Ann. For. Res. 67(2): 51-66, 2024
https://doi.org/10.15287/afr.2024.3467

ANNALS OF FOREST RESEARCH
www.afrjournal.org

Mean annual temperature mainly drives spatial pattern of plant functional traits in inland arid and semi-arid areas

Menglin Li[1,2], Xinbing Zhang[1], Yao Tong[2], Zhe Cao[2], Jihong Huang[2,3]✉, Shichen Zhang[4], Shuyi Xu[2], Yi Ding[2,3], Wendong Wang[5], Alimu Maimaiti[5], Liping Wang[6], Runguo Zang[2,3]

Li M., Zhang X., Tong Y., Cao Z., Huang J., Zhang S., Xu S., Ding Y., Wang W., Maimaiti A., Wang L., Zang R., 2024. Mean annual temperature mainly drives spatial pattern of plant functional traits in inland arid and semi-arid areas. Ann. For. Res. 67(2): 51-66.

Abstract The distribution pattern of different plant functional traits in arid and semi-arid areas and their environmental impact mechanism are still unclear. The aim of this study is to elucidate the spatial distribution patterns of four key plant functional traits and the effects of environmental factors on their variation in inland arid and semi-arid areas and thus provide a reference for the prediction of species distribution and biodiversity conservation in this region. We focused on wild seed plants naturally distributed in Xinjiang, and by reviewing floras and data sharing platforms, we sorted and compiled the species list and distribution, plant functional traits and environmental data, including 3,953 species information, 44,302 county-level distribution records, 3,892 plant functional traits information and 29 environmental variables. Spatial and statistical analyses were utilized to detect the spatial distribution patterns of four key plant traits in 50 × 50 km grid cells. The spatial variation in different functional traits was explored and environmental drivers were identified. The results showed that there were significant latitudinal and altitudinal gradient patterns of plant functional traits, and there were significant spatial correlations between different traits. Among the three types of environmental factors (climate, soil and habitat heterogeneity), climate factors played the most pronounced role in explaining functional traits. Mean annual temperature (MAT) was the most important driver of the spatial distribution patterns of each trait. Overall, vegetative and reproductive growth of plants is more favorable in areas with higher temperatures, abundant precipitation, fertile soils and high habitat heterogeneity, which is mainly reflected in higher plant height, larger leaves, earlier flowering time and longer flowering duration.

Keywords: environmental filtering, biodiversity conservation, trait-environment relationships, climate, soil, habitat heterogeneity

Addresses: [1]Shaanxi Forestry Survey and Planning Institute (Shaanxi Forest Resources Monitoring Center), Xi'an, China | [2]Key Laboratory of Biodiversity Conservation of National Forestry and Grassland Administration, Ecology and Nature Conservation Institute, Chinese Academy of Forestry, Beijing, China. | [3]Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing, China. | [4]Forestry College of Beihua University, Jilin, China. | [5]Institute of Forest Ecology, Xinjiang Academy of Forestry Sciences, Urumqi, China. | [6]The Xinjiang Uygur Autonomous Region Forestry Planning Institute, Urumqi, China.

✉ **Corresponding Author:** Jihong Huang (northalluvion@caf.ac.cn)

Manuscript: received January, 25, 2024; revised October 10, 2024; accepted December 05, 2024.

Introduction

Plant functional traits refer to a series of plant attributes that have potentially significant effects on plant colonization, survival, growth and death, and reflect the mechanisms by which species respond to environmental changes and significantly affect ecosystem function (Weiher et al. 1999, Violle et al. 2007, Chacón-Labella et al. 2023, Hagan et al. 2023). Therefore, the study of plant functional traits is often used as an essential way to explore the mechanisms of local community construction (Diaz et al. 1998, Funk et al. 2017, Jeliazkov & Chase 2024). In the context of global change, how important functional traits respond to environment change at larger scales and how they affect ecosystem function has become one of the central issues that ecologists and biogeographers have focused on extensively (McFadden et al. 2022, Maitner et al. 2023).

The combination of functional traits at large spatial scales provides a new idea to explore biogeographical pattern of biodiversity and ecosystem function (Lamanna et al. 2014, Šímová et al. 2018, Midolo 2024). There are universal and complex associations between plant traits (Westoby 1998, Weiher et al. 1999), and species can weigh these associations to achieve a balance of ecological strategies. Several global-scale studies have confirmed the broad and consistent influence of plant phenotypic traits and their trade-offs on physiological and ecological functions of individual plants (Wright et al. 2004, Kunstler et al. 2016). Furthermore, trade-offs between plant traits reflect the adaptation of plant ecological strategies to different environmental changes (Macek & Lepš 2008, Madsen-Hepp et al. 2023). Studies based on trait-environment relationships have been widely used to explore the mechanisms of plant resource economy and stress tolerance (Diaz et al. 1998, Kunstler et al. 2016, Heilmeier 2019). Although some studies have explored environmental mechanisms of functional plant traits at large-scale (Wright et al. 2004, Swenson et al. 2012, Medeiros et al. 2023), no generally accepted universal laws have been derived, which poses a challenge to the development of predictable trait-environment hypotheses (Shipley et al. 2016).

There is sufficient evidence that spatial patterns of plant traits are closely related to environmental gradients at large-scale (Joswig et al. 2022, Lynn et al. 2023), but studies on trait-environment relationships remain controversial. The main influencing factors of distribution patterns of different plant functional traits are different at different scales.

