

RESEARCH

Open Access



Functional trait response to aridity based on leaf trait network analysis in the Hexi Corridor, China

Yingxiang Miao^{1†}, Haifeng Liu^{1†}, James F. White³, Guoqiang Wu¹ and Shanjia Li^{1,2*}

Abstract

Background Aridity acts as a strong environmental filter for plants and is predicted to intensify in the future, resulting in changes to leaf functional traits. However, few studies explore how interactions of multiple traits result in leaf trait tradeoff strategies along an aridity gradient, and whether trait separation occurs with increasing aridity intensity. This study examines the impact of long-term aridity on 14 plant leaf traits in two arid areas (arid and hyper-arid) in the Hexi Corridor, China. A leaf trait network (LTN) was constructed to study how leaf trait tradeoff strategies differ between the two areas. Structural equation modeling (SEM) was used to identify the direct and indirect effects of aridity and functional diversity (as measured by community weighted means and functional dispersion) on leaf nutrient concentration.

Results LTN shows trait separation, poor synergy among traits, and low resource utilization. Correlation analyses showed that the mass ratio hypothesis is dominant, and aridity is positively correlated with leaf relative water content (RWC) and leaf phosphorus content, and negatively correlated with leaf nitrogen content (LNC). SEM results indicated that LNC is directly affected by aridity, RWC, leaf carbon content, and plant height. Aridity and functional dispersion directly affects leaf phosphorus content.

Conclusions Results indicate that increasing drought weakens plant coordination among specific traits, and the main change in plant trait tradeoff strategies is reflected in the separation of nutrient traits. Exploring the change of the tradeoff among traits along the aridity gradient can better understand the adaptation process of plants to aridity and the process of community function change.

Keywords Aridity, Trait tradeoff strategy, Leaf trait network, Community weighted means, Structural equation model, Hexi Corridor

Introduction

As aridity increases due to climate change, it is crucial to understand how plant traits and ecosystem functions shift along aridity gradients, especially in drylands [1, 2]. Drylands already cover a significant portion of Earth's ecosystems, and their extent is expected to increase with further climate change. Increasing aridity is known to drive shifts in plant trait values, particularly in traits related to water use efficiency and nutrient acquisition [3]. To better understand how traits covary under aridity, it is essential to examine functional traits through

[†]Yingxiang Miao and Haifeng Liu contributed equally to this work.

*Correspondence:

Shanjia Li

lishanjia@lut.edu.cn

¹ School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou 730050, China

² Key Laboratory of Land Surface Process and Climate Change in Cold and Arid Regions, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

³ Department of Plant Biology, Rutgers University, New Brunswick, NJ 08901, USA



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

community metrics such as CWM and FDis. [4]. Two key community metrics, CWM and FDis, are commonly used to describe the functional traits of biological communities [5]. CWM provides insight into the dominant traits in a community [6], capturing how environmental factors, such as aridity, influence trait shifts in response to selection pressures [4]. The mass ratio hypothesis suggests that the traits of dominant species determine the impact of plant communities on ecosystems [7, 8]. Functional dispersion (FDis) measures the average distance between a species and others in a trait space, which reflects the extent of functional differences among communities [9] and how traits change along ecological gradients [10, 11]. The niche complementary hypothesis says that high functional dispersion means high niche differentiation, with species using different strategies for resources [12–14]. As aridity increases, vegetation structure [10, 15], composition [9, 16–18], and plant strategies adapt [19, 20], with significant effects on key elements like carbon, nitrogen, and phosphorus in desert ecosystems [21–24]. Aridity is a key environmental filter that influences ecosystem processes, community structure [25–27], and plant trait strategies, shifting from resource acquisitive to resource conservative strategies [28, 29], yet few studies examine how these strategies change along an aridity gradient.

Functional traits are essential for evaluating plant adaptations, particularly in response to aridity, and provide insights into shifts in resource acquisition strategies [30], and leaf functional traits determine the rate of plant resource capture and utilization, they are variations can reflect patterns of resource allocation or trade-offs among different plant strategies [31]. Plant trait network analysis (PTNs) can be used to test hypotheses for how trait correlations may shift across communities that differ in climate, species, functional richness and/or productivity. PTNs can quantify the overall structure of trait networks that constitute the functional strategies of populations, species, or communities, providing a means for integrating trait functions at larger scales. In these networks, traits are visualized as ‘nodes’ and statistical correlations between traits as connections. This method can calculate parameters that describe the connectivity and complexity of the network, including the design of characteristic functional modules [32]. Recent studies highlight the potential of leaf trait networks (LTNs) to visualize and quantify the relationships among plant traits, especially in response to environmental stressors like aridity [32–34]. Plants can adapt to drought according to multiple strategies (‘avoidance’ or ‘resistance’) adaptation to lower resources or stress would tend to result in a greater independence of traits, and fewer trait correlations. Topological roles of traits in LTN were identified by three node

parameters: degree, closeness and betweenness [35]. The hub trait with a higher degree and closeness means that it has many connections with other traits and has a strong effects on the phenotype of the overall plant community [34]. To quantify the complex relationships between traits by four overall parameters diameter, average path length, average clustering coefficient, and modularity, LTNs provide insights into trait interdependence and segregation across environments. Sub-networks, or modules in LTNs, with strong internal trait connections and minimal external links, suggest the formation of independent trait dimensions, which may reflect functional separation under varying environmental conditions [36]. Consequently, LTNs can test shifts in correlative traits occurring across environments that are decoupled in moister regions but coupled in drier regions [37, 38].

The changes in plant functional traits in arid ecosystems are closely related to global climate gradients. For example, in a study conducted in China, as the latitude changes from cold northern forests to warm, moist tropical forests, the connectivity and complexity of PTNs gradually increase, and species richness also increases accordingly [39, 40]. This trend aligns with our understanding of plant functional traits in arid regions, where plant communities exhibit different functional characteristics under increasing aridity, which may influence the overall function of the ecosystem. Furthermore, global-scale studies have found that for woody plants, the connectivity and complexity of trait networks are lower in polar regions, which is consistent with the trends of trait separation and functional changes in arid ecosystems, suggesting that plant functional traits may be more limited under extreme climatic conditions [34]. The communities in more arid environments show a lower degree of phenotypic integration, consistent with the aforementioned studies [41]. By integrating these studies, we can better understand how plant functional traits change under different climatic conditions, especially the characteristics of trait networks in extreme environments such as arid regions, and their impact on ecosystem function.

