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Spatial Patterns and Influencing Factors of the Leaf Trait Network of *Populus euphratica* Along the Main Stream of the Tarim River

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Abstract: The complex network relationship between leaf traits and their multiple traits is closely related to the environment, and is the result of interactions between various environmental factors such as climate and soil. Based on previous work, we selected 20 *P. euphratica* trees along the desert riparian forest of the main stream of the Tarim River for leaf sample collection and habitat survey. We used 27 leaf traits of *P. euphratica* to visualize the leaf trait network (LTN). Through network structure parameters, such as edge density, diameter, average path length, and average clustering coefficient, the spatial pattern of the LTN and its relationships with 11 soil factors and 19 climatic factors were discussed using principal component analysis and correlation analysis. The results showed that: (1) there were significant differences in the parameters of the leaf trait network of *P. euphratica* along the main stream of the Tarim River. The variation coefficients of the diameter and average path length were the largest, respectively, whereas that of the average clustering coefficient was the smallest. (2) There were both positive and negative correlations between each parameter and soil factors, such as soil water content, total potassium, and organic matter, and climatic factors, such as isothermality, minimum temperature of the coldest month, and precipitation of the wettest month. (3) The explanatory power of climate alone on the leaf traits of *P. euphratica* was generally higher than that of soil factors, indicating that climatic conditions play a more decisive role in shaping the network structure of leaf traits of *P. euphratica*. However, regarding the influence of network modularity, the contribution of soil factors was significant, indicating that the influence of soil conditions on some LTN parameters cannot be ignored.

Keywords: *Populus euphratica*; leaf trait network; soil; climate; adaptation strategies

1. Introduction

Plant functional traits refer to the morphological, physiological, biochemical, and behavioral characteristics of plants in ecosystems. These characteristics are closely related to ecosystem functions and reflect the strategies used by plants to cope with environmental changes [1,2]. As an important aspect of plant functional traits, leaf traits are not only closely related to plant growth, development, and reproduction but are also affected by the external environment and phylogenetic development. It is a bridge between plants and the environment, showing the adaptability and self-regulation ability of plants to complex habitats [3–5]. Under environmental stress, plants usually improve their adaptability by adjusting their leaf functional traits. In addition, as the main organ of photosynthesis and material production, leaves are key to material exchange and energy conversion in plants [6]. Leaf traits directly reflect the photosynthetic capacity of plants and their strategies of resource acquisition, utilization, and distribution [7,8]. Therefore, it is important to understand the changes in leaf functional traits in different environments to explore the environmental adaptability of plants. This helps to reveal the ecological adaptation mechanisms of plants and provides an important scientific basis for the maintenance and management of ecosystem functions.

With the intensification of global environmental change, research on variations in leaf functional traits and their adaptation mechanisms has attracted attention. Studying the changes in plant functional traits with environmental factors is helpful for understanding the physiological and ecological mechanisms of plants under climate change conditions and is of great significance for understanding the survival and distribution of plants [9]. Additionally, climate change and other environmental factors have significant effects on leaf functional traits [10–16]. The variation in leaf functional traits is not only the result of the interaction of environmental factors and phylogenetic history, but also shows dynamic changes in geographical distribution patterns and time scales at global, regional, and local scales [17–19]. The relationship between traits and the environment reflects the optimal adaptation principles for plant growth and adaptation under natural conditions [20]. Therefore, leaf functional traits provide information on environmental changes in the process of plant adaptation to such changes as well as directly reflecting the survival strategies of plants to adapt to environmental changes.

The economic spectrum of plant functional traits reveals an important relationship among plant functional traits. Plant leaf traits are not isolated but are closely related to many other traits [21,22]. Recently, researchers have proposed various theories and methods regarding plant trait networks (PTNs) [23]. By quantifying the complex relationships between multiple leaf traits, a multidimensional network was constructed to explain the relationships between different leaf traits. The study of plant trait networks can comprehensively, multi-dimensionally, and visually analyze and evaluate the relationship between traits, network topology, and hub traits [24]. This allows researchers to explore the key traits of plants in different environments and their relationships with the environment and provide a new way to reveal the adaptation and response mechanisms of plants to environmental and resource changes. The purpose of this study was to explore how the leaf trait network of *P. euphratica* along the main stream of the Tarim River responds to environmental change. By analyzing the spatial variability and driving factors, the adaptive strategies of *P. euphratica* leaf traits in its environment are revealed.

The environment of the main stream of the Tarim River in Xinjiang is complex and varied. It is a typical ecologically fragile area with strong environmental sensitivity, water shortages, sparse vegetation, and severe soil and wind erosion. There are vast desert riparian forests on both sides of the river, and the vegetation is dominated by *P. euphratica*. It is an important tree species in the Salicaceae family. It has strong stress resistance and can adapt to harsh environments such as drought, wind erosion, and saline-alkali soil [25]. It plays an active role in regulating the climate, preventing wind and sand erosion, preventing desert expansion, and protecting oases. Understanding the interactions between *P. euphratica* leaves and the environment is of great significance for revealing the mechanisms of plant adaptation to drought-prone environments. In a previous study [26], the relationship between leaf traits and the environment of *P. euphratica* was been studied. The influence of the climate drought index and river water flow on the leaf trait network of *P. euphratica* was explored using the plant trait network analysis method by determining leaf morphology and functional traits of *P. euphratica* along the main stream of the Tarim River. The lower stratum corneum (LSC), upper stratum corneum (USC), and midvein vascular bundle (MVB) were the central traits of the leaf trait network of *P. euphratica*. It optimizes resource utilization and improves drought resistance by adjusting its leaf traits, thereby exhibiting a high degree of environmental adaptability. However, there are a few reports on the complex relationship network between the multiple leaf traits of *P. euphratica* and their relationships with the environment.

This study used the *P. euphratica* forest on the desert bank of the main stream of the Tarim River in Xinjiang as the research object, and used the leaf trait network and principal component analysis (PCA), variance decomposition analysis (VPA), and other analysis methods to construct the *P. euphratica* leaf trait network along the main stream of the Tarim River. The spatial pattern of the leaf trait network in the entire basin and its relationship with environmental factors, such as climate and soil, were analyzed. The purpose of this study was to analyze how *P. euphratica* adapts to the environment of the main stream of the Tarim River through the integration of leaf traits and adjustment of the relationship between traits, to reveal the adaptation strategy of *P. euphratica* to the environment, ultimately protecting wild *P. euphratica* forests along the Tarim River.

2. Materials and Methods

2.1. Overview of the Study Area and Site Information

The Tarim River flows through the northern Tarim Basin in northwestern China. It is the fifth-longest inland river in the world and the longest river in China. Its main stream is formed by the confluence of the Aksu River, which originates in the Tianshan Mountains, and the Yarkand and Hotan Rivers, which originate in the Kunlun Mountains in the city of Aral. Affected by the climate, the seasonal variation of runoff indicates that the Tarim River is seasonal river [27]. This study was conducted in July 2022, and 20 survey sampling sites were established in the natural *P. euphratica* forest on both sides of the riverbank from east to west along the main stream of the Tarim River, from the source to the end of the river (Figure 1). The sample plots were selected uniformly distant from human disturbance. The latitude and longitude, altitude, vertical riparian distance, and other data for each sample plot were recorded simultaneously. Basic information on the 20 sample plots is provided in Table A1.

