scores for combined functional traits were more common at low and intermediate elevation and declined gradually to high elevation. About 23.0% of the variation in PC1 was accounted for by a GAM fitted to PC1 and elevation, and a strong nonlinear relationship between ecological position along elevation gradient and coordinated functional characteristics was evident.

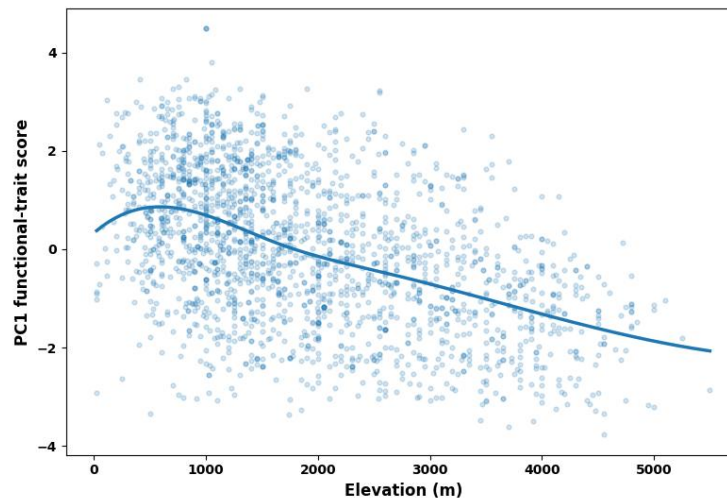


Figure 5. Relationship between elevation and the PC1 functional-trait score

An integrated multivariable model with all four traits accounted for 28.4% of the variance in PC1. Elevation remained the dominant predictor, $\beta = -0.418$, $p < 0.001$, followed by NDVI, $\beta = 0.165$, $p < 0.001$, and soil pH, $\beta = -0.136$, $p < 0.001$. Once these environmental variables were included in the analysis together, AI was not associated with PC1 on its own $\beta = -0.010$, $p = 0.754$. The observed unadjusted trait-AI relationship was however within a wider environmental gradient that was heavily influenced by the elevation, vegetation and edaphic factors.

4. Discussion

In general, the study indicates that plant functional traits are sensitive to aridity gradients, but influenced by larger scale climatic, edaphic, vegetational, and elevational gradients. There were significant differences among Aridity Index quartiles on all traits with the greatest differences being in leaf area and plant height. Seed size and cone size were thus less influenced than vegetative traits. Similar functional composition changes have been documented in other tropical dry forests, where dryness influenced the functional group structure and plant strategies (de Oliveira et al., 2024). A direct response of traits to aridity has also been reported throughout dry forest systems, which bolsters the interpretation that functional traits are related to moisture limitation and associated resource constraint (de Oliveira et al., 2020).

The ecologically more plausible responses are leaf area and plant height, as these traits will have important impacts on light capture, carbon gain, competitive ability, and water use. Drought may cause significant functional trait plasticity, enabling response of populations to changes in water availability (Akman et al., 2021). The drought may also alter the traits that are tolerant to drought to avoidance-based traits (Kramp et al., 2022). In contrast, the same leaf traits have been correlated to survival and community dynamics during severe drought, highlighting their importance in filtering plants in water limiting conditions (Luong et al., 2021). There are also drought-induced coordinated functional changes in cool season grasses (Taleb et al., 2023).

Although there were considerable non-adjusted relationships between AI and all traits, multi-variate analyses indicated that elevation, NDVI, and soil pH had an explanatory effect, and the effect of AI was weakened or not evident for most traits. This finding clearly implies that aridity should not be regarded as a singular driver. Soil hydrology has important effects on the expression of traits, particularly in drylands, where water availability is a function of both climate and soil storage and retention properties (Mens et al., 2023). Similarly, drought evokes different responses in plant root morphologies differing by intensity and plant functional group, emphasizing the significance of belowground modifications for water acquisition (Sun et al., 2024). Given the importance of soil pH and vegetation condition in the current study, this implies a multi-dimensional environmental-filtering framework.

Elevation was the most important negative predictor for leaf area, plant height, seed size and cone size. This discovery suggests that the gradient of the environment may exert greater control on the co-ordinated plant form than high dryness. Alpine research has also shown that functional traits, community composition, and soil processes are reorganized with changes in elevation associated with variations in temperature, moisture, and soils (Schroeder et al., 2024). The interaction between water limitation and elevation can extend to fitness-related traits in mountain plants, as well, during the summer when aridity is a factor (Stanik et al., 2020). The effects are partly responsible for the increased reduction in traits at higher altitudes.

The PCA also indicated that leaf area, plant height, seed size and cone size were on the same multivariate

axis, with PC1 accounting for more than half of the variation in the traits. This coordination suggests that plant responses are organized as cohesive functional tactics instead of as single-trait manipulations. There have been studies of similar coordination between leaf traits under climatic warming in dry systems where several traits change simultaneously to keep the resources in balance (Yu et al., 2022). Trait-network analyses and dryland studies also indicate that environmental stress can alter functional integration and phenotypic diversity (Gross et al., 2024). The organization of such multidimensional traits can affect the distribution and persistence of species in a heterogeneous environment.

The relationship is positive between PC1 and AI, and the highly negative correlation between AI and elevation suggests that the ecological distribution is due to interacting environmental gradients, rather than a linear aridity response. Plants can also adapt functional traits within a species in response to environmental changes such as gradients in aridity (Iozia et al., 2023). At larger scales, aridity is found to interact with plant traits to influence ecosystem functioning in drylands, highlighting that trait-mediated responses have implications beyond the performance of individual species (Eldridge et al., 2024).

Aridity is a factor in functional differentiation, but this effect is influenced by elevation, vegetation productivity and soil characteristics. Interactions of functional strategies are being reflected by stronger responses of vegetative traits and multivariate structure and geographic-elevational patterning of ecological distribution. The results highlight the importance of understanding aridity responses in the context of a multi-dimensional environment and not to assume that pattern of trait variation observed is solely due to climatic dryness.

5. Conclusion

The results of this study indicate systematic changes in plant functional traits along environmental aridity gradients, while also showing that these changes are nested within other elevational, climatic, vegetational and edaphic contexts. In general, Leaf area and Plant height were the most differentiated parameters across Aridity Index quartiles while seed size and Cone size had relatively weaker responses. In unadjusted models, aridity was strongly associated with all four traits, but its independent effects were reduced in models that included other environmental covariates (elevation, NDVI, soil pH). Elevation proved to be the most important negative predictor of functional variation; ecological positioning is thus a key determinant of plant form and strategy. Further, principal component analysis showed a coordinated multivariate trait axis, suggesting that functional characteristics act as integrated ecological strategies, not as individual responses. This trait axis was correlated with aridity, elevation, latitude and longitude which helps to confirm the close relationship of plant functional organization to ecological distribution. In summary, the study indicates that aridity is a factor which promotes trait-mediated differentiation, although this is strongly modulated by interacting environmental gradients. The results highlight the importance of trait-based methods that account for multiple traits when elucidating plant adaptation, environmental filtering and shifting ecological distributions in response to changing climate and landscape conditions in today's spatially and environmentally variable terrestrial ecosystems around the world.

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