The Hexi Corridor is a typical arid region in northwest China with a decreasing precipitation gradient running from southeast to northwest. It is a typical desert ecosystem, and is characterized by limited precipitation and low vegetation cover [24], which consists mainly of annual and perennial species [42]. The elucidation of network of plant functional traits in desert ecosystems is important to clarify the response of the ecosystem to the increasing stress of drought. Here, we constructed a LTN and used structural equation modeling (SEM) to evaluate variation in trait tradeoff strategies occurring with increasing aridity and to identify potential effects of aridity on leaf functional traits in the drylands of the

Hexi Corridor. We propose two hypotheses: 1) Trait segregation occurs in LTNs with increasing aridity, driven by shifts in hub traits such as total water content to leaf succulent degree, and the functional separation of leaf nitrogen and phosphorus content. 2) CWM more effectively explains trait segregation and ecosystem function changes than FDis, as it is strongly associated with aridity and reflects shifts in specific traits such as leaf relative water content, nitrogen, and phosphorus content.

Materials and methods

Study area and aridity gradient

This study was carried out in Hexi Corridor (appx. 27.6×10^4 km²), Gansu Province, China, extending from southeast to northwest. The study area is located at 37°38′–40°36′ N, 94°55′–103°39′ E, and elevation in this region ranges from 1067 m – 1790 m. The sampling sites were set up along the decreasing precipitation gradients (southeast to northwest) of the Hexi Corridor. Field data were collected from 15 dryland sites dominated by annual and perennial species along a regional aridity gradient, comprising hyper-arid and arid areas (Fig. 1).

We used the aridity index (AI) to describe the aridity gradient. AI data from 1970–2000 were retrieved from the Global Aridity Index and Potential Evapotranspiration Climate database (<https://cgiarcsi.community/data/global-aridity-and-pet-database>) [43, 44]. The aridity

level of each site was calculated as $1 - AI$ and ranged from 0.84 to 0.98 [45]. Mean annual precipitation (30 yrs. Average; <https://worldclim.org/data/worldclim21.html>) varied from 39 to 260 mm (mean: 125 mm), and mean annual temperature (30 yrs. Average) varied from 5°C to 10°C (mean: 7.8°C).

To minimize the potential impacts of human activity and other disturbances on soil and vegetation, only sampling sites under pristine or unmanaged conditions and without visible signs of domestic animal grazing, grass/wood collection, engineering restoration, or infrastructure construction were selected. Sampled soil was dry and sites had not received precipitation for at least 3 days prior to sampling. According to the aridity index, the sampling sites encompass two aridity types: arid and hyper-arid. The arid area ($0.8 < AI < 0.95$) is characterized by loamy desert soil and is dominated by perennial species *Reaumuria songarica*, *Artemisia sphaerocephala*, and *Calligonum mongolicum* followed by annual species *Bassia dasyphylla*. The hyper-arid area ($AI > 0.95$) is characterized by a mix of gravel and loamy desert soil and is dominated by perennial species *Lycium ruthenicum*, *Hexinia polydichotoma*, and *Phragmites australis*. The selected plant species were validated by Prof. Shanjia li, and voucher specimens were deposited in the Herbarium, Institute of Botany, Chinese Academy of Sciences. The species information is detailed in Table A1.

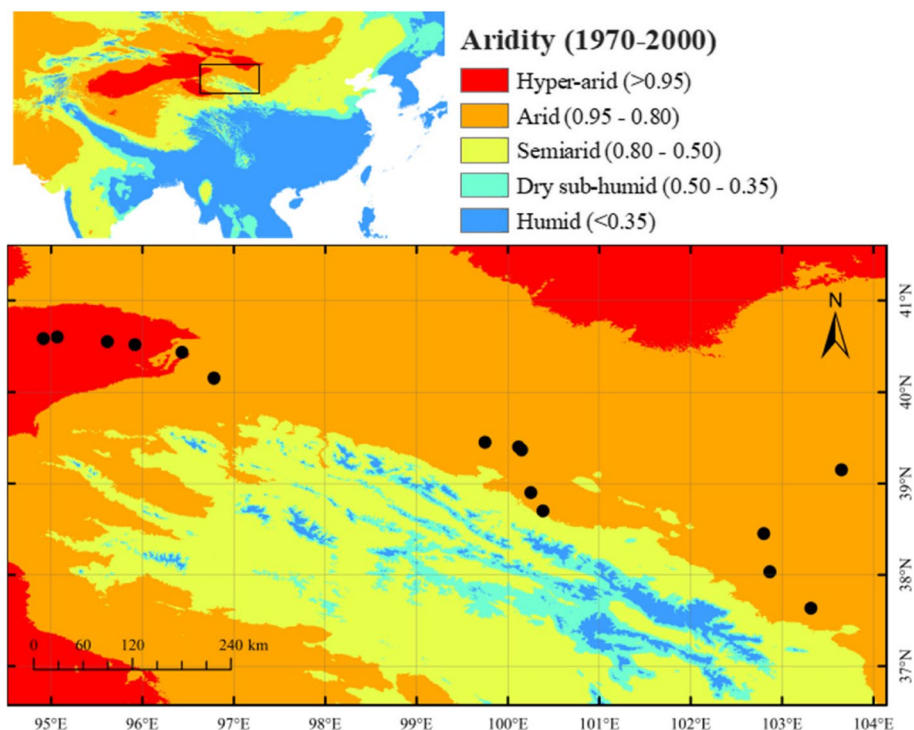


Fig. 1 Map with the location the study sites along the aridity gradient

Vegetation sampling

Vegetation sampling was conducted at the peak of standing biomass from August–September 2020. At each site, five 20 m × 20 m quadrats were established, each separated by 10 m. Three 5 m × 5 m plots were randomly selected from each quadrat, and the density, coverage and height of plants were recorded. We calculated the importance value of each plant plot with the formula: importance value = (relative density + relative coverage + relative height)/3 [46]. Finally, leaves of 27 dominant species with important values > 0.1 in various communities were sampled. 10–30 leaves of each species with good growth, no disease or insect bites were randomly collected, put them into plastic bags in the incubator, and take them back to the laboratory for analysis and testing. We used a soil sampler to randomly collect 3–5 soil samples at depths between 5–20 cm. We sampled a total of 225 plots in 75 quadrats.

Leaf functional traits and functional diversity

Functional traits associated with leaf and plant growth of dominant species (27 species total) were measured for 10–30 leaves belonging to each species in each plot across both desert types. Fresh weight (*FW*) was determined immediately after the samples were brought back to the laboratory, and dry weight (*DW*) was recorded after the samples were dried to constant weight at 75°C. After soaking in deionized water for 4 h, wipe the moisture off the leaf surface with a tissue and measure its saturation weight (*SW*). Leaf bound water (*BW*) and leaf free water (*FW*) were determined by Singh [47]. Specific leaf area was the leaf area per dry mass and determined by scanning fresh and flat leaves and using the ImageJ software. Specific leaf volume (*SLV*) was the leaf area per dry mass and measured by the drainage method. Total water content (*TWC*) = (*FW* - *DW*)/*DW*. Leaf relative water content = (*FW* - *DW*)/(*SW* - *DW*) × 100. Leaf dry matter content = *DW*/*SW* × 100. Leaf thickness was measured using a vernier caliper. Leaf succulent degree was the weight of the leaf per unit area. Leaf carbon content (*LCC*) was determined using the potassium dichromate-sulfuric acid method. Leaf nitrogen content (*LNC*) was measured by an semi-automatic Kjeldahl nitrogen analyzer (Hanon K9840, Jinan, China). Leaf phosphorus content (*LPC*) was determined using molybdenum antimony colorimetry. Other traits are *BW*/*FW* and plant height. These Functional traits were determined using methods described by Cornelissen and Perez-Harguindeguy [48, 49]. All abbreviations with plant traits are detailed in Table A2.

