



1 **Treeline species *Betula ermanii* are more adaptable to alpine environments than**
2 **non-treeline species *Picea jezoensis*: evidence from leaf functional traits**

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4 Renkai Dong^a, Na Li^{a,c}, Mai-He Li^{a,c,e}, Yu Cong^d, Haibo Du^a, Hong S. He^{b,*}

5

6 *^aKey Laboratory of Geographical Processes and Ecological Security in Changbai*
7 *Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal*
8 *University, Changchun 130024, China*

9 *^bSchool of Natural Resources, University of Missouri, Columbia, MO 65211, USA*

10 *^cSwiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903*
11 *Birmensdorf, Switzerland*

12 *^dNortheast Institute of Geography and Agricultural Ecology, Chinese Academy of*
13 *Sciences, Changchun 130102, China*

14 *^eSchool of Life Science, Hebei University, 071002 Baoding, P. R. China.*

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17 *Corresponding author: Hong S. He

18 School of Natural Resources, University of Missouri, Columbia, MO 65211, USA

19 E-mail: HeH@missouri.edu

20



21 **ABSTRACT**

22 Understanding functional trait differences between treeline and non-treeline species is
23 key to exploring their adaptive strategies under environmental stress and predicting
24 subalpine forest dynamics. On Changbai Mountain, *Betula ermanii* dominates over 90%
25 of the treeline zone, while *Picea jezoensis* accounts for over 70% of the lower elevation
26 zone. It remains unclear whether *P. jezoensis*, a treeline genus elsewhere, would
27 eventually shift upward and replace *B. ermanii*. We thus investigated leaf functional
28 traits, their intraspecific variation, and inter-trait relationships for both species along
29 the elevational gradient. *B. ermanii* exhibited higher LDMC, N, P, and gs, but lower
30 WUE and $\delta^{18}\text{O}$ at higher elevations, with the greatest intraspecific variability in
31 photosynthetic and hydraulic traits, and tighter linkages among traits. In contrast, *P.*
32 *jezoensis* exhibited an increase in $\delta^{13}\text{C}$ and a decrease in SLA with elevation,
33 accompanied by the greatest intraspecific variability in photosynthetic traits and weaker
34 correlations among traits. Overall, *B. ermanii* employs a resource-acquisition strategy
35 enabling it to occupy resources and space, while *P. jezoensis* adopts a resource-
36 conserving strategy by emphasizing shade and drought-tolerance, resource
37 conservation, and long-term adaptation at lower elevation, limiting its ability of upward
38 range expansion. These findings enhance our understanding of their adaptive strategies
39 and responses to elevational change, informing predictions of subalpine forest
40 dynamics.

41

42 **Keywords:**

43 Alpine treeline; Climate change; Leaf functional traits; Adaptation strategies; Sub-
44 alpine forest dynamics



45 1. Introduction

46 Global warming is particularly pronounced at high elevations and latitudes
47 (Assessment, 2005; Hagedorn et al., 2014), and has strongly affected global vegetation,
48 especially in cold temperature-limited ecosystems (Pauli et al., 2012). Treelines are
49 important ecological boundaries that are highly sensitive to temperature changes. The
50 formation of upper elevational distribution limits of treeline species is mainly related
51 to growth limitations by low temperature (Körner, 2012). When the climate warms,
52 treeline trees may have faster growth rates, and thus the stem growth increase, and trees
53 migrate upward, and stand density increase (Cong et al., 2022). Similar to the treeline
54 species, climate warming also affects the growth and distribution range of non-treeline
55 species. Except for climate warming, however, changes in distribution patterns of non-
56 treeline species are co-driven also by other factors such as competition with other
57 species (Scherrer et al., 2020; Dong et al., 2024).

58 Many environmental factors, such as temperature, humidity, soil moisture,
59 irradiance, precipitation, and soil physicochemical properties, change substantially
60 along altitudinal gradients over short vertical distances (Read et al., 2014). This can
61 lead to **changes in the functional traits of tree species**, reflecting the combined effects
62 of the environment (Cox et al., 2024).