Almost all studies show that climate is the main factor affecting the distribution pattern of plant traits, and in particular there is widespread controversy as to which is the best predictor of plant traits, temperature or precipitation (Moles et al. 2014). For example, as for plant height, some studies have shown that precipitation is the best explanation factor (Swenson et al. 2012, Liu H et al. 2019), whereas other studies have shown that temperature is the dominant factor (Markku 2014, Yu et al. 2018). As for leaf size, a few studies from the tropics of South and North America have shown that it is more sensitive to precipitation than temperature (Dolph & Dilcher 1980, Ordoñez et al. 2009), whereas a global study confirms that it is more closely related to temperature than precipitation (Moles et al. 2014). As for flowering phenology, in temperate and northern regions, temperature has been considered the main driver (Song et al. 2020), whereas precipitation, rather than temperature, is the main climatic factor in areas with limited precipitation (Peñuelas et al. 2004, Crimmins et al. 2011). Thus it can be seen that these inconsistencies of the dominant affecting the spatial distribution of traits may be caused by a variety of factors, such as spatial scale bias, trait selection and differences in research methods (Borgy et al. 2017). Therefore, exploring the geographic patterns and potential driving mechanisms of plant traits along environmental gradients is a highly complex and significant challenge.

Most recent studies on the geographical distribution pattern and environmental influence mechanism of traits have been carried out based on the single trait-climate relationships (Šímová et al. 2018). Indeed, not only climate but also soil and habitat heterogeneity also play an important role in the distribution of species composition and functional traits (Joswig et al. 2022). Soil nutrient availability is one of the main factors determining the species composition of plant community (Ordoñez et al. 2009). Plant economic traits are driven mainly by soil factors (Joswig et al. 2022). Furthermore, higher habitat heterogeneity provides species with a greater variety of habitat types and available resources, thus accommodating the coexistence of species with a wider range of ecological niches (Rosenzweig 1995). Habitat changes can indirectly affect plant traits by affecting species composition. However, there are still limited studies that quantify the spatial variation of multiple functional traits at different spatial scales, and analyze the adaptation of trait combinations to changes in soil nutrients and regional habitat heterogeneity. There is an urgent need to quantify and grasp these relationships to facilitate understanding of ecosystem function and to predict mechanisms of species composition and distribution under global environmental change (McGill et al. 2006, Hagan et al. 2023).

Among many plant functional traits, plant height and leaf size, representing vegetative traits, and flowering time, representing regenerative traits, have been widely studied as important traits that respond to environmental changes (Matthews & Mazer 2016, Wright et al. 2017), and their important roles are mainly reflected in the following aspects:

(1) Plant height have strong influence on water balance (Liu et al. 2019), light interception capacity and carbon sequestration strategy (Moles et al. 2009), which are key functional traits to evaluate the ecosystem functions such as site quality, aboveground biomass, leaf photosynthesis and species diversity (Wang et al. 2019).

(2) Leaf size directly reflects the light interception capacity of plants (Lusk et al. 2019), significantly affects the energy balance of leaves and water use efficiency of plants (Conesa et al. 2020), and then affects the physiological and biochemical processes of leaves to adapt to external climate changes (Peppe et al. 2011, Wright et al. 2017).

(3) Plants allocate survival resources by strictly controlling flowering time (Song et al. 2020). Flowering phenology is directly related to species fitness (Pfeifer et al. 2006) and is widely considered to be one of the most sensitive traits reflecting plant response to climate change (Chmielewski & Rötzer 2001, Song et al. 2020).

Moreover, plant height, leaf size, flowering phenology and other traits are coordinated with each other, reflecting plant growth, development and reproduction (Westoby 1998, Bucher & Römermann 2021), as well as plant survival strategies and ecosystem functional relationships. However, the relationships and differences between vegetative and regenerative traits adapted to environmental changes are still unclear.

In summary, the study of plant functional traits is important for revealing biogeographic distribution patterns and predicting species composition and distribution mechanisms under global environmental changes. However, trait-trait relationships and trait-environment relationships at different spatial scales are still controversial, and there is limited research on spatial relationships and environmental mechanisms based on multiple traits. To further reveal the above problems, this study focuses on four key functional traits of wild seed plants from Xinjiang, China. They are maximum plant height, leaf size, first flowering time and flowering duration. By quantifying the spatial distribution data of traits and environmental factors in this region, we analyze the geographical distribution pattern of key plant functional traits, understand the relationship and differences of spatial changes of different traits, identify the dominant environmental factors affecting the distribution changes of traits, and further reveal the adaptation mechanism of plant traits to environmental changes in arid areas. This study aims to solve the following questions:

(1) How are the different plant functional traits distributed? Do different traits have the consistent spatial distribution patterns?

(2) What are the dominant environmental factors affecting spatial distribution of plant functional traits? Do different environmental factors have consistent effects on the spatial distribution of different traits?

Materials and Methods

Overview of the study area

Xinjiang is the largest provincial administrative region in China (34°25'~ 49°10'N, 73°40'~ 96°18'E), with a total area of about 1.6 ×106 km^2. It is located in the center of Eurasia, far from the sea, and is a typical semi-arid and arid region (Figure 1).