Soil properties

Soil organic carbon (*SOC*) was determined using the external heating method of potassium dichromate. Alkali-hydrolyzed nitrogen (*AN*) and total nitrogen (*TN*) were determined using the diffusion method, and the semi-automatic Kjeldahl procedure on an auto analyzer (Hanon K9840, Jinan, China), respectively. Total phosphorus (*TP*) and available phosphorus (*AP*) were determined using molybdenum antimony colorimetry after NaOH melting and 0.5 mol·L⁻¹ NaHCO₃ extraction, respectively. Total potassium (*TK*) and available potassium (*AK*) were determined using flame spectrophotometry after NaOH melting and 1 mol·L⁻¹ NH₄OAc extraction, respectively. Soil moisture content (*SW*) was determined using the drying method. Electrical conductivity (*Ec*) and pH were determined using a PHS-3D pH meter produced by Shanghai Precision Scientific Instruments Co., LTD [50]. These soil properties were determined using methods described by Zhang [51]. All abbreviations with soil properties are detailed in Table A2.

Construction and parameters of leaf trait networks

According to the construction method proposed by He [32], a leaf trait network was constructed by taking traits as nodes and the relationships between traits as edges. Plant trait tradeoff strategies were quantified using Pearson correlations among leaf traits. To avoid considering spurious correlations among traits, we selected a threshold ($|r| > 0.2$, $P < 0.05$) to determine whether there was a correlation between traits. All correlations above the threshold were set to 1 and those below the threshold were set to 0, yielding the adjacency matrix $A = [a_{ij}]$ with $a_{ij} \in [0, 1]$. Positive and negative correlations in the adjacency matrix were also assumed to indicate synergistic and trade-off relationships, respectively.

We calculated degree (K_i), closeness (C_i), and betweenness (B_i) to identify the topological roles of different traits in LTN. Degree quantifies all the edges that connect the trait. The trait with a high degree in the trait network represents that it is more connected to other traits, is considered as the hub trait in the trait network. Closeness is the reciprocal of the mean shortest distance between the trait and all other traits. The traits with high closeness are closely related to other traits. Betweenness is the number of all shortest distances that pass through the trait. The higher betweenness of a trait means that the trait is a bridge connecting functional modules and can coordinate the relationship among functional modules. The specific parameter calculations are as follows:

$$K_i = \sum_{j \neq i} a_{ij}$$

where K_i is the degree of trait i , a_{ij} is the strength of the relationship between trait i and j .

$$C_i = \frac{n-1}{\sum_{j=1}^{n-1} d_{ij}}$$

where C_i is the closeness of trait i , d_{ij} is the shortest distance between trait i and j , and n is the number of traits in trait network.

$$B_i = \sum_{jk} \sigma(j, i, k)$$

where B_i is the betweenness of trait i , (j, i, k) is the number of shortest distances between trait j , and trait k that crossed trait i .

To describe the overall topological relationship of LTN, we calculated two parameters to quantify its tightness, namely diameter (D) and average path length (AL), and two parameters to quantify its complexity, namely average clustering coefficient (AC) and modularity (Q). Diameter and average path length quantify the tightness of trait network. Diameter is the maximum and shortest distance between any two connected traits in the trait network. Average path length is the mean shortest path between all traits in the trait network. Lower diameter and average path length mean better synergy between traits, which make plants more efficient in resource use or production. Average clustering coefficient and modularity quantify the complexity of trait network. Average clustering coefficient is the average clustering coefficient of all traits, where the clustering coefficient of the trait is the ratio between the number of actual connected edges and the maximum number of theoretical connected edges among all adjacent traits of the trait. The higher the average clustering coefficient, the better the synergy among the traits, and the higher the differentiation of the leaf function. Modularity is used to quantify how well a trait covaries, and how well it is separated between different functional modules. A higher modularity means that the module is more connected internally, less connected externally and has more functional modules. The specific parameter calculations are as follows:

$$D = \max\{d_{ij}\} (i \neq j)$$

$$AL = \frac{1}{n(n-1)} \sum_{i \neq j} d_{ij}$$

where D and AL are the diameter and average path length of trait network, respectively, d_{ij} is the distance between trait i and j , and n is the number of traits in trait network.

$$AC = \frac{1}{n} \sum_{i=1}^n \frac{2l_i}{t_i(t_i-1)}$$

where AC is the average clustering coefficient of trait network, l_i is the number of edges between adjacent traits of trait i , and t_i is the number of adjacent traits of trait i .

$$Q = \frac{\sum \left[\left(A_{ij} - \frac{k_i k_j}{2m} \right) \tau \right]}{2m}$$

where Q is the modularity of trait network, m is the number of edges, A_{ij} is the element of the A adjacency matrix in row i and column j , k_i is the degree of i , k_j is the degree of j , if j is the same as i , then τ is 1, otherwise it's 0.

We evaluated the stability of the trait centrality by using case-dropping bootstrap, with resampling times $n = 1000$ in each step of case dropping, and computed the resulting average correlations. Correlation Stability coefficient (CS-coefficient) was used to assess this stability, indicating the maximum percentage of cases that could be randomly dropped while retaining results comparable to the original with a correlation coefficient on average above 0.7 (a default threshold) with a 95% confidence interval. These examinations were facilitated by the “BOOTNET” R package [52].

Statistical analysis

The LTN was constructed and visualized using the “igraph” package [53] in R. To obtain uncertainty ranges of these parameters, we randomly resampled plant species 9999 times, and an LTN was established for each bootstrapping. Multi-trait FDis was computed for three leaf traits (RWC, LNC and LPC) that are closely associated with aridity [54]. All calculations of functional diversity metrics were done using the dbFD function of the “FD” package [55] in R [56]. We also tested the significance of Spearman correlations among single-trait CWMs and FDis, multi-trait FDis, aridity, and soil properties, and used the chart. Correlation function of the “PerformanceAnalytics” package [57] for correlation analysis in R. We created an initial SEM (Figure A6) and analyzed the direct and indirect effects of aridity, single-trait CWM, and multi-trait FDis functional metrics. The best-fit SEM model was assessed using the Chi-square test (χ^2), Root mean square residual (RMR), the Root mean square error of approximation (RMSEA), Comparative fit index (CFI), and the Tucker-Lewis index (TLI), we used the AMOS 26.0 package to perform SEM and determine χ^2 , RMR, RMSEA, CFI and TLI [58].