63 Leaf functional traits are closely related to plant survival, growth, and reproduction
64 (Zhang et al., 2023). Different traits and their coordination reflect different ecological
65 strategies among plant species (Lavorel et al., 2012). Leaf economic spectra represent
66 the trade-off between rapid resource acquisition and resource-conserving strategies in
67 plants (Osnas et al., 2013). Plants with leaf traits, such as high specific leaf area, low
68 tissue density, and high nitrogen (N) and phosphorus (P) concentrations, can have high
69 photosynthetic capacity, which is a strategy that permits them rapid access to resources,
70 and such species are typically high-maintenance, poorly defended, and short-lived
71 (Wright et al., 2004). **In contrast, plants with the opposite traits optimize resource**
72 **conservation strategies, with slower returns on investment and longer tissue lifespans**
73 **(Wright et al., 2004).**



74 Plants usually have both strong interspecific and intraspecific variations in
75 functional traits, reflecting heritable genetic make up and growth environment (Jung et
76 al., 2010). These variations reflect the plant responses to environmental and biological
77 interactions. Plasticity in plants varies between growing environments, with a wider
78 range of morphological and physiological variation allowed in suitable environments,
79 and therefore greater phenotypic plasticity (Hulshof et al., 2013). Meanwhile, in
80 stressful environments, the cost of variation in plant traits is increased, leading to
81 reduced phenotypic plasticity (Stotz et al., 2021), and thus smaller intraspecific trait
82 variation. The costs and limitations of phenotypic plasticity are related to the type of
83 trait (Stotz et al., 2021). For example, morphological traits cost more and are thus
84 limited in terms of plasticity under stress conditions. Meanwhile, physiological traits
85 are less cost and reversible, and therefore more plastic (Grime et al., 2002).

86 Functional traits are not independent because of the different plant ecological and
87 physiological needs (Freschet et al., 2015). Many functional traits interact to
88 collectively optimize functioning, enabling plants to apply a variety of strategies in
89 response to environmental change (Díaz et al., 2016). Plant trait networks constructed
90 from nodes (traits) and edges (trait-trait correlations) allow for the visualization of
91 complex trait relationships at the plant level, and the identification of central traits based
92 on topological position in the network (Wei et al., 2023), providing a more complete
93 description of the study of the interactions between functional traits in plants from a
94 systemic perspective. There is controversy about how plant trait networks vary across
95 environments. Woody plants in harsh environments, such as polar and cold regions,
96 showed lower inter-trait connectivity and a higher modularity in their trait networks
97 (Rao et al., 2022). Higher inter-trait connectivity and a lower modularity have been
98 observed in suitable tropical environments (Flores-Moreno et al., 2019). Therefore,
99 lower inter-trait connectivity and a higher modularity may be preferred under harsh
100 environmental conditions that inhibit plant growth. This is because strong trait
101 coordination imposes a cost of construction and does not provide much benefit to plant
102 survival under stressful conditions (Rao et al., 2022).



103 Different factors that shape the distribution patterns of treeline and non-treeline
 104 species may lead to differences in plant adaptation strategies. Some studies have been
 105 conducted on the dynamics and physiological mechanisms of treeline species in
 106 response to climate change (Du et al., 2018; Du et al., 2021). However, relatively few
 107 studies have been conducted on the dynamics and physiological mechanisms of non-
 108 treeline species in response to climate change. Comparisons of leaf functional trait
 109 values, inter- and intraspecific variation in traits, and trait networks between treeline
 110 and non-treeline species can show their adaptive strategies to different environments
 111 from multiple perspectives. These comparisons will help us to understand how treeline
 112 and non-treeline species respond to climate change in terms of trait means, plasticity,
 113 and integration.

114 Located in a biodiversity hotspot and climate-sensitive region, Changbai Mountain
 115 has a complete vertical belt spectrum of vegetation (Zhuang et al., 2017). The treeline
 116 species *B. ermanii* and the non-treeline species *P. jezoensis* on Changbai Mountain are
 117 typical establishment species adapted to the treeline and non-treeline environment.
 118 Therefore, we measured leaf functional traits of *B. ermanii* and *P. jezoensis* along an
 119 altitudinal gradient on the Changbai Mountain. We hypothesize that the harsh alpine
 120 treeline environment will lead to smaller intraspecific variation of *B. ermanii* in their
 121 functional traits than the non-treeline environment (H1), To minimize construction costs
 122 in more stressful environments, treeline species exhibit reduced connectivity among
 123 leaf functional traits. As a result, their trait networks are less interconnected but display
 124 higher modularity compared to those of non-treeline species (H2), and further we
 125 expect, based on the above analyses, that the adaptation strategy of the treeline species
 126 *B. ermanii* is more resource-acquisitive than that of the non-treeline species *P. jezoensis*
 127 (H3).

