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Environmental Gradients and Vegetation Types Alter the Effects of Leaf Traits on the Dominance of Woody Angiosperm Species

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Abstract: Leaf traits can reflect plant photosynthetic capacity, resource utilization strategy and adaptability to the environment. However, whether species' leaf traits are tightly related to the functioning of their community and how that relationship varies with environmental gradients remain largely unexplored. We measured 6 leaf traits, including petiole fineness (PF), specific leaf area (SLA), leaf area (LA), leaf length–width ratio (LLWR), leaf nitrogen content (LN) and leaf phosphorus content (LP), of 733 populations (415 species) of 19 woody angiosperm communities in the eastern Qinghai–Tibetan Plateau across multiple climatic zones or vegetation types. Through meta-analysis and relative importance analysis, the relationship between leaf traits of species and their community dominance and its change with environments were analyzed. The results showed that species dominance was correlated positively with their LA and LP, suggesting that species with high light interception and resource utilization capacity can easily become dominant species in woody angiosperm communities. Along the altitudinal gradient, the effect of PF and SLA on species dominance increased and changed significantly in their pattern, from positive or nonsignificant in temperate forests to negative in alpine and subalpine shrubs, suggesting that increasing petiole mechanical support and lamina protection cost is a dominant leaf growth strategy in stressful high-altitude environments. Our findings demonstrate that the demand for efficient light acquisition and/or utilization and species adaptability or tolerance to specific environmental stress are key mechanisms by which leaf traits govern community composition and functioning.

Keywords: altitudinal gradient; community structure; leaf chemical traits; petiole fineness; specific leaf area; species dominance

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1. Introduction

Leaf traits determine the response of plants to environmental factors and represent various aspects of ecological strategies such as vegetative growth rate, mortality rate, photosynthetic and nitrogen fixation capacity, nitrogen and phosphorus concentration, and even reproductive progress and success [1,2]. In the context of global warming, leaf traits serve as useful tools governing the sensitivity of species to environmental change and their ecological role [3,4]. Thus, it is of great significance to study the variation in leaf traits along environmental gradients to further our understanding of the adaptation strategies of plants to environmental variation [1,5].

Leaf traits can be divided into morphological, chemical and physiological [6,7]. Morphological traits refer to the structure of leaves, including leaf area, specific leaf area, leaf thickness, shape, etc., which can reflect the plant's survival strategies [5,8]. Chemical traits represent leaf chemical investment and affect the physiological process and biochemical activity of leaves [1,9]. Both morphological and chemical traits are easy to measure and are relatively evolutionarily stable [7,10]. In contrast, physiological traits, including net photosynthetic rate, respiration rate, stomatal conductance, etc., reflect the leaf growth and metabolic indices of leaves and have relatively large variations in time and space [11–14]. Because physiological traits are difficult to measure and are variable, they often exhibit significant covariance with morphological and chemical traits used for large-scale or multi-species ecological research [4,5].

Among leaf morphologic traits, leaf size and shape are the first considerations due to their importance for energy balance and hydraulic structure [15–17]. Normally, large or broad–round leaves are considered advantageous in cool, humid or shady habitats because their thick leaf margins induce large resistance to the transport of heat and substances [15,18–20], whereas small or narrow leaves predominate in hot, dry and high-light environments due to their capacity to decrease leaf temperature, avoid leaf damage and maintain leaf water balance [16,21]. However, large or broad leaves are dominant under the conditions of high temperature or light because they can promote leaf carbon acquisition [20,22]. Specific leaf area (SLA), the ratio of leaf area to dry leaf mass, has been used widely to predict growth strategies and responses to environmental change [1,23]. It is a key trait related to the tradeoff between leaf life span and nutrient concentration and photosynthetic rate [24,25]. In general, fast-growing species from nutrient- or water-rich habitats usually have a high SLA to enhance leaf nutrient concentration and photosynthesis [5,24].

Petiole is an important tissue connecting the stem and lamina, which has both mechanical support and transport functions [26,27]. The lamina is the main part of a leaf for conducting photosynthesis to fix carbon, with, consequently, a limited investment in petiole [15,21]. For a given petiole mass, the petiole shape can be long and thin to maximize lamina light interception because petiole elongation can send the lamina to a higher and farther position to avoid overlap with its neighbors [28–30], or be short and thick to provide good mechanical support for the lamina and efficient nutrition/water transport [21,27]. Thus, ‘petiole fineness’ (the ratio of petiole length to petiole diameter) is a reliable indicator of petiole shape and can identify the shift in the tradeoff between leaf light interception and support/transport but has received little attention [27,31].

Nitrogen (N) and phosphorus (P) are two of the most important elements in the ecological cycles [28,32]. The roles of N in enzymatic reactions and of P in protein synthesis are irreplaceable [32–35]. Leaf N and P directly influence photosynthesis and respiration during plant growth and development [14,35]. The study of leaf N and P stoichiometry can contribute to the accurate prediction of ecological responses to global change [3,28], whereby plants increase their leaf N and P concentration with decreasing temperature and (or) available water to maintain the photosynthetic carbon gain [3,4,24,36]. However, this large-scale leaf N and P variation trend have not been supported by local-scale research [3,4,32,34,36], suggesting that some critical knowledge on how leaf stoichiometry patterns respond to environmental change and influence plant performance has not been revealed fully.

Most plant species grow in a community, and their performance in the community is the result of two forces. The first is environmental filtering, which results in the selection of species and their traits that allow adaptation to the environment [37,38]. The second is the role of the ‘community’. Species with varying traits hold distinct community statuses due to their differences in resource utilization and environmental adaptability through interactions [39–41]. The two forces are both trait-related. For plant survival and reproduction, it must exist in an environment consistent with its tolerance level, and its own traits play a crucial role [42]. The combination of different aspects of traits in plants can lead to specific biotic interactions and community structure and ultimately can impact ecosystem function [39]. Therefore, trait-based research is an excellent approach to exploring the community performance of species under the backdrop of global climate change [43]. However, although environmental gradients or community factors in plant trait variation have been revealed frequently [5,17,40,44], few studies considered them together [37,45], which leads to confusion due to the often significant difference among sites or community types in leaf traits along an environmental gradient [2,7] or in the importance of leaf traits in structuring plant communities [38,46]. Thus, the research quantifying the relationship between species leaf traits and their community performance in a multi-trait and multi-community space is crucial in examining plants' local adaptation and community assembly, which still remain largely unexplored [13,17,38,45,46]. Here, using leaf trait data of 733 populations of 415 woody species from 19 sites spanning various climate zones or vegetation types and representing a near 3000 m altitude gradient in an eastern part of the Qinghai–Tibetan Plateau (QTP), we presented the first comprehensive investigation of the environmental variation in the leaf trait–species (community) dominance relationship of an entire woody flora. Specifically, we addressed the following questions:

(1) How do the leaf traits relate to species dominance on a site, and across a number of sites, and are there main leaf traits governing species dominance?