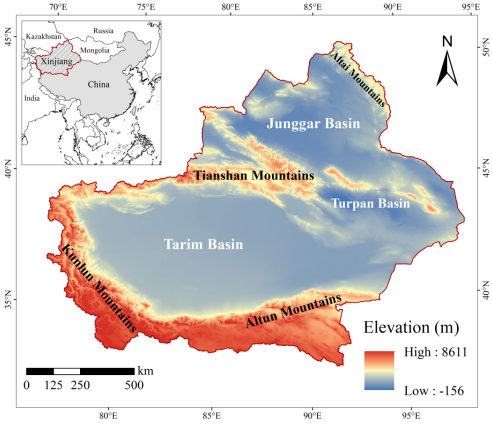

Figure 1 Overview of the study area

This area has a complex terrain, which is gradually raised from north to south, and mostly surrounded by high mountains and plateaus (Xinjiang Investigation Group of Chinese Academy of Sciences 1978). It has a typical geomorphic pattern of "three mountains and two basins". From north to south, they are Altai Mountains, Junggar Basin, Tianshan Mountains, Tarim Basin and Kunlun Mountains. The Tianshan Mountains lie in the middle of Xinjiang and divide it into two halves. It is customary to call the south of the Tianshan Mountains as southern Xinjiang and the north of the Tianshan Mountains as Northern Xinjiang. Xinjiang has a typical temperate continental climate, with large temperature difference between day and night, sufficient sunshine, dry and little rain. The average annual temperature in this area is 4-14°C. Generally, it is low in northern Xinjiang and in plain areas and high in southern Xinjiang and in mountainous areas. The annual precipitation is less than 150 mm. The precipitation distributed uneven and showed more in northern Xinjiang and less in southern Xinjiang, more in mountains and less in basin (Xinjiang Investigation Group of Chinese Academy of Sciences 1978). The complex topography and variable climate conditions have resulted in a rich species composition and vegetation landscape types in this region, which provides an ideal place to detect the spatial distribution patterns of plant traits.

Species distribution data

Seed plant list as well as distribution data in the study were mainly consulted from *Flora Xinjiangensis* (Editorial Committee of Flora Xinjiangensis 1992-2011) and *Brief Flora Xinjiangensis* (Editorial Committee of Flora Xinjiangensis 2014). We compiled information on Latin name, Chinese name, family, genus, distribution county and elevational range, etc. Furthermore, we supplemented, checked and corrected the species list and distribution information by using literature sources and network data sharing platform. The literature included *List of Vascular Plants in Tianshan Mountains* (Pan 2021) and *A Guide to Wild Vascular Plants in Northern Xinjiang* (Yang et al. 2021). The data sharing platforms included iPlant plant species information system (http://www.iplant.cn) and NSII-China National Specimen Resources Platform (http://nsii.org.cn). We excluded all cultivated and introduced species.

Finally, we identified 3,953 wild seed plant species 44,302 records with county-level distribution in Xinjiang.

Trait data

We collected datasets for four plant functional traits: maximum plant height (unit: cm), leaf size (unit: cm^2), first flowering time (unit: month) and flowering duration (unit: months). These trait data were consistent with the sources of species distribution data, and we collated functional trait data for these species alongside the species distribution data. Maximum plant height refers to the maximum known potential height of a species, rather than the average height to avoid plant growth uncertainties and seedling errors (Moles et al. 2009). Leaf size was expressed as the product of average leaf length and average leaf width of single leaf and leaflet (compound leaf species). Previous studies have indicated that the product of leaf length and width had a strong linear correlation with leaf area (Cristofori et al. 2007). First flowering time refers to the month when a plant first blooms. Flowering duration is the total span of months that the plant experiences to complete the entire flowering period. Finally, we collected the trait information of 3,892 species (with at least one known trait value) for subsequent analysis.

Spatial data

The vector data of Chinese county-level administrative divisions and the Digital Elevation Model (DEM) of the study area used in this study are derived from data sharing platforms. The former was obtained from the National Geomatics Center of China - 1:1 million public version of basic geographic information data (2021) (http://www.ngcc.cn), the latter was obtained from the Geospatial Data Cloud website (http://www.gscloud.cn), with a spatial resolution of 30 m.

Environmental data

We collected and sorted out a total of 29 environmental factors in three categories: climate, soil and habitat heterogeneity (Table S1). They are: (1) Climate factors: mean annual temperature (MAT), mean diurnal range (MDR), isothermality, temperature seasonality (TS), maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation (AP), precipitation of wettest month, precipitation of driest month, precipitation seasonality (PS), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter, potential evapotranspiration (PET) and aridity index (AI). (2) Soil factors: soil pH (pH), soil organic carbon content, soil cation exchange capacity (CEC), soil total nitrogen and soil total phosphorus. (3) Habitat heterogeneity factors: elevational range (ER), mean annual temperature range (TR) and annual precipitation range (PR).

Among the above environmental data, 19 climate factors including MAT were derived from the WorldClim database (http://www.worldclim.org), PET and AI were obtained from CGIAR-CSI GeoPortal (https://cgiarcsi.community). The soil data was obtained from the National Earth System Science Data Center, National Science & Technology Infrastructure of China (http://www.geodata.cn). Elevation information was derived from DEM data. Habitat heterogeneity factors: ER, TR and PR were the range (maximum - minimum) of elevation, MAT and AP in each grid cell, respectively. They were often used to reflect topographic and climatic complexity of a region, and were important indicators of habitat heterogeneity (Stein et al. 2015).

Data analysis

Spatial analysis

We used ArcGIS to crop the Chinese county-level administrative division vector data and retained the counties and cities under the jurisdiction of Xinjiang, thus obtaining Xinjiang administrative division data, and superimposed the DEM data to draw an overview map of the study area. Due to the large differences in county areas in Xinjiang, in order to minimize the result deviation caused by unequal areas, we firstly utilized the R software to superimpose the county-level distribution and elevation distribution of species, Xinjiang administrative division data and DEM data to obtain more accurate distribution information of each species in Xinjiang. Secondly, the above species distribution information was transformed into a grid distribution with a spatial resolution of 50 × 50 km, and the species richness information of each grid was further obtained. In order to eliminate the bias brought by the boundary grid to statistical results, subsequent analysis excluded incomplete grids where the actual area of the Xinjiang boundary region was less than 50% of the grid area. Finally, the study area was divided into 765 equal area grid cells with 50×50 km, and 115,732 distribution records were determined based on grid cells.