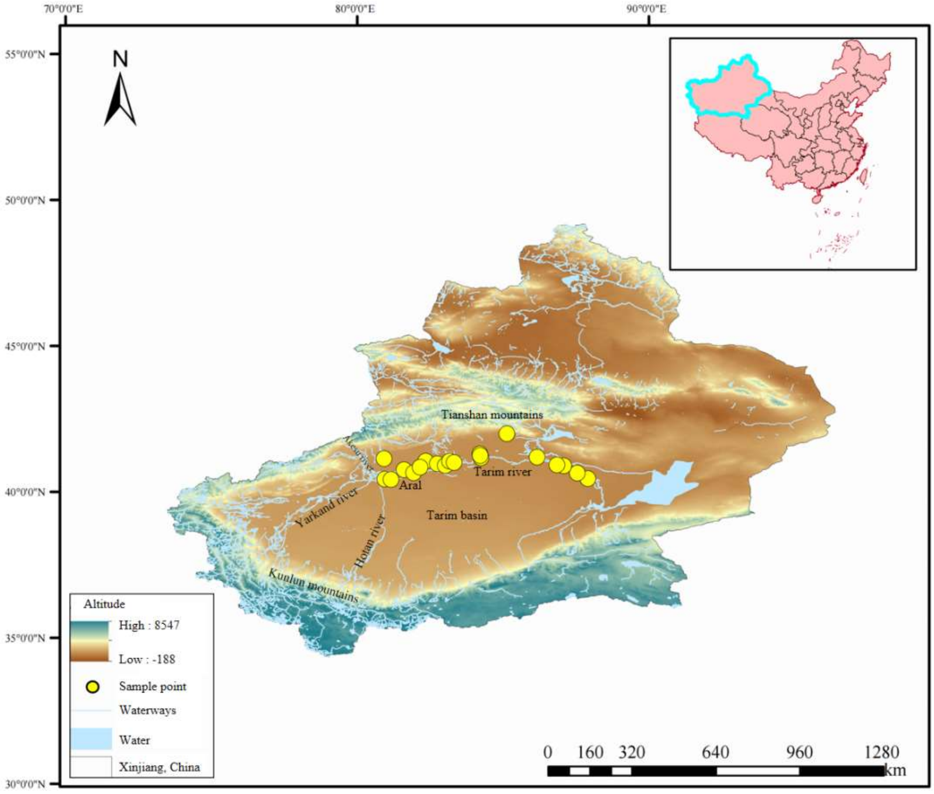

Figure 1. Map of the sampling points.

2.2. Leaf Sample Collection and Pretreatment

Each plot was measured for each tree, and 15 mature *P. euphratica* trees with good growth status and consistent diameter at breast height (DBH) in the range of 20>30 cm were randomly selected as sample plants and their specific DBH was recorded. High-branched scissors were used for sampling. The sampling site covered approximately one third of the lower crown of each *P. euphratica* tree. Healthy leaves at the penultimate third node of the twig were collected from the east, south, west, and north sections of each tree. After sampling was completed, all leaves of the same plant were evenly mixed, and 20 leaves were randomly selected for cutting but retained the main vein and then placed in a reagent bottle containing FAA fixative (70% ethanol: formaldehyde: acetic acid = 90:0.5:0.5). Another 100 leaves were randomly selected and the petiole was removed. The fresh weight of the leaves was first measured, followed by dispersing the leaves flat on a black background plate placed on a ruler, and photographs of the vertical leaves taken for subsequent analyses of leaf morphology indices (Figure 2a). After processing, the samples were returned to the laboratory for subsequent analyses.

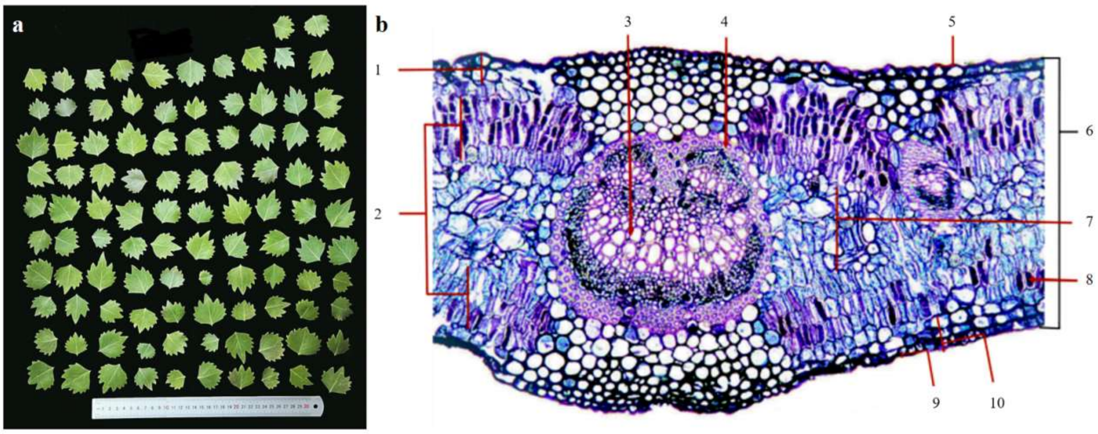

Figure 2. Leaf morphology and leaf anatomical structure. **(a)** Leaf morphology. **(b)** Leaf anatomical structure: **(1)** Upper epidermis; **(2)** Palisade tissue; **(3)** Vascular bundle; **(4)** Sclerenchyma; **(5)** Upper stratum corneum; **(6)** Leaf thickness; **(7)** Spongy tissue; **(8)** Mucous cells; **(9)** Lower stratum corneum; **(10)** Lower epidermis.

2.3. Soil Sample Collection and Pretreatment

Soil profiles were dug near each plant, and three soil samples were taken from each site using a soil auger at depths of 0>20 cm, 20>40 cm, 40>60 cm, 60>80 cm, and 80>100 cm for fresh soil columns. Part of the soil from the base of the soil columns was put into an aluminum box and transported, weighed, and then dried at 105°C in a thermostatic drying oven to determine dry weight and the moisture content of the soil. The rest of the soil samples were transported in sealed bags. Roots and impurities were manually removed and dried naturally in a cool, ventilated place. After air-drying, the soil samples were ground and passed through a 2 mm soil sieve. One part was used to determine soil pH (pH), total salt content (TS), and electrical conductivity (EC), and the other part was ground again and passed through a 0.15 mm soil sieve to determine soil total nitrogen (STN), soil total phosphorus (STP), soil total potassium (STK), and soil organic matter (SOM).

2.4. Determination of Leaf Traits

Leaves collected from the field were washed with deionized water and placed in a constant-temperature drying oven at 105°C for 30 min. The leaves were then dried to a constant weight at 80°C, and their dry weight was measured. The dried leaves were crushed using a pulverizer (15000 r/min), ground, and sieved (0.2 mm) to determine the chemical elements in the leaves. Based on the standard plant trait measurement method [28], we measured 27 leaf traits of *P. euphratica* and divided them into three categories according to their functions: eight leaf morphological traits, including leaf water content (LWC) and specific leaf area (SLA); seven stoichiometric traits, including leaf total nitrogen (LN) and leaf total phosphorus (LP); and 12 anatomical structural traits, including leaf sponge tissue (ST) and leaf palisade tissue (PT). The specific names, abbreviations, and unit information of the traits are detailed in Table A2.

The carbon content of leaf samples was determined using the potassium dichromate oil bath heating method. The nitrogen content was determined using the Kjeldahl method with a Kjeldahl nitrogen analyzer (Hanon, K9840, Shanghai, China). Phosphorus content was determined using an ultraviolet spectrophotometer (INESA, L8, Shanghai, CHINA) following the molybdenum antimony scandium colorimetric method. The potassium content was determined using a flame photometer (INESA, FP4231, Shanghai, CHINA) and the H_2SO_4-H_2O_2 digestion method. The morphological characteristics of the leaves were analyzed using ImageJ (1.53t, 2022). The anatomical structures of the leaves were observed using the paraffin sectioning method (Figure 2b). The paraffin sections were observed under a digital microscope (Leica, Wetzlar, Germany) and analyzed using an image processor (Leica Application Suite V4.0.0 DVD, Wetzlar, Germany).