(2) Across different environmental gradients, whether the relationship between leaf traits and species dominance changes significantly, and which leaf traits are reliable indicators of the local adaptability of woody angiosperm species in a specific environment and their community performance?

To answer these questions, both meta-analysis and relative importance analysis were used to examine the relationships within each site in different climate zones and vegetation types and then across all the sites. We think this study can provide a clear understanding of the importance of leaf trait variation in the local adaptation and community assembly of plants.

2. Materials and Methods

2.1. Study Area

The study area was located on the eastern edge of the Qinghai–Tibetan Plateau (101.38°–104.33° E, 33.45°–35.08° N, about 38,000 km^2), and belongs to a transitional region of semi-humid and semi-arid areas. The altitude difference within the territory is obvious, forming a subtropical–warm temperate–temperate–subalpine–alpine vertical climate zone. Meteorological factors and woody vegetation types also change obviously with altitude (Table 1). Therefore, it is an ideal place to study trait variation in mountain plants.

Table 1. The meteorological parameters and vegetation characteristics of 19 studied sites.

Site	Altitude (m)	Climatic Zone	Vegetation Type	MAT (°C)	FFM (Months)	LGS (Days)	Canopy Height (m)
1	1080	T-S	DEF	14–16	>10	>300	15–20
2	1430	T-S	DEF	12–15	9–10	280–300	15–18
3	1610	T-S	DF	11–14	8–9	260–280	15–18
4	1750	T-S	DF	10–13	7–8	240–270	12–18
5	1880	T-S	DF	9–12	6–7	230–260	12–15
6	1930	Te	DF	8–11	ca. 6	220–250	10–15
7	2080	Te	DF	7–10	5–6	210–240	10–15
8	2170	Te	DF	6–9	ca. 5	210–230	10–12
9	2300	Te	DF	6–8	4–5	200–220	8–12
10	2640	Te	DF	3–6	3–4	180–200	6–10
11	2800	SA	DFS	2–5	ca. 3	170–190	5–9
12	2920	SA	DFS	1–4	2–3	160–180	5–7
13	3100	SA	DFS	0–3	1–2	150–170	3–6
14	3340	SA	DFS	−1 to 1	0–1	140–160	2–5
15	3500	SA	DES	−2 to 0	0	130–150	1–2.5
16	3610	Al	DES	−3 to −1	0	120–150	0.8–1.8
17	3740	Al	DES	−4 to −1	0	120–140	0.6–1.3
18	3840	Al	DES	−5 to −2	0	110–130	0.4–0.8
19	3930	Al	DES	−5 to −3	0	110–120	0.2–0.5

Note: Meteorological parameters, downloaded from National Meteorological Information Center (http://data.cma.cn/, accessed on 25 April 2022), were the approximate range of climate change for many years. Vegetation type was zonal woody-vegetation-type. MAT—mean annual temperature; FFM—the absolute frost-free months;

LGS—the length of the growing season (based on the average phenological performance of the local dominant woody species); T-S—warm temperate–subtropical; Te—temperate; SA—subalpine; Al—alpine; DEF—mixed deciduous–evergreen forest; DF—deciduous forest; DFS—mixed deciduous forest–shrub; DES—mixed deciduous–evergreen shrub.

2.2. Field Sampling

From June to September in 2018 and 2019, we set up 19 study sites with an average altitude gradient of 150 m (Table 1, Figure 1). At each site, 2 to 4 adjacent 300 m × 300 m plots (altogether 41 plots) were sampled to avoid possible sampling bias. These sites can be divided into four vegetation types: mixed deciduous–evergreen forest (DEF), deciduous forest (DF), mixed deciduous forest–shrub (DFS) and mixed deciduous–evergreen shrub (DES), as well as four climatic regions: warm temperate–subtropical (T-S), temperate (Te), subalpine (SA) and alpine (Al). At every plot, leaf materials were gathered from each woody angiosperm species unless they were extremely rare. For leaf materials of the same species (as seen in Supplementary Data), different populations of the same species in the same site were considered as one sample but in different sites were considered as different samples. The total number of samples (populations) in all sites was 733, belonging to 415 angiosperm species in 143 genera of 59 families (based on the Angiosperm Phylogeny Group IV classification system, as updated in 2016). For each sample, three to five well-growing adult individuals were selected. Additionally, for each individual, 2 or 3 branches with 5 to 20 mature, healthy, fully expanded and undamaged leaves on each branch were chosen at the outer canopy to avoid obvious differences in light conditions [20,47]. The picked leaves were then put into a portable refrigerator [47].

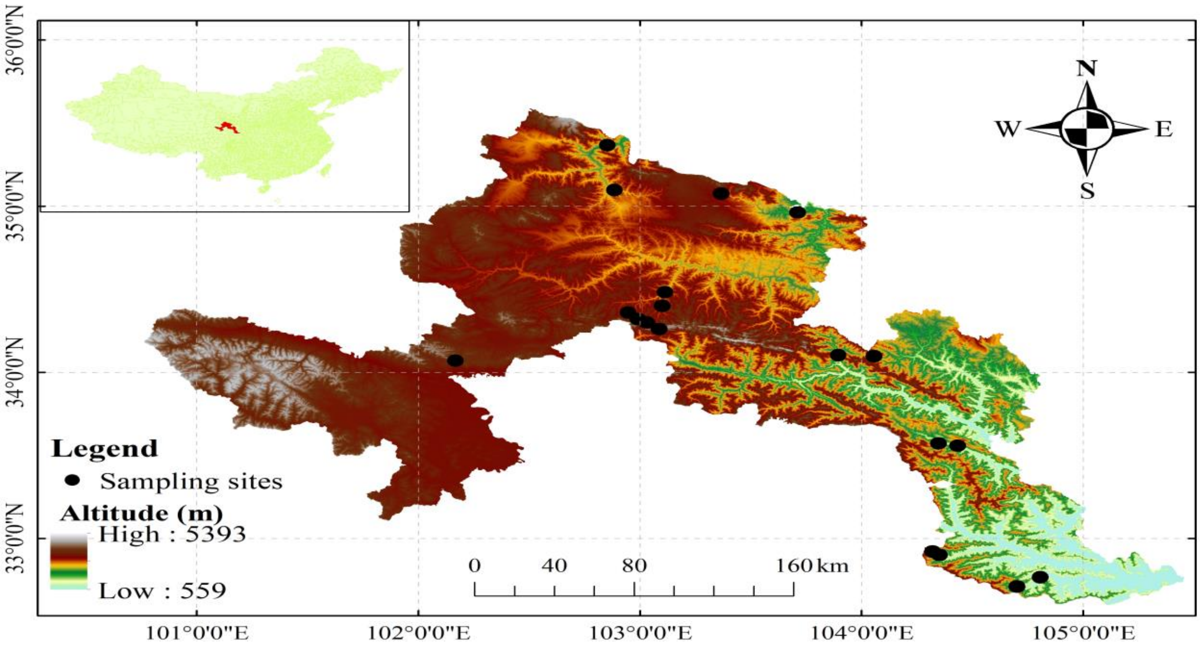

Figure 1. Distribution of the 19 study sites across the eastern edge of the Qinghai–Tibetan Plateau.