Using 'Latin name' as the key field for spatial matching, we used ArcGIS to spatially correlate the species distribution data based on equal-area spatial analysis units with the plant functional trait data, and calculated the average values of plant functional traits of all distributed species in each spatial analysis unit, so as to obtain the spatial distribution data of different plant functional traits.

The Natural breaks (Jenks) segmentation method was used to classify the mean values of different traits, and the spatial distribution patterns of different traits were plotted to characterize the spatial distribution of different plant functional traits within the study area. Based on a 50×50 km equal area spatial unit, spatial data such as longitude, latitude, elevation, and environmental data such as climate, soil, and habitat heterogeneity were resampled separately using spatial analysis tools of ArcGIS. Among them, latitude and longitude are the center point coordinates of each spatial unit, and elevation is the average value of DEM data in each spatial unit.

Climate and soil factors were extracted from the acquired global data, respectively, and resampled using the spatial analysis tool in ArcGIS-Regional Analysis-Display Analysis in Tables to export climate and soil data based on spatial analysis units. The habitat heterogeneity factors, ER, TR, and PR, were extracted and data were exported according to the extreme values of elevation, MAT and AP for each spatial unit of analysis, respectively. All environmental and spatial data derived from resampling will be used for subsequent statistical analysis.

Statistical analysis

Due to the strong correlations between environmental variables, we first performed a preliminary screening of climate factors in order to avoid the bias of multivariate linearity on the statistical model. We retained two widely used climate variables, MAT and AP (Peppe et al. 2011, Moles et al. 2014, Šímová et al. 2018), and excluded variables with a correlation coefficient $r > 0.8$ with both based on the results of the Pearson correlation analysis (Table S2). This step filtered all climatic variables down to nine. Then, the full regression model was constructed for three types of environmental variables: climate, soil and habitat heterogeneity, and the variance inflation factor (VIF) was calculated using the R package 'car' to further filter the environmental variables until $VIF < 6$ for all environment variables (Table S3). The final environmental factors include: (1) climate factors: MAT, MDR, TS, AP and PS. (2) Soil factors: pH and CEC. (3) Habitat heterogeneity factors: ER and PR.

We log-transformed the values of maximum plant height and leaf size to correct for skewness in their distributions and to improve the normality of the residuals in the fitted regression model. We applied the unary least squares regression model to analyze the geographic gradients patterns and pairwise correlations of the spatial variation of different plant traits, and selected the optimal model according to the weight of Akaike Information Criterion (AIC, Supporting Information Table S4). The model with the lowest AIC value was selected to fit the geographical distribution patterns of trait along the latitude, longitude and altitude gradients. Since large-scale spatial data generally have significant spatial autocorrelation, this may lead to an overestimation of the degrees of freedom of the residuals, thus affecting the significance bias of the regression model.

To ameliorate the effect of spatial autocorrelation on significance test, modified t-test were performed using the R package 'SpatialPack' to assess the significance of statistical models (Dutilleul et al. 1993). Use R package 'vegan' to carry out the Variance Partitioning Analysis (VPA), and calculate the proportion of variance explained by climatic, soil, habitat heterogeneity and their combined effects on trait variation. In order to explore the main environmental predictors of plant traits, multiple regression models were constructed for each trait and all screened environmental variables, all of which were standardized before regression analysis.

In order to reduce the complexity of the model and identify the most important environmental factors, the R package 'MuMln' for model selection, retained models with AIC < 2 as candidates, and selected the environment variables in the model with the minimum AIC value to establish the subsequent regression analysis. McFadden's R2 was used to evaluate the goodness of fit of each regression model, and standardized regression coefficients were calculated using the R package 'apaTables' to measure the relative influence of different environmental variables on trait variation.

All spatial analyses were conducted in ArcGIS (10.8), and all statistical analyses were performed in R (4.0) (R Core Team 2021).

Results

Spatial distribution pattern of plant functional traits

The spatial distribution patterns of the four traits showed differences. Maximum plant height was higher in low elevation plains such as Tarim Basin and Junggar Basin, while lower in Tianshan Mountains and Kunlun Mountains (Figure 2a). Leaf size was larger in northern Xinjiang and smaller in southern Xinjiang, especially in Tianshan Mountains and Altai Mountains (Figure 2b). First flowering time was the latest in Kunlun Mountains and earlier in the north and east of Tianshan Mountains (Figure 2c). Flowering duration was longer in Tarim Basin and Turpan Basin, while shorter in Kunlun Mountains (Figure 2d).

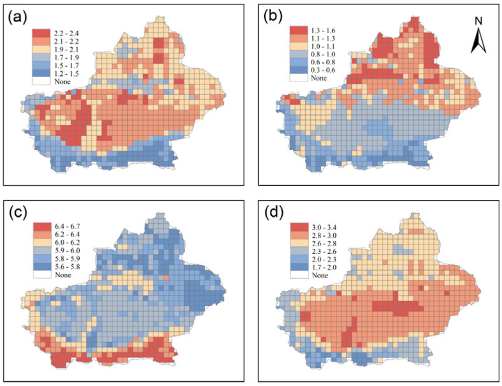

Figure 2 Spatial distribution patterns of plant functional traits in Xinjiang. (a) Maximum plant height, (b) leaf size, (c) first flowering time and (d) flowering duration was based on the spatial distribution patterns of 50×50 km grid cells. The values of maximum plant height and leaf size were log-transformed. Natural breaks (Jenks) method was used to grade the mean values of different traits, which were divided into six grades. The color from red to blue indicated the trait value from high to low, and the white part represented incomplete grid with actual area less than 50% of grid area.