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2.5. Climate Data And Soil Data Acquisition

Data for the 19 climatic factors in this study (Table A3) were obtained from the WorldClim database (www.worldclim.org) [29]. The determination of soil included water content (WC), total salt content (TS), soil organic matter (SOM), soil total nitrogen (STN), soil total phosphorus (STP), soil total potassium (STK), soil carbon-nitrogen ratio (SC:N), soil carbon-phosphorus ratio (SC:P), soil nitrogen-phosphorus ratio (SN:P), electrical conductivity (EC), and soil pH (Table A4). TS was determined using the residue-drying method. WC was determined using the aluminum box drying method. EC was obtained by measuring the soil leaching solution using a conductivity meter. The pH of the soil leachate was measured using a pH meter. The STN and SOM contents were determined using a FLASHSMART elemental analyzer (Thermo Fisher, FlashSmart CN/CNS, GERMANY). The STP was determined using a sodium hydroxide melting method-ultraviolet spectrophotometer (INESA, L8, Shanghai, CHINA). STK was determined using the sodium hydroxide extraction-flame photometric method (INESA, FP4231, CHINA).

2.6. Leaf Trait Network Parameters and Their Ecological Significance

The leaf trait network (LTNs) is a multidimensional network comprising nodes and edges. Nodes represent leaf traits and edges represent relationships between traits. The strength of the trait relationship was determined by calculating the absolute value of Pearson's correlation coefficient (|r|, r>0.2). The correlation coefficient of $P<0.05$ was retained and set to 1. The correlation coefficient below the threshold was set to zero, and an adjacency matrix A=[ai, j] was generated. The edges were then weighed and visualized [30].

The overall characteristics of LTNs are described by their diameter, average path length, edge density, modularity, and average clustering coefficient. The diameter represents the maximum and minimum distances between any two nodes in the network. The average path length is the average shortest path between all the nodes. Edge density is the ratio of the actual edge to the maximum possible edge. A short diameter, short path, and high edge density indicate high synergy between traits. Modularity describes the degree of separation between subnetworks [31], and high modularity indicates that the functional modules are clear. The average clustering coefficient represents the average of clustering coefficient of each trait in the leaf trait network [32], and a high value indicates that some traits have good synergy. The node parameters of LTNs include degree, closeness, and betweenness, which are used to quantify the relationships between traits and identify their topological roles and adaptability in LTNs [33]. The degree represents the number of edges connected to the node, and the high-degree trait is the hub trait of the network. Closeness is the reciprocal of the shortest path length from a specific node to other nodes. The high-closeness trait is closely related to other traits. Betweenness refers to the number of shortest paths through a node, and the high-betweenness trait is the *bridge* or *intermediary* of the functional module.

2.7. Data Analyses

Excel 2007 was used to organize the experimental data, and SPSS19.0 software was used to analyze the data. Network construction and statistical analyses were performed using Origin Drawing (2021) and R (4.3.0 version, 2023).

The R 'igraph' package was used to calculate the parameters of node traits and total LTNs. Variance decomposition analysis (VPA) was performed using the 'vegan' package in R to explain the effects of different environmental factors (climate and soil) on the network parameters.

3. Results

3.1. Leaf Trait Variability of P. euphratica in the Main Stream of Tarim River

Based on the leaf trait dataset of 300 *P. euphratica* trees in 20 plots along the main stream of the Tarim River, spatial variability was studied. The individual variation characteristics of 27 traits of *P. euphratica* leaves in the main stream of the Tarim River (Figure 3a) and the overall variation characteristics of three types of traits (leaf morphological, stoichiometric, and anatomical structure traits) (Figure 3b) are shown.

The degree of variation in the leaf morphological traits ranged from 7.596 to 29.864%. The degree of variation in leaf WC (7.596%) was the smallest, showing weak variation, and the remaining leaf morphological traits showed medium variation. Among them, the single-leaf area (29.865%) and dry weight of a single leaf (29.688%) showed the highest variability.

The degree of variation in the leaf stoichiometric characteristics was between 8.503 and 75.789%. Only the degree of variation of LC (8.503%) was the smallest, showing weak variation. The remaining leaf stoichiometric characteristics showed medium variation, among which the variation in the leaf C:P ratio (5.789%) was the highest.

The degree of leaf anatomical structure trait variation ranged from 9.978 to47.268%; only the degree of variation of the cell tension ratio (9.978%) was the smallest, and the other leaf anatomical structure traits showed medium variation, among which the variation in the midrib vascular bundle (47.268%) was the largest.

The overall leaf anatomical traits of the main stream of the Tarim River showed 28.68% variation, the overall leaf morphological traits showed 20.09% variation, and the overall leaf stoichiometric traits showed 42.02% variation. Leaf stoichiometry exhibited the largest variation among the three leaf traits.

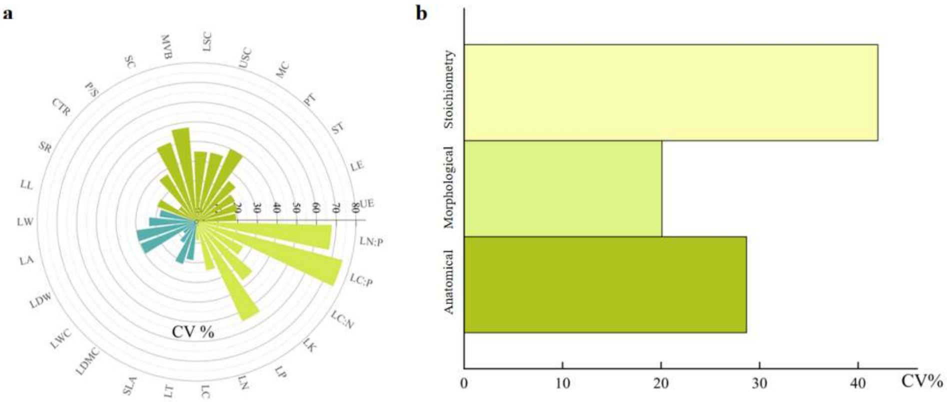

Figure 3. The coefficient of variation of 27 leaf traits and the overall variation characteristics of the three types of leaf traits. **(a)** The coefficient of variation for the 27 leaf traits. **(b)** The overall variation characteristics of three types of leaf traits. (CTR: Cell tension ratio, P/S: The ratio of palisade tissue to sponge tissue, SC: Sclerenchyma, MVB: Median vascular bundle, LSC: Lower stratum corneum, USC: Upper stratum corneum, MC: Mucous cells, PT: palisade tissue, ST: Spongy tissue, LE: Lower epidermal thickness, UE: Upper epidermal thickness, LN:P: Leaf nitrogen to phosphorus ratio, LC:P: Leaf organic matter to phosphorus ratio, LC:N: Leaf organic matter to nitrogen ratio, LK: Leaf total potassium, LP: Leaf total phosphorus, LN: Leaf total nitrogen, LC: Leaf total organic matter, LT: Leaf thickness, SLA: Specific leaf area, LDMC: Leaf dry matter content, LWC: Leaf water content, LDW: Leaf dry weight, LA: Leaf area, LW: Leaf width, LL: Leaf length, and SR: Spongy ratio).