Results

The diameter, average path length, average clustering coefficient, modularity, and number of modules in the LTN varied across arid and hyper-arid areas (Fig. 2a–c, Table 1). The hyper-arid area had a larger diameter (3), average path length (1.60), and modularity (0.09), but lower average clustering coefficient (0.58) than the arid area (Table 1). However, the total area had the lowest average path length (1.35). In total area, total water content showed the highest connectivity (*i.e.*, the best degree, closeness, and betweenness), followed by leaf dry matter content (Figure A1a, d, j), but leaf nitrogen and phosphorus content were not significantly associated with other modules. In the arid area, total water content showed the highest connectivity, followed by leaf carbon content, leaf dry matter content (Figure A1b, e, h). In the hyper-arid area, leaf succulent degree, showed the highest connectivity, followed by specific leaf volume, total water content, leaf dry matter content (Figure A1c, f, i), but leaf phosphorus content was the only module that was not significantly associated with other modules.

A CS-coefficient over 0.35 indicates a high reliability of trait degree closeness and betweenness of arid and

Table 1 Variation in leaf trait network-level parameters between arid and hyper-arid areas

Area	Diameter	Average path length	The average clustering coefficient	Modularity
Arid areas	2	1.58	0.64	0.07
Hyper-arid areas	3	1.60	0.58	0.09
Total areas	2	1.35	0.74	0.05

total areas. The trait degree closeness and betweenness of hyper-arid areas showed a somewhat more sensitive response to case-dropping, with a CS-coefficient less 0.1 (Figure A2).

CWM analysis found that aridity was positively correlated to leaf relative water content, leaf phosphorus content, AN ($P < 0.05$), and TN ($P < 0.05$), and was negatively correlated with leaf nitrogen content (Fig. 3, $P < 0.05$). Leaf nitrogen content was negatively correlated with leaf carbon content ($P < 0.01$), leaf relative water content, leaf phosphorus content, height, and TN ($P < 0.05$). Leaf

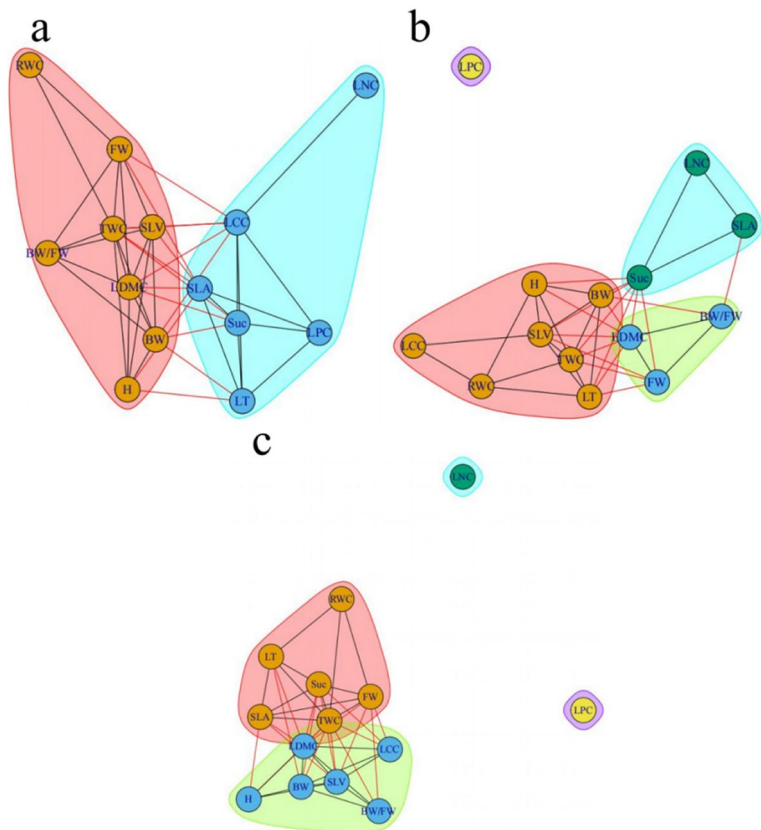


Fig. 2 LTN for fourteen functional traits in arid and hyper-arid areas (**a**, arid area; **b**, hyper-arid area; **c**, total area). Different colors distinguish different functional modules

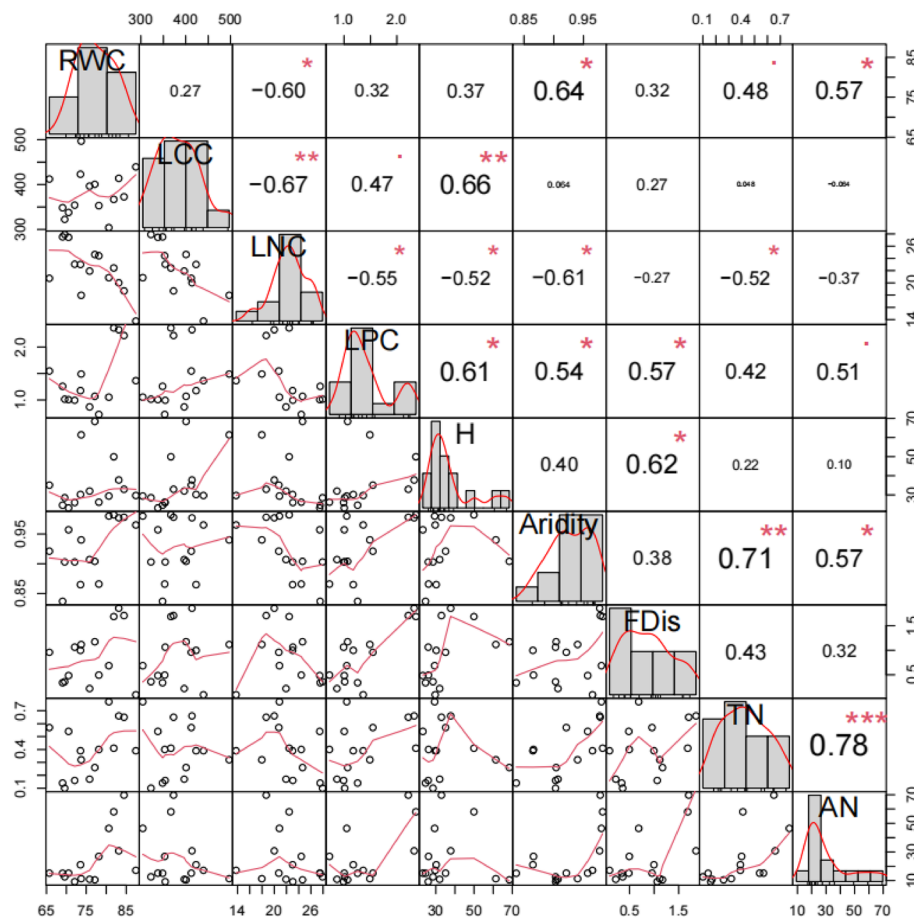


Fig. 3 Spearman correlations of aridity, multi-trait FDis, single-trait CWMs and soil properties. See Figure A3 and A4 for more information on soil properties and functional traits

carbon content was positively correlated with height ($P < 0.01$). Leaf relative water content was positively correlated with AN ($P < 0.05$). Spearman correlations of soil properties and functional traits are presented in Figures A3 and A4. Multi-trait FDis was positively associated with leaf phosphorus content and height (Fig. 3, $P < 0.05$). Single-trait FDis did not have significant correlation with aridity (Figure A5).