All traits showed significant patterns of latitudinal and altitudinal gradients (Figure 3). Among them, the latitudinal gradient pattern of leaf size (R^2 = 0.62) was the most obvious (Figure 3d), whereas altitudinal gradient patterns of maximum plant height (R^2 = 0.75), first flowering time (R^2 = 0.79) and flowering duration (R^2 = 0.64) were the most obvious (Figure 3c,i,l). Leaf size increased significantly with increasing latitude. Maximum plant height, first flowering time and flowering duration showed an unimodal trend along with latitudinal gradient, and the inflection points were about 42°N (Figure 3a,g,j). Maximum plant height and flowering duration first increased and then decreased with increasing latitude, while first flowering time showed the opposite trend. The altitudinal gradient patterns showed that maximum plant height decreased (Figure 3c), leaf size became smaller (Figure 3f), first flowering time delayed (Figure 3i) and flowering duration shortened (Figure 3l) with increasing elevation. There was no obvious trend in four plant traits with longitudinal gradient.

Correlations of spatial distribution of different plant functional traits

Significant correlations were found between pairs of different traits (Figure 4).

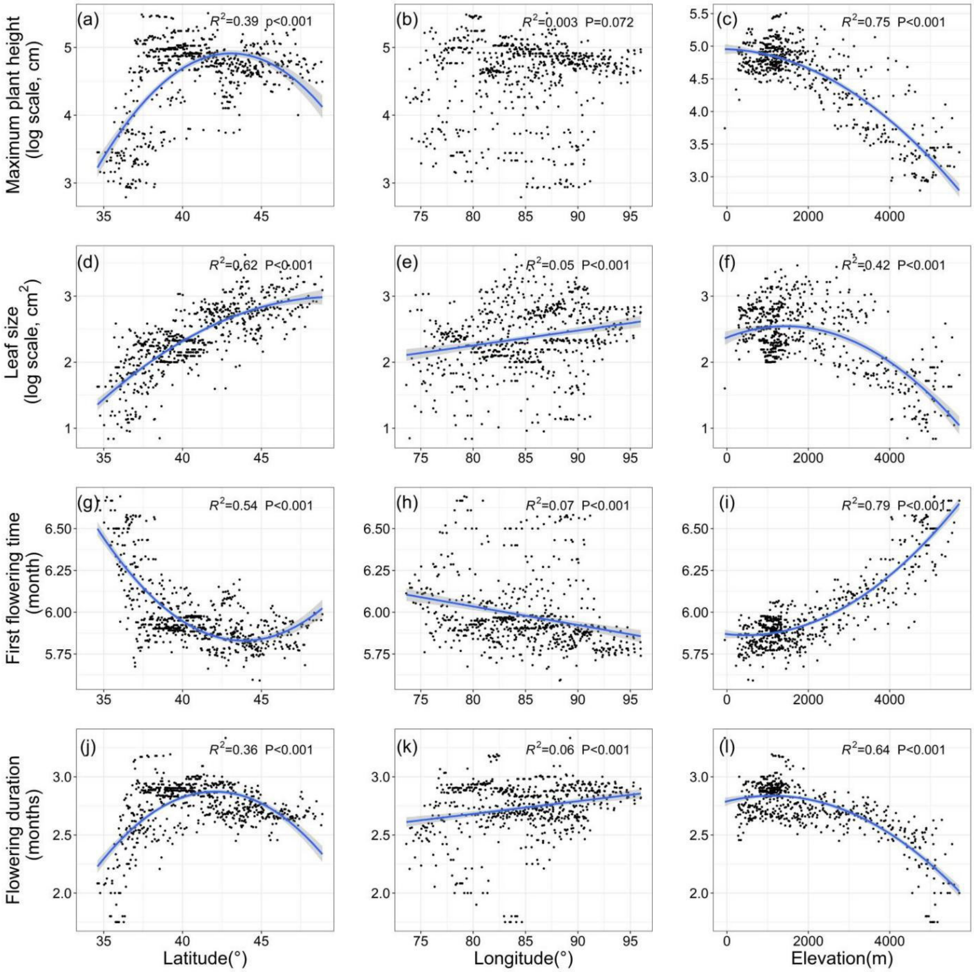

Figure 3 Geographic gradients distribution patterns of plant functional traits in Xinjiang. The variation trends of maximum plant height, leaf size, first flowering time and flowering duration along latitudinal gradient (first column), longitudinal gradient (second column) and elevational gradient (third column). The values of maximum plant height and leaf size were log-transformed. We selected the best models according to the AIC weight. The model fit was quadratic regression in latitudinal and elevational gradient, and linear in longitudinal gradient. The blue line represented regression fit line, and the gray part represented 95% confidence interval.