2.3. Leaf Traits

For each population, we measured six leaf traits (Table 2), including four leaf morphological traits: petiole fineness (PF), specific leaf area (SLA), leaf area (LA) and leaf length–width ratio (LLWR), and two leaf chemical traits: leaf nitrogen content (LN) and leaf phosphorus content (LP). These traits were measured as follows.

Table 2. Ecological significance of six leaf traits.

Trait	Abbreviation	Values	Ecological Significance
Petiole fineness	PF	Ratio	Photosynthetic capacity, nutrient cycling, signal transduction
Specific leaf area	SLA	mm^2 mg^{-1}	Competitive ability, growth rate, stress tolerance
Leaf area	LA	cm^2	Competitive ability, growth rate, stress tolerance
Leaf length–width ratio	LLWR	Ratio	Light capture
Leaf N concentration	LNC	mg g^{-1}	Metabolic activity, growth rate, nutrient cycling
Leaf P concentration	LPC	mg g^{-1}	Metabolic activity, growth rate, nutrient cycling

2.3.1. LA and LLWR

For each population, 5–20 leaves (or 2–4 large leaves) from different individuals were mixed, representing 1 replicate. In each replicate, all selected leaves were carefully placed on a flatbed scanner (HP LaserJet 1320) to avoid overlap and fully expand bent or contracted leaves. LA was determined by analyzing the scanned leaf pictures of three to four repetitions with Image J software (http://rsb.info.nih.gov/ij, accessed on 1 October 2019). Leaf length, leaf width and petiole length were also determined by analyzing scanned pictures (8 to 15 leaves were randomly selected for each population), and LLWR was calculated as: LLWR = leaf length/leaf width.

2.3.2. SLA

The scanned leaves were dried at 65 °C to a constant mass and weighed to the nearest 0.0001 g. SLA was calculated as: SLA = leaf area/leaf dry weight.

2.3.3. PF

A spiral micrometer (at 0.001 mm) was used to measure the petiole diameter—the diameter of the middle position from the lamina base to the end of the petiole. If the petiole was cylindrical in shape, its diameter was used directly, whereas if it was ellipsoidal or even flattened, the average of the maximum and minimum diameter was used. For each population, the average diameter value of 10 petioles was finally used. PF was calculated as: PF = petiole length/petiole diameter.

2.3.4. LN and LP

Three to five healthy, intact leaves were selected from each population. The leaves were dried to constant weight in an oven at 70 °C, and then ground to a fine powder. Leaf powder of 0.100 g was digested with 5 mL of H_2SO_4 and then measured using an automated discrete analyzer (Smartchem 450, AMS Alliance, Rome, Italy) to obtain its leaf nitrogen and leaf phosphorus contents.

2.4. Community Investigation and Species Dominance

Dominance is used to indicate a species' performance and status in a community, but there are differences in its definition and calculation. For a woody community, species dominance can be calculated from one or more of the following indices: species abundance, frequency, density, cover, height, diameter at breast height (DBH) and basal stem. We excluded DBH and basal stem because they are not indices suitable for all woody species (i.e., trees and shrubs). Leaf is a typical vegetative organ, and its traits are tightly related to plant vegetative growth and resource utilization. Thus, we did not consider abundance, frequency and density, the indices showing the individual number or the occurrence probability of a species within the community, reflecting mainly species' dispersal, generation or recovery ability (rather than their space occupancy and resource utilization capacity) that are often related to plant reproductive traits [48]. Ultimately, cover and (average individual) height were selected to calculate species dominance because they represent space occupancy and light interception capacity of plants in horizontal and vertical directions, respectively.

Each plot was divided into nine subplots of 100 m × 100 m in order to ensure an accurate estimate of species cover. Based on the method of Burrascano et al. [35], we visually assigned each species in each subplot a cover value (named 'C′') using an ordinal cover class scale: 1 (<0.5%), 2 (0.5%–1%), 3 (1%–2%), 4 (2%–5%), 5 (5%–10%), 6 (10%–15%), 7 (15%–20%) and, thereafter, every 10% up to 100%, and an adult individual height class scale ('H′'): 1 (<0.3 m), 2 (0.3–0.6 m), 3 (0.6–1.0 m), 4 (1.0–1.8 m), 5 (1.8–3.2 m), 6 (3.2–5.6 m), 7 (5.6–10.0 m), 8 (10.0–17.7 m) and 9 (17.7–31.6 m). For each site, the maximum C and H were defined as Cmax and Hmax, respectively, and the relative cover (C') and adult height (H') of species x can be calculated as $C'x = Cx/Cmax$ and $H'x = Hx/Hmax$. The dominance (D) of species x (Dx) is the mean value of $C'x$ and $H'x$. In the following, we used D as species community performance, and the results related to species cover (C) or adult height (H) are shown in Figures S1–S3.

2.5. Data Analysis

Data on PF, SLA, LA and LLWR were log-transformed before analysis to fit a normal distribution. We first performed a meta-analysis to assess the binary relationship between species dominance (D) and each of the leaf traits and the difference in the relationship among the sites. Effect size of each binary relationship for each site was analyzed by applying the random effects model with 'Metafor' package. The mean effect size across sites and for each climate zone or vegetation type was calculated by weighting each site-specific effect size by its corresponding standard error. The 95% confidence interval (CI) of the mean effect was generated by bootstrapping with 4999 iterations. We used between-group heterogeneity ($Q_{between}$) to determine the differences in effect size between sites and tested its significance. For each site, we then performed a relative importance analysis (a part of multiple regression analysis with D as the dependent variable and all six leaf traits as independent variables) to quantify the contribution of each leaf trait to D. All of the above analyses were performed in R 4.2.2.

3. Results

3.1. Environmental Variation in the Relationships between Species Dominance and Their Leaf Traits

Across all sites, the meta-analysis showed that the mean effect size was significantly positive for the D-LA and D-LP relationships, while non-significantly negative for the D-LLWR and D-SLA relationships and non-significantly positive for the D-PF and D-LN relationships (Figures 2 and 3). Along the altitudinal gradient, the effect size of the D-PF relationship decreased significantly ($Q_{between} = 17.338$, $p < 0.001$). This relationship is significantly positive in temperate and subtropical forests (T-S and Te, or DEF and DF) but non-significantly different from zero in subalpine forests and shrubs (SA or DFS) and significantly negative in alpine shrub (Al or DES). The effect size of the D-SLA relationship also decreased significantly with altitude ($Q_{between} = 16.345$, $p = 0.001$), from non-significantly different from zero in temperate and subtropical forests to significantly negative in subalpine/alpine forests or shrubs (Figures 2 and 3). The D-LA relationship of all climate zones and vegetation types was similar ($Q_{between} < 1.722$, $p > 0.632$) and significantly positive. Although altitudinal variations in the effect size of the D-LN, D-LP, and D-LLWR relationships were statistically non-significant (p of $Q_{between}$ were all > 0.1), the effect size of the D-LN and D-LP relationships was relatively high and (marginally) significantly positive at the lowest altitude (T-S and DEF). However, the D-LLWR relationship was relatively low and significantly negative in the middle-altitude DF and Te. In addition, when the C- or H-leaf trait relationship was examined by using a meta-analysis, similar patterns were found with the D-leaf trait relationship except for non-significant differences in the H-SLA relationship among the climate zones (Figures S1 and S2).