The model that included aridity, FDis, leaf relative water content, height, leaf phosphorus and carbon content was the best fit $\chi^2 = 1.44$, $P = 0.99$; RMR = 0.04; RMSEA = 0.00; CFI = 1.00; TLI = 1.49 (Table A3) and explained 86% of the variance in leaf nitrogen content (Fig. 4). SEM showed that aridity, leaf carbon content, and leaf relative water content had a negative direct impact on leaf nitrogen content (Table 2). Increasing aridity directly increased leaf relative water content and leaf phosphorus content, but did not affect FDis. FDis had positive direct impacts on leaf phosphorus content and positive indirect impacts on leaf nitrogen content via positive influence on height and leaf carbon content. Increasing height directly

increased leaf carbon and nitrogen content but its negative total impact on leaf nitrogen content (Table 2).

Discussion

As a hub trait of plant response to aridity, leaf succulent degree refers to the amount of water storage capacity in the leaves themselves, high leaf succulent degree is usually a typical characteristic of slow-growing or pressure-tolerant species, low leaf succulent degree is a typical characteristic of fast-growing species [17]. As aridity intensifies, the hub trait of LTN changes from total water content to leaf succulent degree. This shift suggests that plants in hyper-arid regions rely more on water storage in their leaves to cope with prolonged drought conditions. A high leaf succulent degree allows plants to store more water, helping them endure dry periods. This trait indicates plants' ability to thrive under stress, suggesting that in hyper-arid areas, ecosystem services related to water retention, carbon sequestration, and biodiversity maintenance are potentially enhanced by the prevalence of succulent species. Although hub traits varied with

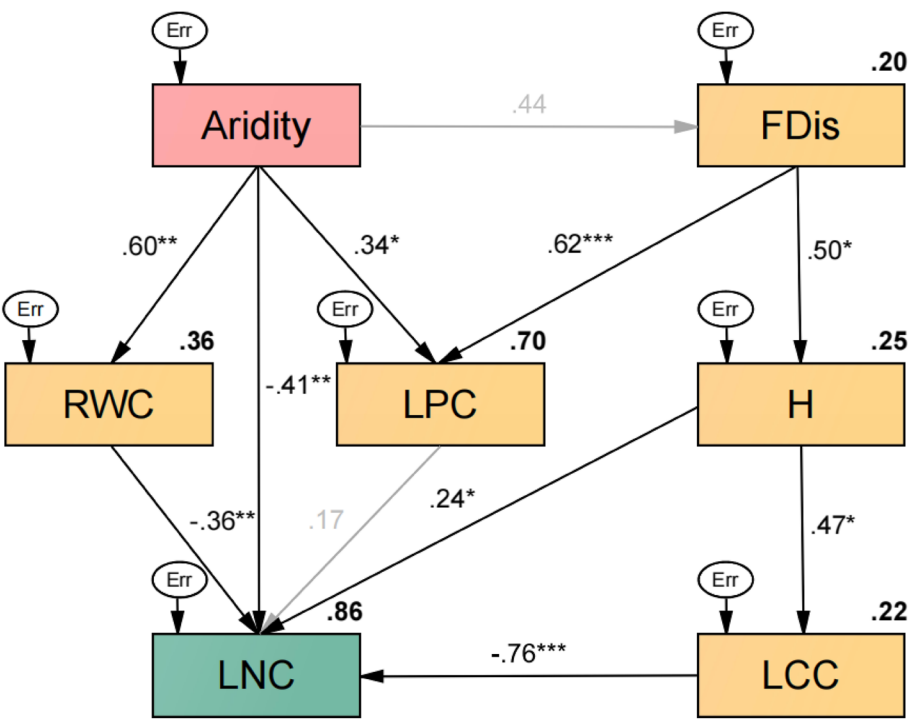


Fig. 4 SEM accounting for direct and indirect relationships of aridity, single-trait CWMs, and multi-trait FDis functional metrics. Note: Single headed arrows indicate paths. The unexplained error is indicated by “Err.” Numbers on paths represent standardized regression weights. Total explained variance (R^2) of variables is listed on the top right corner of each rectangle. *, **, and *** indicate significance along the paths at levels of $P < 0.05$, $P < 0.01$, and $P < 0.001$

Table 2 The total, direct, and indirect standardized effects on LNC from the structural equation model

Predictor	Pathways	Effect	Predictor	Pathways	Effect
Aridity	Direct	−0.415	LPC	Direct	0.173
	Indirect	−0.138		Indirect	NS
	Total	−0.553		Total	0.173
FDis	Direct	NS	LCC	Direct	−0.758
	Indirect	0.048		Indirect	NS
	Total	0.048		Total	−0.758
H	Direct	0.237	RWC	Direct	−0.363
	Indirect	−0.358		Indirect	NS
	Total	−0.121		Total	−0.363

NS Non-significant relationships

aridity, total water content and leaf dry matter content were consistently at the center of leaf trade-off strategies. Total water content represents the total amount of water stored in the plant, while leaf dry matter content refers to the accumulation of non-water substances in the leaves, which reflects the plant’s biomass. In arid environments, plants need to maintain adequate water storage (total water content) while also ensuring enough leaf dry matter content to sustain photosynthesis, drought resistance,

and growth. The stability of total water content and leaf dry matter content indicates that these two traits are critical for plant growth, survival, and adaptation to drought. They help regulate plant physiological functions through water and biomass management, thus affecting overall ecosystem stability. The result suggests that total water content and leaf dry matter content are coupled [41], meaning there is a stable correlation between the two (Figure A4). The coupling may represent an adaptive strategy that plants can efficiently cope with water scarcity by regulating these traits together.