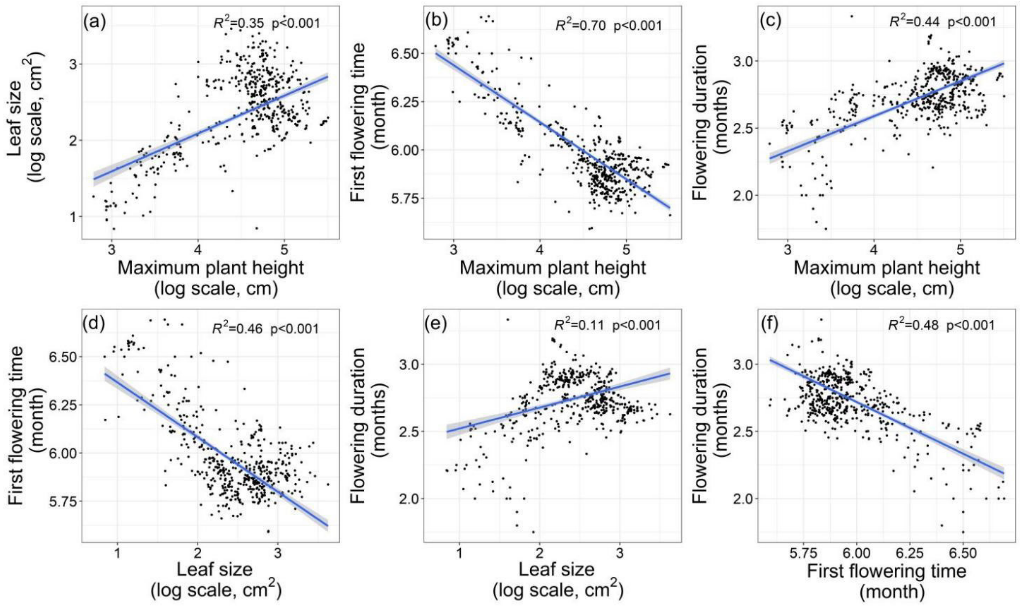

Figure 4 Pairwise correlations between different plant functional traits in Xinjiang. The values of maximum plant height and leaf size were log-transformed. The blue line represented linear regression fit line, and the gray part represented 95% confidence interval.

Maximum plant height was positively correlated with leaf size and flowering duration (Figure 4a,c), and negatively correlated with first flowering time (Figure 4b). Leaf size was negatively correlated with first flowering time (Figure 4d) and positively correlated with flowering duration (Figure 4e). First flowering time was negatively correlated with flowering duration (Figure 4f). Among them, maximum plant height had the strongest correlation with first flowering time ($R^2 = 0.70$), while leaf size had the weakest correlation with flowering duration ($R^2 = 0.11$). The correlation between maximum plant height and flowering traits (mean $R^2 = 0.57$) was significantly stronger than that between leaf size and flowering traits (mean $R^2 = 0.28$).

Environmental factors affecting spatial distribution of plant functional traits

Effects of different types of environmental factors on spatial variation in plant functional traits

All three categories of environmental factors, climate, soil and habitat heterogeneity, had significant effects on variation in trait patterns (Figure 5). They had the highest total explanatory variance for first flowering time (Figure 5c) and the lowest for leaf size (Figure 5b).

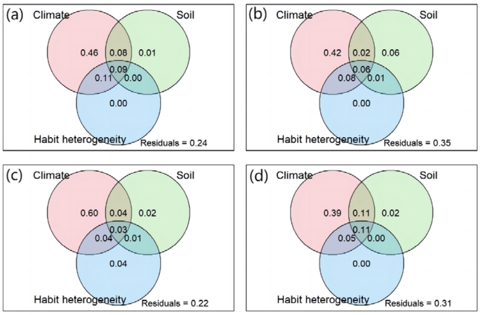

Figure 5 Variance decomposition of climate, soil and habitat heterogeneity on (a) maximum plant height, (b) leaf size, (c) first flowering time and (d) flowering duration in Xinjiang. Residuals represent variance values that were not explained by the variance decomposition model. The numbers in the circles represented variances explained independently or jointly by climate, soil and habitat heterogeneity.

The climate factor had the highest independent explanatory variance for all four traits, accounting for the proportion of total variance: maximum plant height 60.53%, leaf size 64.62%, first flowering time 76.92% and flowering duration 56.52%. The combination of climate and soil, climate and habitat heterogeneity, and three types of environmental factors may also explain a certain proportion of trait variation. Overall, climate played an overwhelming role in explaining spatial variation in traits, while soil and habitat heterogeneity were only weakly explained.

Dominant environmental factors affecting spatial variation in plant functional traits

Environmental factors had a significant and strong effect on spatial distribution of plant functional traits, with the regression model achieving a mean R2 of 0.72 for four traits (Figure 6). Overall, the first environmental predictor of different traits was MAT, which explained considerably more than other environmental variables, the second predictor was CEC. In addition, there were relatively strong effects of AP on leaf size and ER on first flowering time. All environmental factors with significant effects on maximum plant height except PS were positive (Figure 6a). Only MDR, PS and DR had negative effects on leaf size (Figure 6b). All environmental variables with significant effects on first flowering time except PS had negative effects (Figure 6c). All environmental variables that significantly affected flowering duration had positive effects (Figure 6d).

The effects of environmental factors on the distribution of functional traits in different plants were different. Although MAT was found to be the dominant factor affecting all traits, the extent and effect of its influence on traits varied (Figure 6). MAT had the strongest effect on flowering duration (r = 1.09) and the weakest effect on leaf size (r = 0.70). MAT only had a negative explanatory effect on first flowering time, but a positive explanatory effect on other traits. MAT explained maximum plant height and flowering duration far more than other factors, but CEC was relatively prominent for leaf size and first flowering time. In addition, there were significant differences in the explanatory effects of environmental factors on different traits. For example, MDR and TS only had no effect on