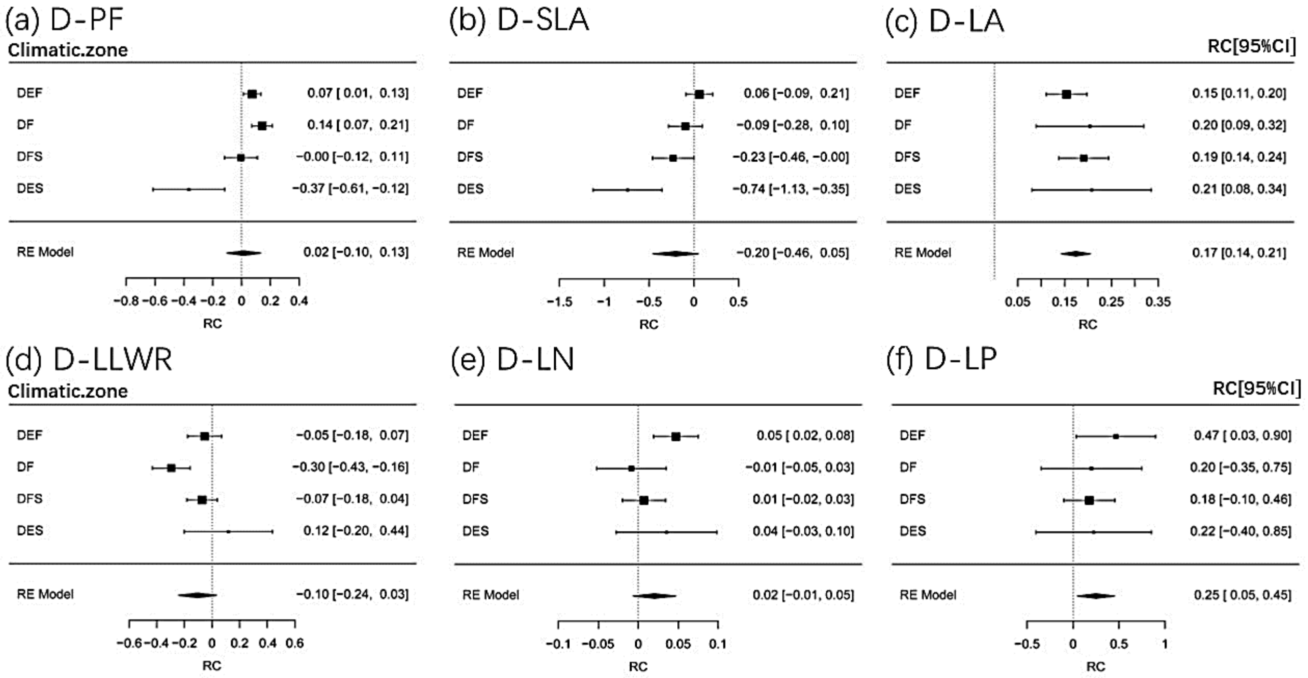

Figure 2. Mean effect size and 95% confidence intervals (CIs) of the relationship between species dominance (D) and petiole fineness (PF, (**a**)), specific leaf area (SLA, (**b**)), leaf area (LA, (**c**)), leaf length–width ratio (LLWR, (**d**)), leaf nitrogen (LN, (**e**)) or leaf phosphorus (LP, (**f**)) for different climate zones. T-S—warm temperate–subtropical; Te—temperate; SA—subalpine; Al—alpine.

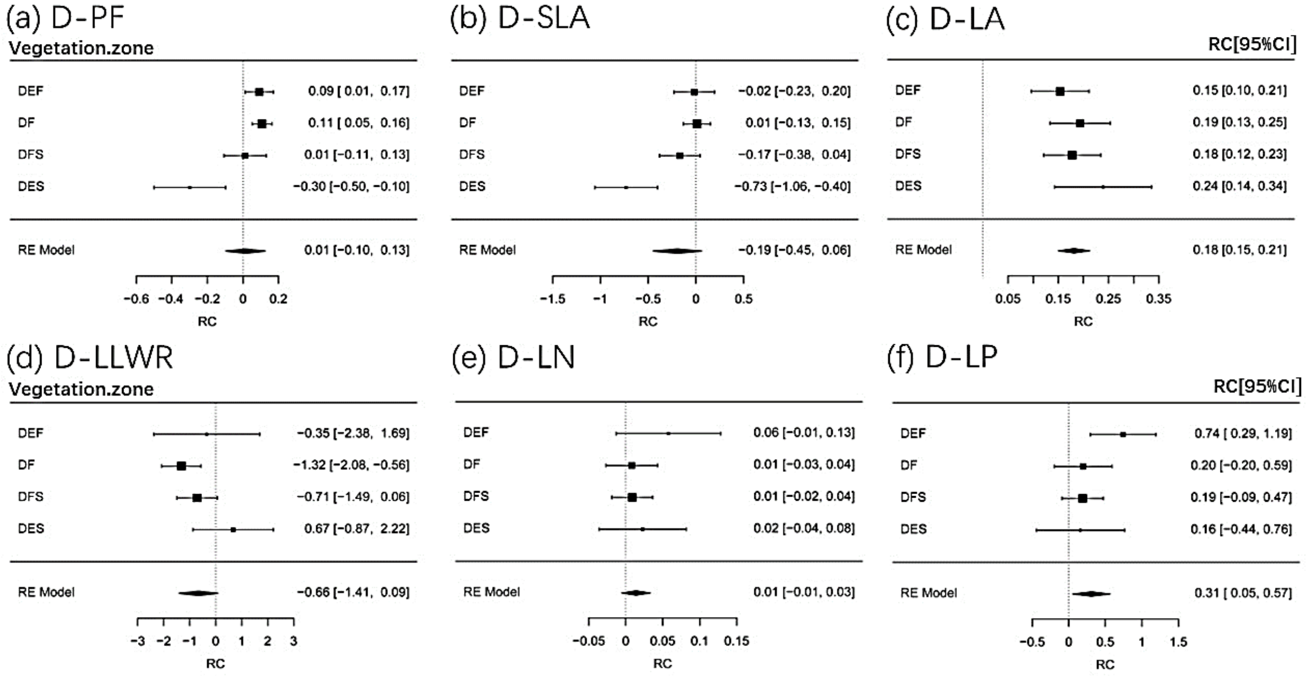

Figure 3. Mean effect size and 95% confidence intervals (CIs) of the relationship between species dominance (D) and petiole fineness (PF, (**a**)), specific leaf area (SLA, (**b**)), leaf area (LA, (**c**)), leaf length–width ratio (LLWR, (**d**)), leaf nitrogen (LN, (**e**)) or leaf phosphorus (LP, (**f**)) for different vegetation types. DEF—mixed deciduous–evergreen forest; DF—deciduous forest; DFS—mixed deciduous forest–shrub; DES—mixed deciduous–evergreen shrub.