3.2. *Spatial Variability of Leaf Trait Network of P. euphratica in the Main Stream of Tarim River*

The network of each plot and whole-leaf traits was constructed (Figure 4), and the network parameters were calculated. In the entire reach of the main stream of the Tarim River, the maximum, minimum, and average values of the network parameters of the 20 sample points (Table A5) and the variability of the overall network parameters were as follows (Figure 5): the maximum average path length of the network was 4.595, the minimum value was 1.343, the average value was 2.150, and the coefficient of variation was 32.971%. The maximum diameter was 11.170, the minimum diameter was 3.090, the average diameter was 5.166, and the coefficient of variation was 35.359%. The maximum edge density was 0.247, the minimum was 0.101, the average was 0.136, and the coefficient of variation was 25.183%. The maximum value of the average clustering coefficient was 0.727, the minimum value was 0.434, the average value was 0.535, and the coefficient of variation was 17.214%. The maximum modularity was 0.674, the minimum was 0.265, the average was 0.555, and the coefficient of variation was 19.336%. Among them, the variability in the diameter was the largest and the variability in the average clustering coefficient was the smallest.

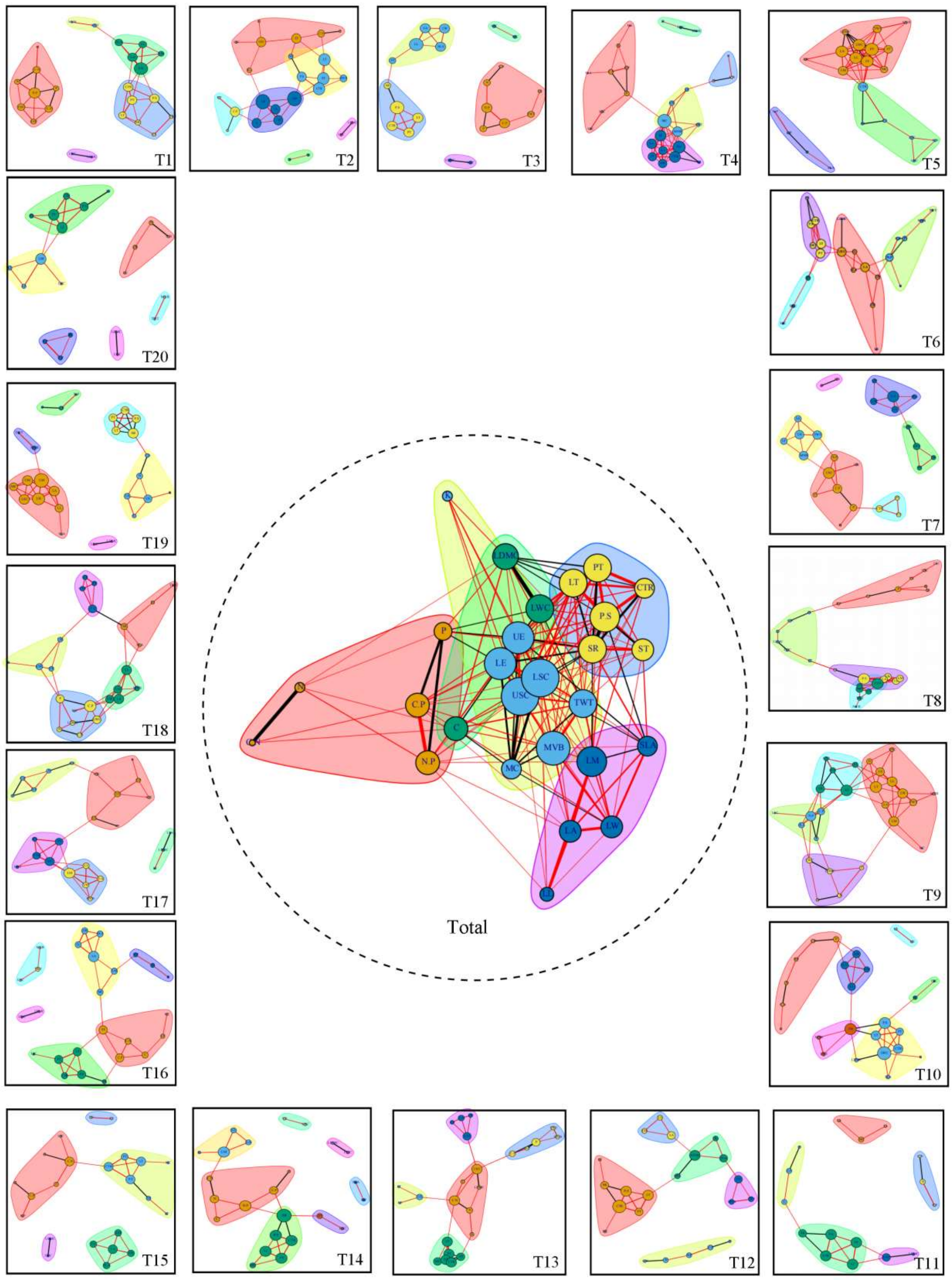

Figure 4. Leaf trait network and whole leaf trait network of *P. euphratica* in 20 sampling sites (T1–T20) in the main stream of Tarim River. Note: Features with the same background color belong to the same module; the red line shows a positive correlation, the black line shows a negative correlation, the line width indicates the strength between traits, and the node size indicates the degree of the trait. K: Leaf total potassium, LDMC: Leaf dry matter content, PT: Palisade tissue, LT: Leaf thickness, CTR: Cell tension ratio, LWC: Leaf water content, P.S: The ratio of palisade tissue to sponge tissue, P: Leaf total phosphorus, UE: Upper epidermis thickness, SR: Spongy ratio, ST: Sponge tissue, LE: Lower epidermis thickness, LSC: Lower stratum corneum, USC: Upper stratum corneum, TWT: Sclerenchyma, N: Leaf total nitrogen, C.P: Leaf organic matter to phosphorus ratio, C: Leaf total organic matter, MVB: Midvein vascular bundle, LM: Leaf dry weight, SLA: Specific leaf area, C.N: Leaf organic matter to nitrogen ratio, N.P: Leaf nitrogen to phosphorus ratio, MC: Mucilage cells, LA: Leaf area, LW: Leaf width, and LL: Leaf length.

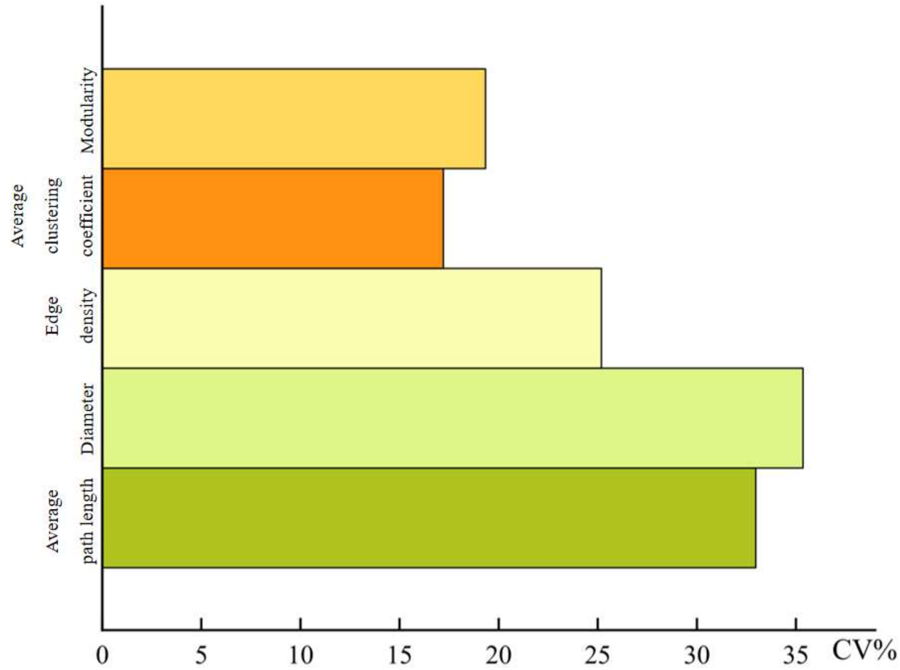

Figure 5. The variability of network parameters in the main stream of Tarim River.