Network parameters revealed weak synergistic interactions among traits, the utilization rate of plant resources and production efficiency were lower in the hyper-arid area [32]. The relationship between the functional modules is weak, but the internal relationship is close, and there are functional differences between the functional modules [59]. In both the total and hyper-arid areas, the LTN separated two separate modules (leaf nitrogen and phosphorus content), which is different from the study of [33]. As aridity increased, plants shift from a unified trait strategy (e.g., combined nitrogen and phosphorus management) toward specialized and separated vegetative trait strategies. This independence allows plants to optimize their nutrient-use strategies based on specific

resource availability. Such changes reflect the plants' adaptive responses to optimize limited resources (water and nutrients), increasing their drought tolerance. This specialized modularization of traits influences critical ecosystem services in arid areas, such as nutrient cycling efficiency and soil stabilization. On the one hand, a clear division of nutrient-related traits allows plants to maximize survival and growth under harsh conditions, indirectly maintaining ecosystem function despite limited resources [22]. On the other hand, low network connectivity does not indicate functional irrelevance [60]. Resource availability, plant size, economic efficiency, and element concentration limit the traits of any plant organ, so traits are coordinated to some extent [61]. These findings suggest that increasing aridity may compromise ecosystem functions related to nutrient cycling and water use efficiency.

Spearman correlation analyses showed that CWM, but not FDis, was significantly associated with aridity, supporting the importance of CWM functional metrics in plant community responses, a finding that diverges from those of [4]. Aridity resulted in shifts in mean trait values along the gradient and directly affected leaf relative water, nitrogen and phosphorus content. Therefore, aridity was one of the important drivers of dominant species traits reflected by CWMs. This is consistent with previous findings that CWM traits determine ecosystem function [62], thus supporting the mass ratio hypothesis. Leaf relative water content is an important indicator of plant water status and, as other work has found, it increases with aridity intensification [16], indicating that plant drought tolerance increases due to water limitation [28]. Consistent with work by Xiong et al. [22], leaf phosphorus content was positively correlated with aridity, which may explain why leaf phosphorus content was separated trait in LTNs. Leaf nitrogen content is negatively correlated with aridity and TN, indicating that variation in aridity influences leaf element variation more than soil properties do. It is possible that the gravelly soils in our study area have high element concentrations, but that these nutrients are inaccessible to plants [41]. Leaf carbon content and plant height showed no significant correlation with aridity, consistent with global analyses such as those conducted by Delgado-Baquerizo et al. [23], likely due to physiological trait diversity among perennial species. While Spearman correlations yield simplified trait associations, structural equation modeling (SEM) offers deeper insight into trait trade-off strategies under arid conditions [63].

The separation path of leaf nitrogen content and leaf phosphorus content was determined by SEM results. As aridity intensifies, the dominant species are mainly perennials. According to the mass ratio hypothesis, the

traits of the dominant species can largely represent the influence of the community on the ecosystem function. Leaf relative water content is negatively correlated with leaf nitrogen content in the direct path, which is consistent with the studies of Gong et al. [64]. The reason may be the dominant species leaves respond directly to water stress by increasing leaf relative water content, thus reducing transpiration rate, closing stoma, reducing photosynthesis and carbon dioxide absorption, yellowing leaves, affecting chlorophyll synthesis, and further reducing leaf nitrogen content [16, 65, 66]. Moreover, total carbon fixation depends strongly on the availability of nitrogen, especially when plants are exposed to drought conditions [67]. Compared to leaf nitrogen content, multi-trait FDis can better explain increases in leaf phosphorus content and height, it indicated that rapidly growing perennial species were functionally similar, sharing traits adapted to aridity [4, 68], a strategy that results in reductions in leaf nitrogen content. Through the aridity and plant trait tradeoff, the separation traits are correlated with nutrient concentration, which means that the community gradually loses the function of using nutrient elements and further reduces the ecosystem function. With increasing aridity, the niche decreases, and the separation traits may be associated with water and carbon acquisition.

Although Leaf Trait Networks (LTN) effectively reveal plant adaptation strategies and nutrient modularization under drought conditions, their application still has limitations. The low connectivity in LTN does not necessarily indicate functional irrelevance among traits; some indirect interactions may occur through soil or below-ground processes, which might not be clearly visible in network analyses. Moreover, multi-scale ecosystem dynamics (such as root traits, plant morphology, or phenological changes) and trait relationships under multiple stress conditions (e.g., simultaneous drought, temperature extremes, and saline-alkaline) are difficult to capture within the traditional LTN framework. Additionally, LTN approach primarily identifies trait associations through correlations rather than causal relationships, limiting deeper insights into trait evolution mechanisms and ecological processes.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12870-025-06658-9>.

Supplementary Material 1.

Acknowledgements

This work was supported by National Natural Science Foundation of China (grant number: 41961007), Opening Fund of Key Laboratory of Land Surface

Process and Climate Change in Cold and Arid Regions, CAS (grant number: LPCC2023003). English language services provided by Unruh, Micah Leigh.

Authors' contributions

SL: conceived and designed the research; YM, HL: performed the experiments, analyzed and collected the data, wrote and edited the manuscript; SL, JW, GW: edited the manuscript and provided scientific guidance. YM and HL contributed equally to this manuscript.

Funding

This work was supported by National Natural Science Foundation of China (grant number: 41961007), Opening Fund of Key Laboratory of Land Surface Process and Climate Change in Cold and Arid Regions, CAS (grant number: LPCC2023003).

Data availability

The data that support the findings of this study are openly available in "Dryad" at <https://doi.org/10.5061/dryad.3j9kd51nx>.

Declarations

Ethics approval and consent to participate

The collection of leaf samples was approved by the Forestry Bureau of Gansu Province.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 21 November 2024 Accepted: 30 April 2025