3.2. The Relative Importance of Leaf Traits in Species Dominance

Across 19 sites, LA was the strongest predictor of D variation, with a mean explanatory power of 0.165, followed by SLA (0.069), LN (0.050), PF (0.044) and LP (0.042), whereas LLWR (0.027) was the worst predictor. The altitudinal gradient in the relative importance of leaf traits in D variation was significant. At the low altitude (sites 1~9), LA was often the only significant predictor of D variation, with the explanatory power ranging from 0.079 to 0.211, whereas PF had the lowest explanatory power, ranging from 0.003 to 0.064 (Figure 4). At the middle and higher altitudes (sites 10~17), the explanatory power of LA on D decreased, but that of other leaf traits increased, often resulting in a lack of dominant leaf traits predicting D change. At the highest altitude (sites 18~19) where the predictive power of LA regarding D change was low, SLA and PF were the strongest predictors. In addition, the total explanatory power of leaf traits on D increased with altitude (ranging from 0.186 to 0.804), with SLA and PF (sometimes LN) contributing most to the increasing explanatory power (Figure 4).

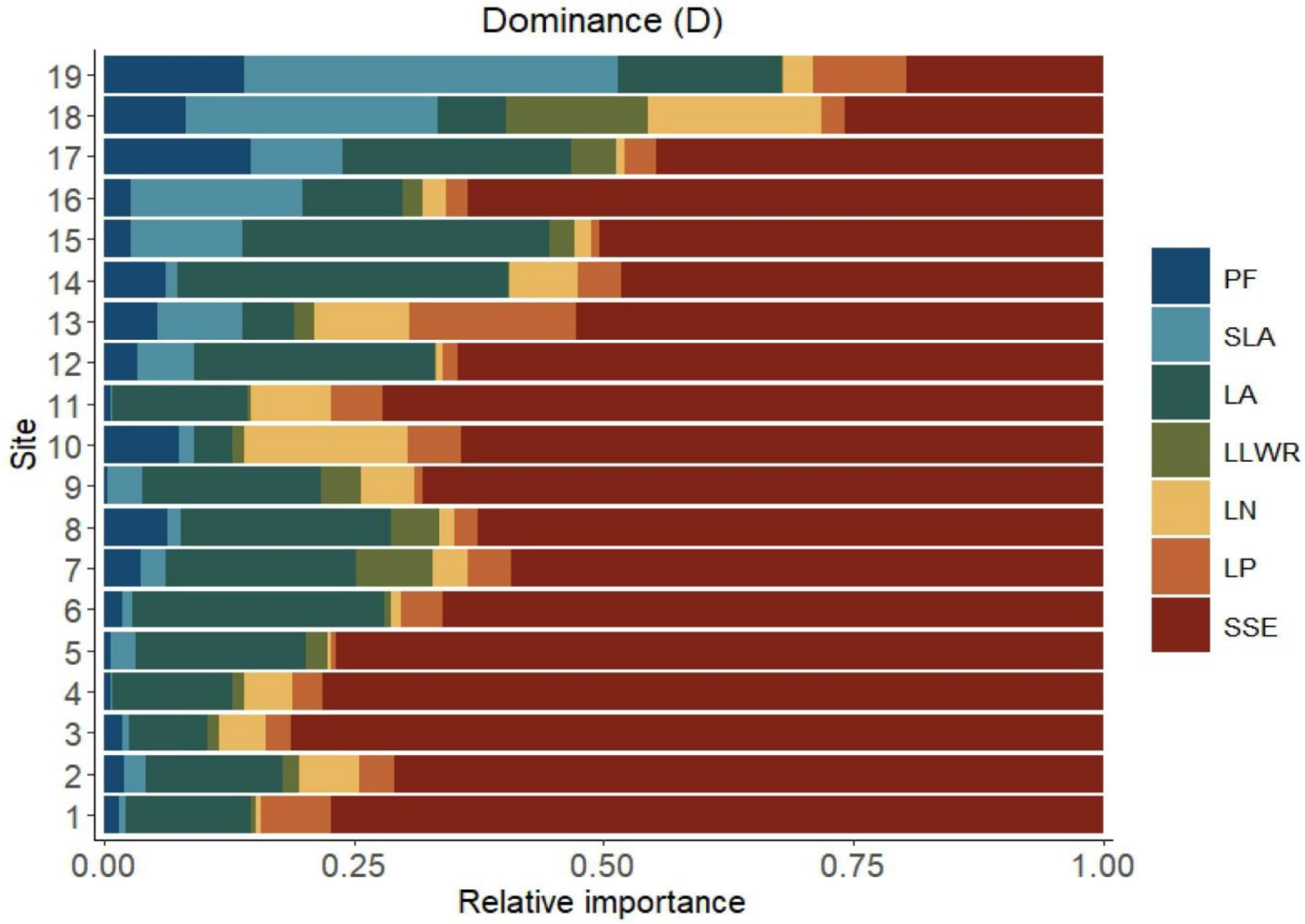

Figure 4. The relative importance of leaf traits on species dominance (D) at 19 studied sites (woody communities, as seen in Table 1). The horizontal axis is the relative importance of leaf traits, and the vertical axis is different sites. The leaf traits from left to right on the histogram are petiole fineness (PF), specific leaf area (SLA), leaf area (LA), leaf length–width ratio (LLWR), leaf nitrogen (LN) and leaf phosphorus (LP). SSE—sum-squared error.

4. Discussion

We showed different patterns for the relationship between species community performance and their leaf morphological and chemical traits. These relationships also differed significantly among the studied sites, climate zones and vegetation types. Overall, leaf area was the best predictor of species dominance, but the explanatory power of leaf area and other leaf traits changed significantly with altitude and among climate zones or vegetation types. Below, we explore the trends behind our findings, their possible causes and the implications of these trends.