3.3. Relationship Between Leaf Trait Network of P. euphratica and Soil Factors in the Main Stream of Tarim River

PCA analysis of the 11 soil factors (Figure 6) showed that the first four principal components accounted for 90.7% of the original information, whereas the first (PC1-1), second (PC1-2), third (PC1-3), and fourth (PC1-4) principal components explained 35.5, 29.1, 13.9, and 12.2% of the original information, respectively. SOM, WC, and STK were selected as representative indicators, and correlation analysis was performed using network parameters (Figure 7). The results showed that the average path length, diameter, and modularity of the leaf trait network were negatively correlated with WC, STK, and SOM, whereas edge density and average clustering coefficient were positively correlated. Modularity was significantly negatively correlated with STK and SOM ($P<0.05$).

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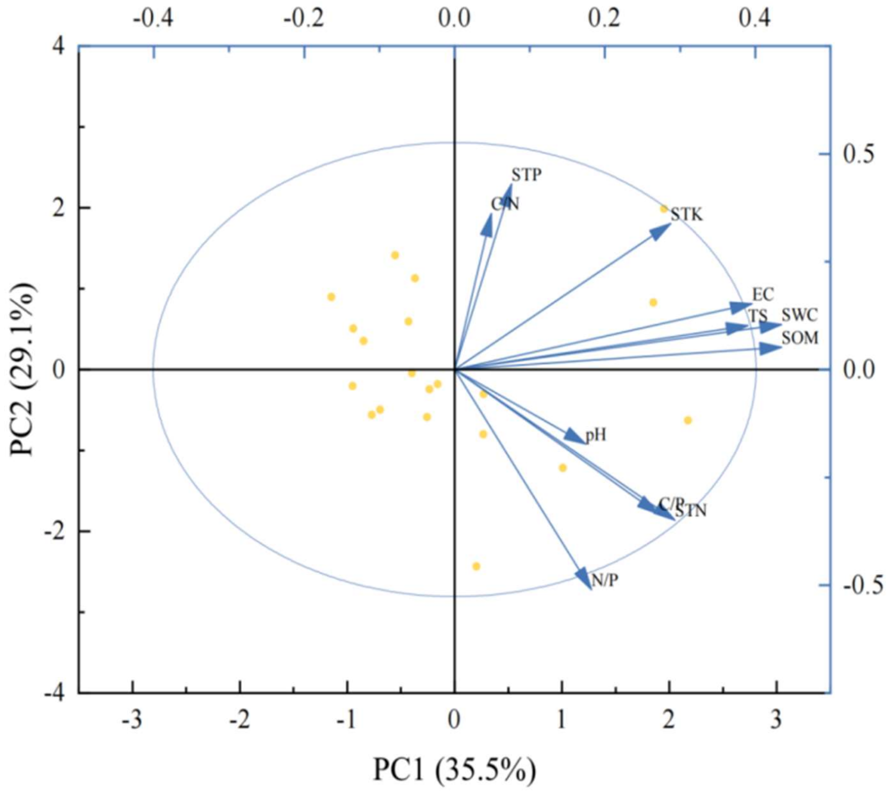

Figure 6. PCA analysis of soil factors. Note: C/N: Soil organic matter to nitrogen ratio, STP: Soil total phosphorus, STK: Soil total potassium, EC: Electrical conductivity, TS: Total salt, SWC: Water content, SOM: Soil total organic matter, pH: pH, C/P: Soil organic matter to phosphorus ratio, STN: Soil total nitrogen, and N/P: Soil nitrogen : phosphorus ratio.

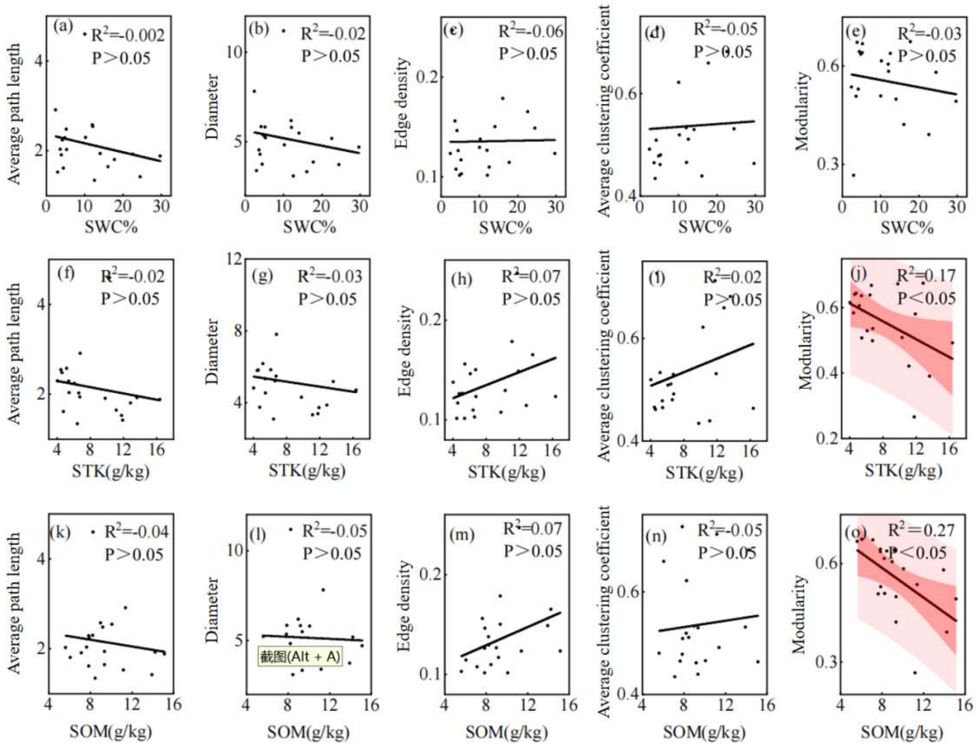

Figure 7. The relationships between overall parameters of leaf traits network and soil factors. Note: The shaded red area represents the 95% confidence interval and the black line represents the linear regression fit. SWC: Water content, STK: Soil total potassium, SOM: Soil total organic matter.

3.4. Relationship Between Leaf Trait Network of P. euphratica and Climatic Factors Along the Main Stream of Tarim River

The PCA analysis of the 19 climatic factors (Figure 8) showed that the first three principal components accounted for 87.21% of the original information, and the first (PC1-1), second (PC1-2), and third (PC1-3) principal components accounted for 60.89, 15.23, and 11.09% of the original information, respectively. BIO03, BIO06, and BIO13 were selected as representative indicators to further analyze their correlation with the network parameters (Figure 9). The results showed that the average path length, diameter, and modularity of the leaf trait network were negatively correlated with BIO03, whereas edge density and average clustering coefficients were positively correlated with BIO03. The average clustering coefficient was also significantly positively correlated with BIO03 (P<0.05). The average path length, diameter, and modularity of the leaf trait network were positively correlated with BIO06, and the average path length and diameter were significantly positively correlated with BIO06 (P<0.05), while the edge density and average clustering coefficient were negatively correlated with BIO06. The average clustering coefficient was significantly negatively correlated with BIO06 (P<0.05). The average path length, diameter, and edge density of the leaf trait network were positively correlated with BIO13; the diameter was significantly positively correlated with BIO13 (P<0.05), but negatively correlated with the average clustering coefficient and modularity.