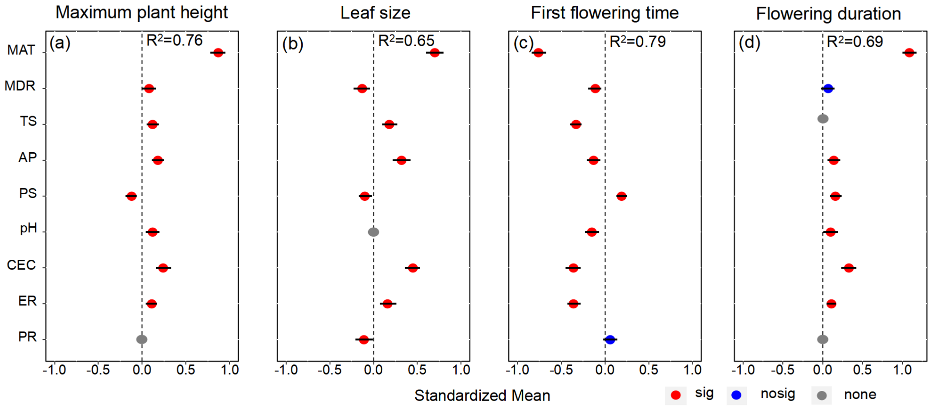

Figure 6 Explanatory effects of different environmental factors on spatial distribution of (a) maximum plant height, (b) leaf size, (c) first flowering time and (d) flowering duration. The best regression models were selected to explain maximum plant height, leaf size, first flowering time and flowering duration according to AIC weight. The effect coefficient for each explanatory variable had been normalized to indicate the relative contribution of that variable to each regression model. Different colored dots represented different impact effects, with red indicating significant impact, blue indicating insignificant impact and grey indicating no impact. The black line on the dot was the error bars. The dashed line was the zero-effect line, with the left side representing negative effect and the right side representing positive effect.
Abbreviations: MAT = mean annual temperature, MDR = mean diurnal range, TS = temperature seasonality, AP = annual precipitation, PS = precipitation seasonality, pH = soil pH, CEC = soil cation exchange capacity, ER = elevational range, PR = annual precipitation range.

flowering duration, or not significant effect, PR only significantly explained leaf size, while soil pH only had no effect on leaf size.

Discussion

Based on the spatial distribution patterns and environmental influence mechanisms of plant functional traits in Xinjiang, we found significant difference in the spatial distribution patterns of maximum plant height, leaf size, first flowering time and flowering duration. Although different traits showed significant distribution patterns along with latitudinal and altitudinal gradients, the patterns of between different traits were not consistent. We found that environmental factors have significant and strong effects on plant traits. Among them, the trait-climate relationships were the strongest. The first predictor of spatial variation in all traits was MAT, and the second predictor was CEC. However, trait-environment relationships differed overall between different plant traits, mainly in terms of different environmental predictors or different shapes of the trait-environment relationships.

Significant latitudinal and altitudinal gradient patterns of plant functional traits

We found significant latitudinal and altitudinal gradient patterns in different traits, and the overall trend of traits with altitudinal gradients was more pronounced than with latitudinal gradients. Latitude patterns of plant traits at large-scale, especially at global-scale, are not uncommon (Lamanna et al. 2014, Wright et al. 2017). Although the latitude span in this study area is relatively limited, we can still find some interesting phenomena, such as maximum plant height, first flowering time and flowering duration show a single peak along latitude, with a turning point around 42°N, which is the location of the Central Tianshan Mountain range.

The Tianshan Mountain, which lies in the middle of Xinjiang, is an important dividing line for physical geography and vegetation level. There are clear differences in climate, soil, flora, and vegetation types on the north and south sides of the Tianshan Mountains (Xinjiang Investigation Group of Chinese Academy of Sciences 1978), which coincides with the latitudinal single-peak patterns of trait variation in this region. Moreover, due to the huge difference in altitude, vegetation in the mountainous areas of Xinjiang shows vertical zonation with altitude (Xinjiang Geography Institute of Chinese Academy of Sciences 1987). This is also confirmed by our results. The argument that maximum plant height decreases, leaf size decreases and flowering phenology delays with increasing altitude has been generally confirmed in previous studies (Macek & Lepš 2008, Rafferty et al. 2020). Altitude is often highly complex indirect gradient that are closely related to climate, soil, solar radiation and many other environmental variables that are critical to plant growth and survival (Körner 2007). As the altitude increases, there are environment features such as lower temperature, less precipitation, and increased solar radiation. Such adverse conditions will filter out some species that are less competitive (Cornwell et al. 2006).

Significant and strong functional plant trait-environment relationships

Trait-environment relationships, a set of plant attributes that are closely related to specific environmental conditions, are a result of the filtering effects of climate, disturbance, land-use change, and biological conditions (Diaz et al. 1998). Different plant traits showed significantly stronger environmental signals in Xinjiang, in line with expectation of a strong and predictable trait-environment relationships (Lavorel & Garnier 2002, Shipley et al. 2016). The variability and plasticity of traits may help species to overcome rapidly changing and harsh environmental conditions (Heilmeier 2019). As a result, plants adapt to different environmental changes by trade-offs in trait-environment relationships (Macek & Lepš 2008, Kunstler et al. 2016, Lynn et al. 2023).

We also found that the relationships between different plants functional traits and environment was mainly represented by the traits-climate relationship, the variance explanation ratio of climate factors to plant traits was considerably higher than that of soil factors or habitat heterogeneity factors, and more than 50% of the spatial variation of the four traits was independently explained by climate. Previous studies have shown that climate change has a globally consistent and driving effect on natural ecosystems (Parmesan & Yohe 2003). In general, climate factors play a decisive role in the distribution of functional traits on global or larger scales, whereas at smaller scales, soil, topography or habitat heterogeneity may be more critical to the distribution of traits (Liu X & Ma 2015).

Effects of temperature on spatial variation in plant functional traits

Although different traits showed significant environmental effects, not all environmental indicators were good predictors of plant traits. We found that MAT was the best explanatory factor for all traits, and its explanatory role was significantly higher than other environmental variables. This likely indicates that temperature is the key dominant factor shaping the trait variation in Xinjiang. This result is consistent with plant traits showing significant latitudinal and altitudinal gradient patterns, as temperature usually shows highly similar trends with latitude and altitude (Halbritter et al. 2013). It is often assumed that moisture conditions should be the most important environmental factor limiting plant growth in arid and semi-arid regions (Moles et al. 2009), but our results confirm that temperature is considerably more important than precipitation in explaining plant functional traits in Xinjiang. This may be related to the complex topography and hydrothermal distribution of the study area. Located far from the sea and surrounded by high mountains, Xinjiang forms a typically arid climate region, characterized by minor and uneven distribution of water resources, undeveloped surface runoff, and large areas without water flow (Xinjiang Geography Institute of Chinese Academy of Sciences 1987).