4.1. Overall Trends

Leaves are the major plant organs conducting photosynthesis and being in contact with the atmospheric environment [3,5]. Thus, species whose leaf traits have high light interception and utilization and strong environmental adaptability or tolerance are more likely to dominate plant communities [37,38,49]. Our finding that leaf area was the best leaf trait predicting (significantly positively related to) species dominance, height and cover in most sites and almost all climate zones and vegetation types (Figures 2, 3, S1 and S2) supports the widespread importance of the light acquisition capacity of species in their community performance [50,51]. The finding also implies that, in most woody communities, interspecific light competition is ubiquitous, and large leaves can help species form a dense canopy to intercept light effectively and accumulate carbon quickly [16,28,33,52]. These species, thus, tend to grow tall and occupy a wide space, which, in turn, enhances their light competition. Similarly, the overall positive relationship between species dominance and their LN and LP (or the negative relationship with LLWR) suggests that high leaf N or P content and broad–round leaf shape, associated with high light interception, high photosynthetic efficiency and rapid nutrient accumulation [15,16,18–20,34], enable woody angiosperms to grow tall and have a wide crown. The more significant association of species dominance with leaf P content than leaf N content potentially implies stronger P limitation on leaf photosynthetic efficiency in the QTP region [3,33].

4.2. Pattern of Different Climate Zones or Vegetation Types

The role of petiole fineness in affecting species dominance differed significantly among climate zones or vegetation types. In temperate or subtropical forests, species dominance was positively related to petiole fineness, whereas dominant species of subalpine/alpine forests or shrubs were characterized by low petiole fineness. This suggests that enhancement of petiole elongation for maximizing light interception is an optimum leaf growth strategy under high competition for light in low-altitude closed and tall forests [15,26,29,30], whereas strong petiole shortening for maximizing lamina support is common for dominant species in the stressful alpine and subalpine areas where leaves are exposed to the strong natural drag forces (wind blowing, snow covering, air-moisture freezing, etc.) [19,21,27]. The dominant species of subalpine/alpine forests or shrubs, but not of temperate forests, were also characterized by low SLA. The reason may be that low SLA, associated with many lamina cell layers and a high proportion of protective tissue in the leaf epidermis, can decrease the leaf transpiration rate and increase leaf protection against high solar radiation or low temperatures [11,20], which help high-altitude dominant species thrive under stressful environments. These dominant species can create a low-stress microhabitat for high-SLA non-dominant species. On the contrary, in temperate forests with mild climates, long growth periods and without significant environmental pressure, woody species may obtain similar benefits from high SLA (high photosynthetic efficiency but short leaf lifespan) and low SLA (slow photosynthate production but extended leaf longevity) [5,22,24,25], resulting in a weak association of species SLA with their community performance.

The positive effect of leaf N and P content on species dominance was stronger in the lowest-altitude warm temperate–subtropical forests (T-S and DEF) than in the other climate zones or vegetation types. The lowest altitude is characterized by high temperature, high humidity and a long growing season. Dominant species can benefit from high leaf N and P concentrations at the lowest altitude for their long-time advantages in photosynthetic efficiency and nutrient accumulation [32,53]. This may be important for species to maintain their community performance, especially when they need to consume large amounts of fixed carbon through respiration [3,14,34]. Surprisingly, the D-LLWR relationship was significantly negative in the mid-altitude temperate deciduous forests (Te and DF) but was non-significant in the other woody communities. For a given leaf area, light interception and photosynthetic or transpiration rates were higher for broad–round leaves (low LLWR) than long–narrow ones [12,31]. This result implies that, in temperate deciduous forests where environmental stress is low, temperatures are suitable, but the growing season is relatively short, and the time for leaf development and photosynthesis is limited. Broad–round leaves (low LLWR) can help plants accumulate more nutrients during a growing season [17,18]. A long growing season in the lowest-altitude warm temperate–subtropical forests may allow for uncoupling species dominance from their leaf shape to a large extent. The reason why broad–round leaves are not dominant in the high-altitude subalpine and alpine areas may be that they are prone to strong natural drag forces and high temperature loss (caused by transpiration) on the lamina surface [1,10,12,19].

Our data show that, with increasing altitude, the total explanatory power of leaf traits on species dominance increased and the leaf traits additional to leaf area, especially petiole fineness and SLA, contributed significantly to species dominance. This indicates that, in the low-altitude forests lacking environmental stress, interspecific light competition should be the only primary factor affecting the role of leaf traits in the woody community assembly [46]. As environmental stress increases with altitude, species' environmental adaptability or tolerance becomes increasingly important in determining their survival and abundance [54]. Different leaf traits, representing the adaptability of plants to different environmental stresses, are, thus, statistically significantly related to their community performance.

5. Conclusions

We provide evidence that leaf traits change significantly with environmental gradients, as well as strongly influence the local adaptation of plant species. In most woody communities, leaf area is the most important trait affecting (positively) species community performance, implying that woody species within the community follow a resource acquisition strategy, most of the time, and focus on efficient light acquisition and utilization. Among all the selected leaf traits, the association of petiole fineness or SLA with species dominance changes most dramatically with altitudes, climate zones and vegetation types, indicating that they are reliable leaf traits for predicting the environmental adaptability of woody species and their community performance in a given environment. In addition, with the increase in altitude, the total explanatory power of leaf traits on species dominance increases, supporting the view of a great impact of plant biological traits on community assembly in stressful environments.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14050866/s1, Figure S1: Mean effect size and 95% confidence intervals (CIs) of the relationship between species cover class (C, part A) or adult height class (H, part B) and petiole fineness (PF, a), specific leaf area (SLA, b), leaf area (LA, c), leaf length–width ratio (LLWR, d), leaf nitrogen content (LN, e) or leaf phosphorus content (LP, f) for different climate zones. T-S—warm temperate-subtropical; Te—temperate; SA—subalpine; Al—alpine; Figure S2: Mean effect size and 95% confidence intervals (CIs) of the relationship between species cover class (C, part A) or adult height class (H, part B) and petiole fineness (PF, a), specific leaf area (SLA, b), leaf area (LA, c), leaf length–width ratio (LLWR, d), leaf nitrogen content (LN, e) or leaf phosphorus content (LP, f) for different vegetation types. Abbreviations of leaf traits are as specified in Figure S1. DEF—mixed deciduous–evergreen forest; DF—deciduous forest; DFS—mixed deciduous forest–shrub; DES—mixed deciduous–evergreen shrub; Figure S3: The relative importance of leaf traits on species cover class (C) or height class (H) at 19 sites (woody communities, as seen in Table 1). The horizontal axis is the relative importance of leaf traits, and the vertical axis is different sites. The leaf traits from left to right on the histogram are petiole fineness (PF), specific leaf area (SLA), leaf area (LA), leaf length–width ratio (LLWR), leaf nitrogen (LN) and leaf phosphorus (LP). SSE—sum-squared error; Supplementary Data: A comparison of 6 leaf traits for 415 woody species (733 populations) in 19 studied sites. PF—petiole fineness; LA—leaf area (cm^2); SLA—specific leaf area (cm^2/g); LLWR—leaf length–width ratio; LN—leaf nitrogen content (%); LP—leaf phosphorus content (%).