Published online: 07 May 2025

References

- Cherlet M, Hutchinson C, Reynolds J, Hill J, Sommer S, VON, M. G. World atlas of desertification. Luxembourg: Publication Office of the European Union; 2018.
- Huang J, Yu H, Guan X, Wang G, Guo R. Accelerated dryland expansion under climate change. *Nat Clim Chang*. 2016;6(2):166–71. <https://doi.org/10.1038/nclimate2837>.
- Welles SR, Funk JL. Patterns of intraspecific trait variation along an aridity gradient suggest both drought escape and drought tolerance strategies in an invasive herb. *Ann Bot*. 2021;127(4):461–71. <https://doi.org/10.1093/aob/mcaa173>.
- Nunes A, Köbel M, Pinho P, Matos P, de Bello F, Correia O, Branquinho C. Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. *Agric For Meteorol*. 2017;239:176–84. <https://doi.org/10.1016/j.agrformet.2017.03.007>.
- Lavorel S, Grigulis K, McIntyre S, Williams NS, Garden D, Dorrough J, & Bonis A. Assessing functional diversity in the field—methodology matters!. *Functional Ecol*. 2008;22(1):134–147. <https://doi.org/10.1111/j.1365-2435.2007.01339.x>.
- Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, & Zarovali MP. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann Botany*. 2007;99(5):967–985. <https://doi.org/10.1093/aob/mcl215>.
- Grime JP. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol*. 1998;86(6):902–10. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Ricotta C, Moretti M. CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*. 2011;167(1):181–8. <https://doi.org/10.1007/s00442-011-1965-5>.
- Valencia E, Maestre FT, Le Bagousse-Pinguet Y, Quero JL, Tamme R, Börger L, & Gross N. Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*. 2015;206(2):660–671. <https://doi.org/10.1111/nph.13268>.
- Lablerté E, Legendre P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*. 2010;91(1):299–305. <https://doi.org/10.1890/08-2244.1>.
- Villéger S, Mason NW, Moullot D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*. 2008;89(8):2290–301. <https://doi.org/10.1890/07-1206.1>.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. The influence of functional diversity and composition on ecosystem processes. *Science*. 1997;277(5330):1300–2. <https://doi.org/10.1126/science.277.5330.1300>.
- Mouchet MA, Villéger S, Mason NW, Moullot D. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol*. 2010;24(4):867–76. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>.
- Tobner CM, Paquette A, Reich PB, Gravel D, Messier C. Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*. 2014;174(3):609–21. <https://doi.org/10.1007/s00442-013-2815-4>.
- Le Bagousse-Pinguet Y, Soliveres S, Gross N, Torices R, Berdugo M, Maestre FT. Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proc Natl Acad Sci*. 2019;116(17):8419–24. <https://doi.org/10.1073/pnas.1815727116>.
- Zegaoui Z, Planchais S, Cabassa C, Djebbar R, Belbachir OA, Carol P. Variation in relative water content, proline accumulation and stress gene expression in two cowpea landraces under drought. *J Plant Physiol*. 2017;218:26–34. <https://doi.org/10.1016/j.jplph.2017.07.009>.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, & Villar R. The worldwide leaf economics spectrum. *Nature*. 2004;428(6985):821–827. <https://doi.org/10.1038/nature02403>.
- Michelaki C, Fyllas NM, Galanidis A, Aloupi M, Evangelou E, Arianoutsou M, Dimitrakopoulos PG. An integrated phenotypic trait-network in thermo-Mediterranean vegetation describing alternative, coexisting resource-use strategies. *Sci Total Environ*. 2019;672:583–92. <https://doi.org/10.1016/j.scitotenv.2019.04.030>.
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol*. 2009;182(3):565–88. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>.
- Ronzhina DA, Ivanova LA, Ivanov LA. Leaf functional traits and biomass of wetland plants in forest and steppe zones. *Russ J Plant Physiol*. 2019;66(3):393–402. <https://doi.org/10.1134/S1021443719030129>.
- Belnap J. Biological phosphorus cycling in dryland regions. *Phosphorus in action*. Berlin: Springer; 2011.
- Xiong J, Dong L, Lu J, Hu W, Gong H, Xie S, & Deng J. Variation in plant carbon, nitrogen and phosphorus contents across the drylands of China. *Functional Ecol*. 2022;36(1), 174–186. <https://doi.org/10.1111/1365-2435.13937>.
- Delgado-Baquerizo M, Eldridge DJ, Maestre FT, Ochoa V, Gozalo B, Reich PB, Singh BK. Aridity decouples C: N: P stoichiometry across multiple trophic levels in terrestrial ecosystems. *Ecosystems*. 2018;21(3):459–68. <https://doi.org/10.1007/s10021-017-0161-9>.
- Wang M, Su Y, Yang X. Spatial distribution of soil organic carbon and its influencing factors in desert grasslands of the Hexi Corridor. *Northwest China PLoS one*. 2014;9(4):e94652. <https://doi.org/10.1371/journal.pone.0094652>.
- de Oliveira ACP, Nunes A, Rodrigues RG, Branquinho C. The response of plant functional traits to aridity in a tropical dry forest. *Sci Total Environ*. 2020;747:141177. <https://doi.org/10.1016/j.scitotenv.2020.141177>.
- Maestre FT, Eldridge DJ, Soliveres S, Kéfi S, Delgado-Baquerizo M, Bowker MA, & Berdugo M. Structure and functioning of dryland ecosystems in a changing world. *Ann Rev Ecol Evol Systematics*. 2016;47:215. <https://doi.org/10.1146/annurev-ecolsys-121415-032311>.
- Koutroulis AG. Dryland changes under different levels of global warming. *Sci Total Environ*. 2019;655:482–511. <https://doi.org/10.1016/j.scitotenv.2018.11.215>.
- Yao S, Akram MA, Hu W, Sun Y, Sun Y, Deng Y, & Deng J. Effects of water and energy on plant diversity along the aridity gradient across dryland in China. *Plants*. 2021;10(4):636. <https://doi.org/10.3390/plants10040636>.
- Carvajal DE, Loayza AP, Rios RS, Gianoli E, & Squeo FA. Population variation in drought-resistance strategies in a desert shrub along an aridity