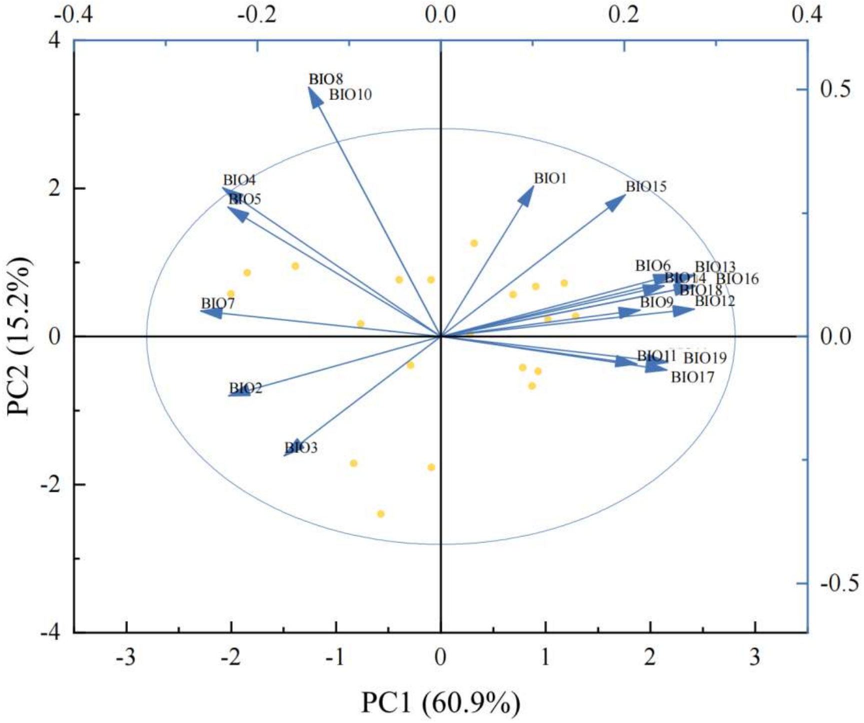

Figure 8. PCA analysis of climate factors. Note: BIO7: Temperature annual range, BIO5: Max temperature of warmest month, BIO4: Temperature seasonality, BIO8: Mean temperature of wettest quarter, BIO10: Mean temperature of warmest quarter, BIO1: Annual mean temperature, BIO15: Precipitation seasonality, BIO6: Min temperature of coldest month, BIO13: Precipitation of wettest month, BIO14: Precipitation of driest month, BIO16: Precipitation of wettest quarter, BIO18: Precipitation of warmest quarter, BIO9: Mean temperature of driest quarter, BIO12: Annual precipitation, BIO11: Mean temperature of coldest quarter, BIO19: Precipitation of coldest quarter, BIO17: Precipitation of driest quarter, BIO3: Isothermality, and BIO2: Mean diurnal range.

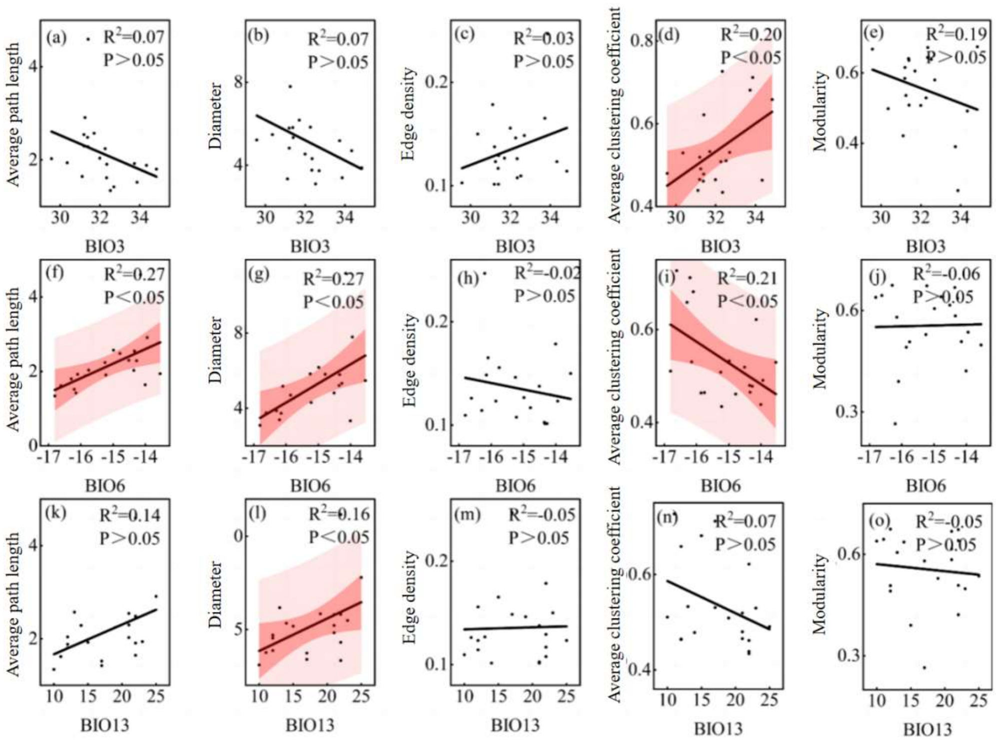

Figure 9. Relationship between overall parameters of leaf traits network and climatic factors. Note: The shaded red area represents the 95% confidence interval and the black line represents the linear regression fit. BIO3: Isothermality, BIO6: Min temperature of coldest month, BIO13: Precipitation of wettest month.

3.5. Effects of Climate and Soil on Network Parameters of Leaf Traits

The effects of climate and soil on the leaf trait network of *P. euphratica* were quantified using VPA (Figure 10). The results showed that climate, soil, and the interactions thereof had a common effect on the average path length, diameter, edge density, average clustering coefficient, and modularity. The combined effects of climate and soil explained 57% of the average path length. In the single effect, climate had a greater impact on the average path length, with an interpretation of 53.96%, whereas the single effect of soil was small, with an interpretation of 5.2%. In the interaction analysis, these two factors explained 2.1% of the variation. The combined effects of climate and soil accounted for 55% of the diameter. In the single effect, climate had a greater influence on diameter, explaining 50.53%. The single effect of soil was small, and the explanation was 4.35%. In the interaction analysis, these two factors explained 0.18% of the variation. The combined effects of climate and soil accounted for 71% of edge density. In the single effect, climate had a greater influence on edge density, with an explanatory degree of 50.73%. The single effect of soil was small, with an explanatory degree of 33.79%. In the interaction analysis, these two factors explained 13.34% of the variation. The combined effects of the climate and soil accounted for 70% of the average clustering coefficients. Among the individual effects, climate had the greatest impact on the average clustering coefficient, with an interpretation degree of 63.47%. The individual effect of the soil was small, with an interpretation degree of 10.19%. In the interaction analysis, the two factors explained 3.36% of variation. The combined effects of the climate and soil accounted for 88% of the average clustering coefficients. Among the individual effects, soil had the greatest impact on the average clustering coefficient, with an interpretation degree of 50.45%. The individual effects of the climate were relatively small, with an interpretation degree of 43.90%. In the interaction analysis, these two factors explained 6.07% of the variation. Simultaneously, we found that the nodal parameters of some leaf traits in the LTN were also related to climate and soil factors (Tables A6–A8).

Figure 10. Interpretation degree of climate and soil to network parameters.

4. Discussion

4.1. The Relationship Between Leaf Trait Network of P. euphratica and Soil Factors in the Main Stream of Tarim River

In the main stream of the Tarim River, the variability in average path length and diameter was large, indicating that the interaction and connection between leaf traits of *P. euphratica* may be more diversified. The variability in edge density and modularity may be affected by the availability of resources and environmental conditions, such as climate and soil [34]. These factors may promote the leaf trait network to form a closer or more dispersed network structure to maximize the resource utilization efficiency. The variability of the average clustering coefficient indicates the local connectivity and trait tendency of leaf traits of *P. euphratica*, which reflects the heterogeneity of environmental conditions in the main stream of the Tarim River Basin and makes the leaf trait network of *P. euphratica* adopt different strategies when forming functional groups or modules.