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References

1. Meng, T.-T.; Wang, H.; Harrison, S.P.; Prentice, I.; Ni, J.; Wang, G. Responses of leaf traits to climatic gradients: Adaptive variation versus compositional shifts. *Biogeosciences* **2015**, *12*, 5339–5352. [CrossRef]
2. Yao, L.; Ding, Y.; Yao, L.; Ai, X.; Zang, R. Trait Gradient Analysis for Evergreen and Deciduous Species in a Subtropical Forest. *Forests* **2020**, *11*, 364. [CrossRef]
3. Han, W.; Fang, J.; Guo, D.; Zhang, Y. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol.* **2005**, *168*, 377–385. [CrossRef] [PubMed]
4. Ordoñez, J.C.; Van Bodegom, P.M.; Witte, J.P.M.; Wright, I.J.; Reich, P.B.; Aerts, R. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob. Ecol. Biogeogr.* **2009**, *18*, 137–149. [CrossRef]
5. Cheng, X.; Ping, T.; Li, Z.; Wang, T.; Han, H.; Epstein, H.E. Effects of environmental factors on plant functional traits across different plant life forms in a temperate forest ecosystem. *New For.* **2021**, *53*, 125–142. [CrossRef]
6. Mao, W.; Li, Y.-L.; Zhang, T.-H.; Zhao, X.-Y.; Huang, Y.-X.; Song, L.-L. Research advances of plant leaf traits at different ecology scales. *J. Desert Res.* **2012**, *32*, 33–41.
7. Wang, R.; Yu, G.; He, N.; Wang, Q.; Zhao, N.; Xu, Z. Latitudinal variation of leaf morphological traits from species to communities along a forest transect in eastern China. *J. Geogr. Sci.* **2016**, *26*, 15–26. [CrossRef]
8. Zhang, L.; Luo, T.-X. Advances in ecological studies on leaf lifespan and associated leaf traits. *Chin. J. Plant Ecol.* **2004**, *28*, 844.
9. Bon, M.P.; Böhner, H.; Kaino, S.; Moe, T.; Bråthen, K.A. One leaf for all: Chemical traits of single leaves measured at the leaf surface using near-infrared reflectance spectroscopy. *Methods Ecol. Evol.* **2020**, *11*, 1061–1071.
10. Wright, T.E.; Kasel, S.; Tausz, M.; Bennett, L.T. Leaf traits of *Eucalyptus arenacea* (Myrtaceae) as indicators of edge effects in temperate woodlands of south-eastern Australia. *Aust. J. Bot.* **2013**, *61*, 365–375. [CrossRef]
11. Niklas, K.J. A mechanical perspective on foliage leaf form and function. *New Phytol.* **1999**, *143*, 19–31. [CrossRef]
12. Malhado, A.C.M.; Whittaker, R.J.; Malhi, Y.; Ladle, R.J.; Ter Steege, H.; Butt, N.; Aragão, L.; Quesada, C.A.; Murakami-Araujo, A.; Phillips, O.L. Spatial distribution and functional significance of leaf lamina shape in Amazonian forest trees. *Biogeosciences* **2009**, *6*, 1577–1590. [CrossRef]
13. Herrera, C.M.; Medrano, M.; Bazaga, P. Continuous within-plant variation as a source of intraspecific functional diversity: Patterns, magnitude, and genetic correlates of leaf variability in *Helleborus foetidus* (Ranunculaceae). *Am. J. Bot.* **2015**, *102*, 225–232. [CrossRef] [PubMed]
14. Rowland, L.; Zaragoza-Castells, J.; Bloomfield, K.J.; Turnbull, M.H.; Bonal, D.; Burban, B.; Salinas, N.; Cosio, E.; Metcalfe, D.J.; Ford, A. Scaling leaf respiration with nitrogen and phosphorus in tropical forests across two continents. *New Phytol.* **2017**, *214*, 1064–1077. [CrossRef]
15. Niinemets, Ü.; Portsmuth, A.; Tobias, M. Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. *New Phytol.* **2006**, *171*, 91–104. [CrossRef]
16. Peppe, D.J.; Royer, D.L.; Cariglino, B.; Oliver, S.Y.; Newman, S.; Leight, E.; Enikolopov, G.; Fernandez-Burgos, M.; Herrera, F.; Adams, J.M. Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. *New Phytol.* **2011**, *190*, 724–739. [CrossRef]