- gradient: Interplay between phenotypic plasticity and ecotypic differentiation. *Perspect Plant Ecol Evol Syst.* 2017;29:12–19. <https://doi.org/10.1016/j.ppees.2017.10.001>
30. Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. Let the concept of trait be functional! *Oikos.* 2007;116(5):882–92. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
 31. Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, & Gorné LD. The global spectrum of plant form and function. *Nature.* 2016;529(7585):167–171. <https://doi.org/10.1038/nature16489>
 32. He N, Li Y, Liu C, Xu L, Li M, Zhang J, & Yu G. Plant trait networks: improved resolution of the dimensionality of adaptation. *Trends Ecol Evol.* 2020;35(10):908–918. <https://doi.org/10.1016/j.tree.2020.06.003>
 33. Kleyer M, Trinogga J, Cebrián-Piqueras MA, Trenkamp A, Fløjgaard C, Ejrnæs R, & Blasius B. Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. *J Ecol.* 2019;107(2):829–842. <https://doi.org/10.1111/1365-2745.13066>
 34. Flores-Moreno H, Fazayeli F, Banerjee A, Datta A, Kattge J, Butler EE, & Reich PB. Robustness of trait connections across environmental gradients and growth forms. *Global Ecol Biogeography.* 2019;28(12):1806–1826. <https://doi.org/10.1111/geb.12996>
 35. Deng Y, Jiang YH, Yang Y, He Z, Luo F, Zhou J. Molecular ecological network analyses. *BMC Bioinformatics.* 2012;13:1–20. <https://doi.org/10.1186/1471-2105-13-113>.
 36. Cohen R, Havlin S. Complex networks: structure, robustness and function. Israel: Cambridge University Press; 2010.
 37. Yin Q, Wang L, Lei M, Dang H, Quan J, Tian T, & Yue M. The relationships between leaf economics and hydraulic traits of woody plants depend on water availability. *Sci Total Environ.* 2018;621, 245–252. <https://doi.org/10.1016/j.scitotenv.2017.11.171>
 38. Li LE, McCormack ML, Ma C, Kong D, Zhang Q, Chen X, & Guo D. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecol Letters.* 2015;18(9):899–906. <https://doi.org/10.1111/ele.12466>
 39. Li Y, Liu C, Sack L, Xu L, Li M, Zhang J, He N. Leaf trait network architecture shifts with species-richness and climate across forests at continental scale. *Ecol Lett.* 2022;25:1442–57.
 40. Li Y, Liu C, Xu L, Li M, Zhang J, He N. Leaf Trait networks based on global data: Representing variation and adaptation in plants. *Front Plant Sci.* 2021;12:710530.
 41. Medeiros CD, Trueba S, Henry C, Fletcher LR, Lutz JA, Méndez Alonzo R, Kraft NJB, & Sack L. Simplification of woody plant trait networks among communities along a climatic aridity gradient. *J Ecol.* 2025;00:1–17. <https://doi.org/10.1111/1365-2745.70010>
 42. Zhang K, Li M, Su Y, Yang R. Stoichiometry of leaf carbon, nitrogen, and phosphorus along a geographic, climatic, and soil gradients in temperate desert of Hexi Corridor, northwest China. *J Plant Ecol.* 2020;13(1):114–21. <https://doi.org/10.1093/jpe/rtz045>.
 43. Zomer RJ, Trabucco A, Bossio DA, Verchot LV. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agr Ecosyst Environ.* 2008;126(1–2):67–80. <https://doi.org/10.1016/j.agee.2008.01.014>.
 44. Trabucco A, Zomer RJ. Global aridity index and potential evapotranspiration (ETO) climate database v2. CGIAR Consort Spat Inf. 2018;10:m9.
 45. Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein MD, Quero JL, & Zaady E. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature.* 2013;502(7473):672–676. <https://doi.org/10.1038/nature12670>
 46. Wang M, Wan P, Guo J, Xu J, Chai Y, Yue M. Relationships among leaf, stem and root traits of the dominant shrubs from four vegetation zones in Shaanxi Province, China. *Israel J Ecol Evol.* 2017;63(2):25–32.
 47. Singh V, Pallaghy CK, & Singh D. Phosphorus nutrition and tolerance of cotton to water stress: II. Water relations, free and bound water and leaf expansion rate. *Field Crops Res.* 2006;96(2–3):199–206. <https://doi.org/10.1016/j.fcr.2005.06.011>
 48. Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, & Poorter H. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian J Botany.* 2003;51(4):335–380. <https://doi.org/10.1071/BT02124>
 49. Perez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jau-reguiberry P, & Cornelissen JHC. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian J Botany.* 2006;64(8):715–716. https://doi.org/10.1071/BT12225_CO
 50. Li S, Wang H, Gou W, White JF, Kingsley KL, Wu G, Su P. Leaf functional traits of dominant desert plants in the Hexi Corridor, Northwestern China: Trade-off relationships and adversity strategies. *Global Ecol Conserv.* 2021;28:e01666. <https://doi.org/10.1016/j.gecco.2021.e01666>.
 51. Zhang GL, Gong ZT. Soil survey laboratory methods. Beijing: Science Press; 2012.
 52. Ye Z, Mu Y, Van Duzen S, Ryser P. Root and shoot phenology, architecture, and organ properties: An integrated trait network among 44 herbaceous wetland species. *New Phytol.* 2024;244:436–50.
 53. Csardi G, Nepusz T. The igraph software package for complex network research. *InterJournal, complex systems.* 2006;1695(5):1–9.
 54. Wu J, Wurst S, Zhang X. Plant functional trait diversity regulates the nonlinear response of productivity to regional climate change in Tibetan alpine grasslands. *Sci Rep.* 2016;6(1):1–10. <https://doi.org/10.1038/srep35649>.
 55. Laliberté E, Legendre P, Shipley B, & Laliberté ME. "Package 'fd'" Measuring functional diversity from multiple traits, and other tools for functional ecology. 2014:0-12.
 56. Team RC. R: A Language and Environment for Statistical Computing, R fuoundation for statistical. Computing. 2020.
 57. Peterson BG, Carl P, Boudt K, Bennett R, Ulrich J, Zivot E, & Cornilly D. Package 'PerformanceAnalytics': R Team Cooperation. 2018:13-14.
 58. Hu W, Ran J, Dong L, Du Q, Ji M, Yao S, & Deng J. Aridity-driven shift in biodiversity–soil multifunctionality relationships. *Nat Commun.* 2021;12(1):1–15. <https://doi.org/10.1038/s41467-021-25641-0>
 59. Armbruster WS, Pélabon C, Bolstad GH, Hansen TF. Integrated phenotypes: understanding trait covariation in plants and animals. *Philosophical Transact Royal Soc B: Biol Sci.* 2014;369(1649):20130245. <https://doi.org/10.1098/rstb.2013.0245>.
 60. Lienin P, Kleyer M. Plant leaf economics and reproductive investment are responsive to gradients of land use intensity. *Agr Ecosyst Environ.* 2011;145(1):67–76. <https://doi.org/10.1016/j.agee.2011.03.015>.
 61. Yang Y, Kang L, Zhao J, Qi N, Li R, Wen Z, & Zheng H. Quantifying leaf trait covariations and their relationships with plant adaptation strategies along an aridity gradient. *Biology.* 2021;10(10):1066. <https://doi.org/10.3390/biology10101066>
 62. Zhang Q, Buyantuev A, Li FY, Jiang L, Niu J, Ding Y, & Ma W. Functional dominance rather than taxonomic diversity and functional diversity mainly affects community aboveground biomass in the Inner Mongolia grassland. *Ecol Evol.* 2017;7(5):1605–1615. <https://doi.org/10.1002/ece3.2778>
 63. White SR, Bork EW, Cahill JF Jr. Direct and indirect drivers of plant diversity responses to climate and clipping across northern temperate grassland. *Ecology.* 2014;95(11):3093–103. <https://doi.org/10.1890/14-0144.1>.
 64. Gong Y, Ling H, Lv G, Chen Y, Guo Z, Cao J. Disentangling the influence of aridity and salinity on community functional and phylogenetic diversity in local dryland vegetation. *Sci Total Environ.* 2019;653:409–22. <https://doi.org/10.1016/j.scitotenv.2018.10.358>.
 65. Aroca R. Plant responses to drought stress. Berlin: Springer; 2012.
 66. Pietragalla J, Mullan DM, Reynolds MP. Physiological breeding II: a field guide to wheat phenotyping. Mexico: Cimmyt; 2012.
 67. Ågren GI, Wetterstedt JM, Billberger MF. Nutrient limitation on terrestrial plant growth—modeling the interaction between nitrogen and phosphorus. *New Phytol.* 2012;194(4):953–60. <https://doi.org/10.1111/j.1469-8137.2012.04116.x>.
 68. Chen R, Ran J, Huang H, Dong L, Sun Y, Ji M, & Deng J. Life history strategies drive size-dependent biomass allocation patterns of dryland ephemerals and shrubs. *Ecosphere.* 2019;10(4):e02709. <https://doi.org/10.1002/ecs2.2709>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.