WC, STK, and SOM are important indices that reflect soil fertility, fertilizer supply capacity, and plant growth status. The negative correlation between the average path length, diameter, modularity, WC, STK, and SOM indicated that when the content of WC, STK, and SOM was high, the connection degree of the leaf trait network increased, and the network structure was more concentrated. This indicates that in environments with abundant resources, the interaction between leaf traits is closer [35], and the network structure is more concentrated and efficient. Simultaneously, the decrease in modularity indicated that the functional modules were closely connected under better soil conditions, and the differences between different modules were reduced. Modularity was significantly negatively correlated with STK and SOM, indicating that these had a greater impact on the functional modules of the leaf trait network. Abundant soil resources reduced the modularity of the leaf trait network, reflecting the common utilization and interdependence of resources between the functional modules of leaf traits in *P. euphratica*. There was a positive correlation between WC, STK, SOM, edge density, average, and the clustering coefficient. This is likely because a resource-rich environment with high WC, STK, and SOM promotes direct interactions between leaf traits and builds a closer network structure.

4.2. Relationship Between Leaf Trait Network of P. euphratica and Climatic Factors Along the Main Stream of Tarim River

High isothermality indicates that the climate in the region is relatively stable [36]. Average path length, diameter, and modularity were negatively correlated with BIO03, indicating that the leaf

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trait network of *P. euphratica* tended to form a more compact and centralized structure in areas with relatively small temperature changes and relatively stable environments. This may be because under relatively stable temperature conditions, the interactions between traits are more frequent and the synergy is better, resulting in a decrease in the average path length and diameter, whereas higher isothermality may reduce niche differentiation and the modularity of the network [37]. The edge density and average clustering coefficient were positively correlated with BIO03, indicating that in an environment with small temperature fluctuations, the connectivity of the *P. euphratica* leaf trait network and the relationships between traits increased. There was a significant positive correlation between BIO03 and the average clustering coefficient, indicating that only specific traits, rather than all traits in the network, had better synergy and that the leaf traits of *P. euphratica* tended to form specific functional modules to achieve their functions. This may be an adaptation to resource utilization efficiency and survival strategies in the environment, reflecting the important relationship between the closely related and mutually supportive leaf traits of *P. euphratica*.

The average path length and diameter were significantly positively correlated with BIO06, which was likely due to the weakening of the synergy between the leaf network traits in the low-temperature environment, and the structure of the leaf trait network became more dispersed. *P. euphratica* adapts by adjusting its physiological and morphological characteristics. Edge density and average clustering coefficient were significantly negatively correlated with BIO06. This significant negative correlation indicates that *P. euphratica* may reduce the relationship between leaf traits in cold environments and aggregate traits into specific functional modules to resist low-temperature stress, thereby improving the ability to adapt to the environment.

Precipitation during the wettest months is the most significant climatic factor affecting tree height growth [38]. The positive correlation between BIO13 and average path length, diameter, and edge density showed that with an increase in the precipitation of the wettest month (BIO13), the overall independence of leaf traits increased. The average clustering coefficient and modularity were negatively correlated with BIO13, indicating that under high-precipitation conditions, the connections between traits were looser, the local aggregation of the leaf trait network was lower, and the network structure was more dispersed. With increasing rainfall, the leaf trait network module showed a trend of loose internal and tight external connections.

Climatic factors are the main environmental factors affecting the average path length, diameter, edge density, and average clustering coefficient. The explanation for the individual effects is generally stronger than that for soil factors. The influence on the average clustering coefficient was the most significant, with an explanatory degree of 63.47%. Although the explanatory power of soil factors alone is relatively small, the contribution of soil factors is a significant influence on modularity, which indicates that the influence of soil factors on some leaf trait network parameters cannot be ignored, especially when interacting with climatic factors that can significantly change the structure of the leaf trait network. Overall, soil factors also significantly affected specific trait parameters; however, climatic factors were usually dominant.

5. Conclusions

The average path length, diameter, and edge density in the leaf trait network of *P. euphratica* in the main stream of the Tarim River had a large degree of variation between 20 sampling points, and the overall leaf network parameters had a large spatial variability. Under the influence of different soil and climatic factors, the leaf trait network is promoted to form a closer or more dispersed network structure, thereby maximizing resource utilization efficiency.

Leaf trait networks were significantly affected by environmental factors. Average path length, diameter, and modularity were negatively correlated with water content, soil total potassium, and soil total organic matter, whereas edge density and average clustering coefficient were positively correlated with these soil factors. The negative correlations between modularity and soil total potassium and soil total organic matter were significant. In addition, these leaf trait network parameters were also related to climatic factors, among which average path length, diameter, and modularity were negatively correlated with isothermality and positively correlated with min temperature of coldest month. In contrast, the edge density and average clustering coefficient were positively correlated with isothermality but negatively correlated with min temperature of coldest month, and the correlation between the average clustering coefficient and these two climatic factors was significant. The average path length, diameter, and edge density of the leaf trait network were positively correlated with precipitation of wettest month, whereas the average clustering coefficient and modularity were negatively correlated with precipitation of wettest month, and the diameter was positively correlated with precipitation of wettest month.

Climatic factors play a decisive role in shaping the network structure of leaf traits and are the main environmental factors affecting the network parameters of leaf traits of *P. euphratica*. The degree of interpretation of individual effects was generally higher than that of the soil factors; However, soil factors had the greatest influence on the modularity when acting alone. The interactions between soil and climatic factors contributed to all leaf trait network parameters. Although the interpretation was relatively small, climatic and soil factors alone did not affect the leaf trait network. Interactions between these factors also shaped the spatial variability of leaf traits to a certain extent. However, compared to soil factors, climatic factors can significantly change the structure of the leaf trait network. Crucially, the variation in the *P. euphratica* leaf trait network was mainly driven by environmental factors.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

Author contributions: C.P.: Conceptualization; Formal analysis; Investigation; Methodology; Software; Validation; Visualization; Roles/Writing- original draft; and Writing- review and editing. S.Y.: Data curation; Investigation; Methodology; Software; Validation; Visualization; and Roles/Writing- original draft. W.H.: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; and Writing- review and editing. J.W.: Data curation; Investigation; Software; Visualization. S.S.: Investigation; Software; Visualization. P.Z.: Investigation; Software; Visualization. P.J.: Supervision; and Writing- review and editing.

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Data Availability Statement: The data and code that supports the findings of this study are available in the supplementary material of this article. The data that support the findings of this study are openly available in the WorldClim database at https://www.worldclim.org.

Conflicts of Interest: None declared.

Appendix A

Table A1. Sample point information.

Sample point	Longitude/ °E	Latitude/ °N	Altitude/ m	Distance from bank/ km
T1	80.916	41.137	1084	18.475
T2	80.944	40.437	1025	1.093
T3	81.155	40.425	1018	9.569
T4	81.6	40.757	1001	2.982
T5	81.929	40.654	994	0.828
T6	82.152	40.845	988	0.614
T7	82.343	41.053	978	2.954
T8	82.743	40.963	970	0.261
T9	83.015	40.904	962	0.969
T10	83.162	41.052	957	0.774
T11	83.316	41.006	955	0.993
T12	84.202	41.3	932	3.596

T13	84.213	41.245	934	0.957
T14	84.238	41.172	933	0.524
T15	85.127	41.994	974	4.346
T16	86.163	41.19	891	0.171
T17	86.843	40.924	874	1.85
T18	87.076	40.894	868	12.269
T19	87.541	40.645	856	4.994
T20	87.904	40.454	845	0.045

Table A2. Classification units and abbreviations for leaf traits.