Due to water constraints, extensive deserts and gravel deserts are found in the two basins of northern and southern Xinjiang, indicating that precipitation is generally less and at the same level in habitats where plants are widely distributed. Moreover, Xinjiang is rich in solar-thermal resources, which are highly beneficial for plant growth and development. Therefore, we suggest that when precipitation is highly scarce in arid regions and light and heat conditions are very favorable, changes in precipitation may no longer be the most critical limiting factor for plant growth and survival.

Contribution of soil to spatial distribution of plant functional traits

CEC is an important soil index to evaluate nutrient availability for plant growth, and a higher CEC generally represents a higher soil fertility level (Ross & Ketterings 1995). In this study, CEC was the second predictor explaining variation in all plant traits, especially for leaf size. It is obvious that plant traits such as plant height and leaf size that can use nutrients quickly have a growth advantage in habitats where soil nutrients are abundant (Ordoñez et al. 2009). This is because plants growing in fertile soil environments produce large amounts of litter, which produce macronutrient elements that are further returned to the soil, thus maintaining high soil fertility level. However, the relationships between plant traits and soil at large-scale are often easily overlooked.

Several studies based on global scales have confirmed that soil fertility indicators explain differences in leaf traits across sites even better than climate (Ordoñez et al. 2009), and that soils are more focused on explaining plant economic traits (Joswig et al. 2022). It has also been shown that predicting the effect of soil nutrient availability on plant productivity is one of the biggest uncertainties in future climate change predictions (Hungate et al. 2003). Global climate change may affect soil nutrient availability on relatively shorter time scales, and plant species composition on longer time scales (Rustad et al. 2001). Therefore, quantifying the effect of soil on variation in plant traits at different spatial scales needs to be further investigated (Lavorel & Garnier 2002, McGill et al. 2006).

Trade-off relationships between plant functional traits

This study found significant relationships between vegetative and regenerative traits, which showed that plants with higher height and larger leaves tended to bloom earlier, especially between maximum plant height and first flowering time, which was consistent with the conclusions of previous studies (Fitter & Fitter 2002, Sun & Frelich 2011). In order to ensure sufficient time for accumulation to improve the survival rate of offspring, taller plants allocate resources by controlling the timing of early flowering to coordinate vegetative growth and reproductive growth replacement (Sun & Frelich 2011). The temporal trade-off between leaf growth and senescence is essential to minimize the risk of low temperature events and maximize carbon gain during the growing season (Bucher & Römermann 2021). Larger leaves favor the accumulation of abundant nutrients for reproduction and growth. The close relationships between leaf functional traits and flowering phenology have been widely confirmed (König et al. 2018, Bucher & Römermann 2021). Trade-off relationships between plant traits are the result of adaptation of their ecological strategies to environmental changes (Maitner et al. 2023).

In general, environmental variables played a more important role in explaining regenerative traits than vegetative traits in Xinjiang, especially the environmental explanation of the first flowering time reaches 79%, indicating that the flowering strategy of plants is highly sensitive to environmental changes (Song et al. 2020). Flowering marks the transition from vegetative growth to reproductive growth (Kushwaha et al. 2011), and the selection of the best flowering time plays a crucial role in the survival and reproduction of plants (Rafferty et al. 2020). We also find that the intensity and effect of different environmental factors on the interpretation of different traits differed, reflecting the uniformity and variability of the adaptation of plant traits to environmental changes. The intensity and direction of adaptation of species ecological strategies to environmental changes varies across regions and even within the same region (Parmesan & Yohe 2003). Therefore, we urgently need to master more trait-trait and trait-environment relationships to understand the ecological hot issues such as community species coexistence, ecosystem function, and species range formation (Midolo 2024, Wiethase et al. 2024).

Conclusions

We analyzed the geographical distribution patterns and environmental drivers of four important plant functional traits: maximum plant height, leaf size, first flowering time and flowering duration of seed plant in Xinjiang. In general agreement with existing research findings and theoretical expectations, the main findings of this study are as follows:

(1) Plant functional traits showed significant latitudinal and altitudinal gradient patterns in inland arid or semi-arid areas. There is a unimodal trend in maximum plant height and flowering traits along with latitudinal gradient.

(2) Different traits showed significant correlations and environmental signals. Of all four traits, maximum plant height is most closely related to first flowering time. Among the three types of environmental variables, the trait-climate relationships are the strongest.

(3) MAT is the dominant environmental influencing factor for spatial variation in all four traits, and its explanatory contribution is significantly higher than other environmental factors, but the explanatory degree and effect of MAT on different traits are different.

(4) CEC is the second predictor for all traits, especially for leaf size. It is necessary to quantify the effect of soil conditions on distribution of plant traits at different spatial scales.

This study quantifies the geographical patterns and environmental mechanisms of key plant functional traits in a typical inland arid and semi-arid area, with a focus on clarifying the associations and differences between trait-trait relationships and trait-environment relationships. Our results enrich the spatial pattern of plant functional trait at region level, and provide guidance for species composition and range prediction as well as biodiversity conservation in arid and semi-arid areas.

Acknowledgments

We are particularly grateful to the associate editor and reviewers for their valuable comments on the manuscript. Any research in the paper not carried out by us is fully acknowledged in the manuscript. All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication.

Funding

This study was financially supported by the Special Foundation for National Science and Technology Basic Research Program of China (2019FY101604-2) and the National Natural Science Foundation of China (32071648).

Conflict

The authors declare there is no conflict of interest.

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