17. Li, Y.; Zou, D.; Shrestha, N.; Xu, X.; Wang, Q.; Jia, W.; Wang, Z. Spatiotemporal variation in leaf size and shape in response to climate. *J. Plant Ecol.* **2020**, *13*, 87–96. [CrossRef]
18. Leigh, A.; Sevanto, S.; Close, J.; Nicotra, A. The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant Cell Environ.* **2017**, *40*, 237–248. [CrossRef]
19. Louf, J.-F.; Nelson, L.; Kang, H.; Song, P.N.; Zehnbauer, T.; Jung, S. How wind drives the correlation between leaf shape and mechanical properties. *Sci. Rep.* **2018**, *8*, 16314. [CrossRef]
20. Kang, X.; Li, Y.; Zhou, J.; Zhang, S.; Li, C.; Wang, J.; Liu, W.; Qi, W. Response of Leaf Traits of Eastern Qinghai-Tibetan Broad-Leaved Woody Plants to Climatic Factors. *Front. Plant Sci.* **2021**, *12*, 679726. [CrossRef]
21. Li, Y.; Kang, X.; Zhou, J.; Zhao, Z.; Zhang, S.; Bu, H.; Qi, W. Geographic Variation in the Petiole–Lamina Relationship of 325 Eastern Qinghai–Tibetan Woody Species: Analysis in Three Dimensions. *Front. Plant Sci.* **2021**, *12*, 2339. [CrossRef] [PubMed]
22. Wright, I.J.; Reich, P.B.; Cornelissen, J.H.; Falster, D.S.; Groom, P.K.; Hikosaka, K.; Lee, W.; Lusk, C.H.; Niinemets, Ü.; Oleksyn, J. Modulation of leaf economic traits and trait relationships by climate. *Glob. Ecol. Biogeogr.* **2005**, *14*, 411–421. [CrossRef]
23. Guo, Z.; Lin, H.; Chen, S.; Yang, Q. Altitudinal patterns of leaf traits and leaf allometry in bamboo *Pleioblastus amarus*. *Front. Plant Sci.* **2018**, *9*, 1110. [CrossRef] [PubMed]
24. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **2001**, *82*, 453–469. [CrossRef]
25. Kayama, M.; Kitaoka, S.; Wang, W.; Choi, D.; Koike, T. Needle longevity, photosynthetic rate and nitrogen concentration of eight spruce taxa planted in northern Japan. *Tree Physiol.* **2007**, *27*, 1585–1593. [CrossRef] [PubMed]
26. Niinemets, Ü.; Al Afas, N.; Cescatti, A.; Pellis, A.; Ceulemans, R. Petiole length and biomass investment in support modify light interception efficiency in dense poplar plantations. *Tree Physiol.* **2004**, *24*, 141–154. [CrossRef] [PubMed]
27. Filartiga, A.L.; Klimeš, A.; Altman, J.; Nobis, M.P.; Crivellaro, A.; Schweingruber, F.; Doležal, J. Comparative anatomy of leaf petioles in temperate trees and shrubs: The role of plant size, environment and phylogeny. *Ann. Bot.* **2022**, *129*, 567–582. [CrossRef]
28. Sarlikioti, V.; De Visser, P.; Marcelis, L. Exploring the spatial distribution of light interception and photosynthesis of canopies by means of a functional–structural plant model. *Ann. Bot.* **2011**, *107*, 875–883. [CrossRef]
29. Perez, R.P.; Dauzat, J.; Pallas, B.; Lamour, J.; Verley, P.; Caliman, J.-P.; Costes, E.; Faivre, R. Designing oil palm architectural ideotypes for optimal light interception and carbon assimilation through a sensitivity analysis of leaf traits. *Ann. Bot.* **2018**, *121*, 909–926. [CrossRef]
30. Zhong, M.; Castro-Díez, P.; Puyravaud, J.P.; Sterck, F.J.; Cornelissen, J.H. Convergent xylem widening among organs across diverse woody seedlings. *New Phytol.* **2019**, *222*, 1873–1882. [CrossRef]
31. Takenaka, A. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. *Ecol. Res.* **1994**, *9*, 109–114. [CrossRef]
32. Wang, J.; Wen, X.; Zhang, X.; Li, S.; Zhang, D.-Y. Co-regulation of photosynthetic capacity by nitrogen, phosphorus and magnesium in a subtropical Karst forest in China. *Sci. Rep.* **2018**, *8*, 7406. [CrossRef] [PubMed]
33. Anten, N.P.; Hirose, T. Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. *Oecologia* **2001**, *129*, 186–196. [CrossRef] [PubMed]
34. Reich, P.B.; Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 11001–11006. [CrossRef]
35. Burrascano, S.; Ripullone, F.; Bernardo, L.; Borghetti, M.; Carli, E.; Colangelo, M.; Gangale, C.; Gargano, D.; Gentilesca, T.; Luzzi, G. It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests. *J. Veg. Sci.* **2018**, *29*, 98–109. [CrossRef]
36. Wang, L.; Zhao, G.; Li, M.; Zhang, M.; Zhang, L.; Zhang, X.; An, L.; Xu, S. C: N: P stoichiometry and leaf traits of halophytes in an arid saline environment, northwest China. *PLoS ONE* **2015**, *10*, e0119935. [CrossRef]
37. Šímová, I.; Violle, C.; Kraft, N.J.; Storch, D.; Svenning, J.C.; Boyle, B.; Donoghue, J.C.; Jørgensen, P.; McGill, B.J.; Morueta-Holme, N. Shifts in trait means and variances in North American tree assemblages: Species richness patterns are loosely related to the functional space. *Ecography* **2015**, *38*, 649–658. [CrossRef]
38. E-Vojtkó, A.; de Bello, F.; Durka, W.; Kuehn, I.; Goetzenberger, L. The neglected importance of floral traits in trait-based plant community assembly. *J. Veg. Sci.* **2020**, *31*, 529–539. [CrossRef]
39. Illa, E.; Ninot, J.M.; Anadon-Rosell, A.; Oliva, F. The role of abiotic and biotic factors in functional structure and processes of alpine subshrub communities. *Folia Geobot.* **2017**, *52*, 199–215. [CrossRef]
40. Akram, M.A.; Zhang, Y.; Wang, X.; Shrestha, N.; Malik, K.; Khan, I.; Ma, W.; Sun, Y.; Li, F.; Ran, J. Phylogenetic independence in the variations in leaf functional traits among different plant life forms in an arid environment. *J. Plant Physiol.* **2022**, *272*, 153671. [CrossRef]
41. Han, Z.-Q.; Liu, T.; Liu, H.-F.; Hao, X.-R.; Chen, W.; Li, B.-L. Derivation of species interactions strength in a plant community with game theory. *Ecol. Model.* **2019**, *394*, 27–33. [CrossRef]
42. Winemiller, K.O.; Fitzgerald, D.B.; Bower, L.M.; Pianka, E.R. Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* **2015**, *18*, 737–751. [CrossRef] [PubMed]
43. Šímová, I.; Rueda, M.; Hawkins, B.A. Stress from cold and drought as drivers of functional trait spectra in North American angiosperm tree assemblages. *Ecol. Evol.* **2017**, *7*, 7548–7559. [CrossRef]

44. Akram, M.A.; Wang, X.; Hu, W.; Xiong, J.; Zhang, Y.; Deng, Y.; Ran, J.; Deng, J. Convergent variations in the leaf traits of desert plants. *Plants* **2020**, *9*, 990. [CrossRef] [PubMed]
45. Siefert, A.; Fridley, J.D.; Ritchie, M.E. Community functional responses to soil and climate at multiple spatial scales: When does intraspecific variation matter? *PLoS ONE* **2014**, *9*, e111189. [CrossRef]
46. Mori, A.S.; Shiono, T.; Koide, D.; Kitagawa, R.; Ota, A.T.; Mizumachi, E. Community assembly processes shape an altitudinal gradient of forest biodiversity. *Glob. Ecol. Biogeogr.* **2013**, *22*, 878–888. [CrossRef]
47. Gagliardi, S.; Martin, A.R.; Virginio Filho, E.d.M.; Rapidel, B.; Isaac, M.E. Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes. *Agric. Ecosyst. Environ.* **2015**, *200*, 151–160. [CrossRef]
48. Zhao, R.; Zhang, H.; An, L. Plant size influences abundance of floral visitors and biomass allocation for the cushion plant *Thylacospermum caespitosum* under an extreme alpine environment. *Ecol. Evol.* **2019**, *9*, 5501–5511. [CrossRef]
49. Poorter, L.; Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **2006**, *87*, 1733–1743. [CrossRef]
50. Selaya, N.G.; Oomen, R.J.; Netten, J.J.; Werger, M.J.; Anten, N.P. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *J. Ecol.* **2008**, *96*, 1211–1221. [CrossRef]
51. Thakur, D.; Rathore, N.; Chawla, A. Increase in light interception cost and metabolic mass component of leaves are coupled for efficient resource use in the high altitude vegetation. *OIKOS* **2019**, *128*, 254–263. [CrossRef]
52. Falster, D.S.; Westoby, M. Leaf size and angle vary widely across species: What consequences for light interception? *New Phytol.* **2003**, *158*, 509–525. [CrossRef] [PubMed]
53. Kang, H.; Zhuang, H.; Wu, L.; Liu, Q.; Shen, G.; Berg, B.; Man, R.; Liu, C. Variation in leaf nitrogen and phosphorus stoichiometry in *Picea abies* across Europe: An analysis based on local observations. *For. Ecol. Manag.* **2011**, *261*, 195–202. [CrossRef]
54. Arévalo, J.R.; Delgado, J.D.; Otto, R.; Naranjo, A.; Salas, M.; Fernández-Palacios, J.M. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspect. Plant Ecol. Evol. Syst.* **2005**, *7*, 185–202. [CrossRef]