Classification	Full name	Unit	Abbreviation
Leaf morphological traits	Leaf length	cm	LL
	Leaf width	cm	LW
	Leaf area	cm^2	LA
	Leaf dry weight	g	LDW
	Leaf water content	%	LWC
	Leaf dry matter content	g	LDMC
	Specific leaf area	cm^2/g	SLA
	Leaf thickness	μm	LT
Stoichiometric characteristics	Leaf total organic matter	g/kg	LC
	Leaf total nitrogen	g/kg	LN
	Leaf total phosphorus	g/kg	LP
	Leaf total potassium	g/kg	LK
	Leaf organic matter : nitrogen ratio	\	LC:N
	Leaf organic matter : phosphorus ratio	\	LC:P
	Leaf nitrogen : phosphorus ratio	\	LN:P
Leaf anatomical structure traits	Sponge tissue	μm	ST
	Upper epidermis thickness	μm	UE
	Lower epidermis thickness	μm	LE
	Mucilage cells	$μm^2$	MC
	Palisade tissue	μm	PT
	Upper stratum corneum	μm	USC
	Lower stratum corneum	μm	LSC
	Midvein vascular bundle	$μm^2$	MVB
	Sclerenchyma	$μm^2$	SC
	ratio of palisade tissue to sponge tissue	%	P/S
	Cell tension ratio	%	CTR
	Spongy ratio	%	SR

Table A3. Soil factors.

Full name	Unit	Abbreviation
Water content	%	WC
Electrical conductivity	μs/cm	EC
Total salt	g/kg	TS
pH	\	pH
Soil total organic matter	g/kg	SOM
Soil total nitrogen	g/kg	STN
Soil total phosphorus	g/kg	STP
Soil total potassium	g/kg	STK
Soil organic matter : nitrogen ratio	\	SC:N
Soil organic matter : phosphorus ratio	\	SC:P
Soil nitrogen : phosphorus ratio	\	SN:P

Table A4. Climate factors.

Climate factors	Full name
BIO1	Annual mean temperature
BIO2	Mean diurnal range (mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (×100)
BIO4	Temperature seasonality (standard deviation ×100)
BIO5	Max temperature of warmest month
BIO6	Min temperature of coldest month
BIO7	Temperature annual range (BIO5-BIO6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

Table A5. Network parameters of 20 sampling points.

Sample point	Average path length	Diameter	Edge density	Average clustering coefficient	Modularity
T1	1.422	3.731	0.149	0.531	0.58
T2	1.882	4.697	0.123	0.464	0.492
T3	1.802	3.871	0.114	0.659	0.674
T4	1.923	5.176	0.165	0.681	0.39
T5	1.523	3.39	0.247	0.712	0.265
T6	2.24	5.837	0.146	0.508	0.529
T7	1.907	4.307	0.108	0.434	0.673
T8	4.595	11.17	0.129	0.621	0.508
T9	1.643	3.333	0.178	0.439	0.421
T10	2.91	7.796	0.123	0.491	0.536
T11	1.939	5.479	0.15	0.529	0.498
T12	2.483	5.814	0.117	0.462	0.641
T13	2.297	4.821	0.138	0.519	0.616
T14	2.546	5.791	0.101	0.466	0.584
T15	2.028	5.212	0.103	0.48	0.668
T16	2.286	5.331	0.102	0.478	0.636
T17	2.571	6.173	0.127	0.533	0.606
T18	2.037	4.537	0.156	0.465	0.507
T19	1.615	3.758	0.126	0.727	0.644
T20	1.343	3.09	0.11	0.511	0.639
MAX	4.595	11.17	0.247	0.727	0.674
MIN	1.343	3.09	0.101	0.434	0.265
AVERAGE	2.15	5.166	0.136	0.535	0.555

Table A6. Relationship between degree of network nodes and environmental factors.

Trait	BIO3	BIO6	BIO13	SWC%	STK(g/kg)	SOM(g/kg)
LL	.461*	/	/	/	.552*	/
LDW	/	/	/	/	/	/
LT	/	/	/	/	/	/
LW	/	/	/	/	/	/
LA	.490*	/	/	/	.498*	/
LDMC	/	/	/	/	/	/
SLA	/	/	/	/	/	/
LWC	/	/	/	-.461*	/	/
LSC	/	-.649**	-.582**	/	/	/
USC	/	/	/	/	/	/
MC	/	/	/	/	/	/
MVB	/	/	/	/	/	.444*
P/S	/	/	/	/	/	/

PT	/	/	/	/	/	.482*
SR	/	/	/	/	/	/
ST	/	/	/	/	/	/
TWT	/	/	/	/	/	/
LE	/	/	/	/	/	/
UE	/	/	/	/	/	/
CTR	/	/	/	/	/	.518*
LC	-.505*	.568**	/	/	/	/
LC:N	/	/	/	/	/	/
LC:P	/	/	/	/	/	/
LK	/	/	/	.454*	/	.449*
LN	/	/	/	/	-.448*	/
LN:P	/	/	/	/	/	/
LP	/	/	/	/	/	/

*: At $P<0.05$ (two-tailed), the correlation was significant. **: At $P<0.01$ (two-tailed), the correlation was significant.

Table A7. Relationship between network node closeness and environmental factors.

Trait	BIO3	BIO6	BIO13	SWC%	STK(g/kg)	SOM(g/kg)
LL	/	/	/	/	/	/
LDW	/	/	/	/	/	/
LT	/	-.456*	/	/	/	/
LW	/	/	/	/	/	/
LA	/	/	/	/	/	/
LDMC	/	/	-.586**	/	/	/
SLA	/	/	/	/	/	/
LWC	/	/	-.578**	/	/	/
LSC	.512*	/	/	/	/	/
USC	/	/	/	/	/	/
MC	/	/	/	/	/	/
MVB	/	/	/	/	/	/
P/S	/	/	/	/	/	/
PT	/	-.526*	/	/	/	/
SR	/	/	/	/	/	/
ST	/	/	/	/	/	/
TWT	/	/	-.446*	/	/	/
LE	/	/	/	/	/	/
UE	/	/	/	/	/	/
CTR	/	/	/	/	/	/
LC	/	/	/	/	/	/
LC:N	/	/	/	/	/	/
LC:P	/	-.646**	-.492*	/	/	/

LK	/	/	/	/	/	/
LN	/	/	/	/	/	/
LN:P	/	/	/	/	/	/
LP	/	-.497*	/	/	/	/

*: At *P*<0.05 (two-tailed), the correlation was significant. **: At *P*<0.01 (two-tailed), the correlation was significant.

Table A8. Relationship between the betweenness of network nodes and environmental factors.

Trait	BIO3	BIO6	BIO13	SWC%	STK(g/kg)	SOM(g/kg)
LL	/	/	/	/	/	/
LDW	/	/	/	/	/	/
LT	-.820*	.828*	/	/	/	/
LW	/	/	/	/	/	/
LA	/	/	/	/	/	/
LDMC	/	/	/	/	/	/
SLA	/	/	/	/	/	/
LWC	/	/	/	/	/	/
LSC	.785*	-.858*	/	/	/	/
USC	/	/	/	/	/	/
MC	/	/	/	/	/	/
MVB	/	/	/	/	/	/
P/S	/	/	/	/	/	/
PT	/	/	/	/	/	/
SR	/	/	/	/	/	/
ST	/	/	/	/	/	/
TWT	/	/	/	/	/	/
LE	/	/	/	/	/	/
UE	/	/	/	/	/	-.798*
CTR	/	/	/	/	.795*	.774*
LC	/	/	/	/	/	/
LC:N	/	/	/	/	/	/
LC:P	/	/	/	/	/	/
LK	/	/	/	/	/	.828*
LN	/	/	/	/	/	/
LN:P	/	/	/	/	/	/
LP	/	/	/	/	/	/

*: At *P*<0.05 (two-tailed), the correlation was significant. **: At *P*<0.01 (two-tailed), the correlation was significant.

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