128

129 2. Materials and methods

130 2.1. Study area

131 Changbai Mountain (41°41'49" to 42°25'18" N; 127°42'55" to 128°16'48" E) is a



dormant volcano and also is the highest mountain in Northeast China with its summit at 2696 m a.s.l. The area has a temperate continental climate, with a mean temperature of -7.3 to 4.9 °C in the growing season and annual precipitation of 800 to 1800 mm. The volcanic eruption of 946 AD destroyed most of the vegetation and formed a spectrum of vertical zones over a long period of succession. From top to bottom, the vegetated landscapes are alpine tundra ($>2,000$ m a.s.l.), deciduous broad-leaved *B. ermanii* forests (1,700–2,000 m a.s.l.), alpine coniferous spruce-fir forests (1,100–1,700 m a.s.l.), and mixed coniferous and broad-leaved forests (740–1,100 m a.s.l.). *B. ermanii* is a treeline species. Although the elevation of the forest line is 2000 m, *B. ermanii* can still be distributed upward to 2200 m, and *P. jezoensis* is the main established species of the cloud fir forest. During the growing season, for every 100 m of elevation gain, the mean annual atmospheric temperature in the understory of the area decreased by approximately 0.68 °C and the mean annual atmospheric humidity in the understory increased by approximately 0.93% (Reich et al., 1998).

2.2 Experimental design and sampling

We selected *B. ermanii* as a representative treeline species and *P. jezoensis* as a non-treeline species for this study. This selection reflects the unique composition of the treeline in the Changbai Mountain region, where *B. ermanii* predominates, constituting over 90% of the treeline species population. In contrast, *P. jezoensis* is mainly distributed along the lower boundary of the *B. ermanii* range, accounting for more than 70% of the tree species population in this zone. These distribution patterns make *P. jezoensis* an ideal representative of non-treeline species. We set up experimental plots comprising a total of 12 plots at 100 m intervals within the main distribution range of the treeline species *B. ermanii* (1700–2200 m) and the non-treeline species *P. jezoensis* (1300–1800 m). The plots were in the natural native forest far away from the highway, with the trees in the sample plots in good growing conditions and with moderate spacing between each other. We conducted on-site field measurements and tree sampling in August 2023 (peak of the growing season). Our study focuses on the relative spatial variations in leaf functional traits of the two species by analyzing data from different



161 elevation points. Although the leaf functional traits varies annually, the relative the
162 seasonal trends within a year remain stable (Islam et al., 2024). Therefore, the
163 measurements from one year are sufficient in this study. Five healthy and representative
164 adult trees ($n = 5$, $N = 60$) were selected at each elevation, with a space >100 m apart,
165 with no obvious damage or deformities and generally uniform light conditions. In situ,
166 photosynthetic traits measurement and sample collection were performed for each tree.

167 **2.3 Measurement of leaf functional traits**

168 The measurements were conducted on August 6, 2023, during the peak of the
169 growing season. Leaf photosynthetic parameters were measured using a CIRAS-3
170 portable photosynthesis measurement system from 9:00 to 15:00 each day, with
171 chamber conditions set to 25°C , CO_2 concentration at $400 \mu\text{mol mol}^{-1}$,
172 photosynthetically active radiation at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and relative humidity of 50 –
173 60% , under favorable weather conditions. In the field, different sunny branches from
174 the upper part of the tree crown were selected, and immediately cut with high pruning
175 shears, and then inserted into buckets filled with water to prevent gas embolism from
176 affecting the photosynthetic physiology of the plant-related leaves. A total of 6–8 latest
177 fully extended, healthy, and disease-free leaves were selected for assessment. The
178 measured parameters included net photosynthetic rate (A), transpiration rate (Tr),
179 intercellular carbon dioxide concentration (Ci), stomatal conductance (gs), and water
180 use efficiency (WUE).

181 After the photosynthetic parameters measurements were completed, 30–50 leaves
182 similar to those used for the photosynthetic parameter measurements, were taken and
183 placed in a holding box, and brought back to the experimental station for leaf area
184 scanning (Li-3000C). The scanned leaves were first measured for fresh weight and then
185 placed in a desiccator (70°C) for drying to obtain the leaf dry weight. The dried samples
186 were brought back to the laboratory for elemental analysis.

187 Leaf carbon (C) and nitrogen (N) contents were measured using an elemental
188 analyzer (EA300, Hanon Instruments, China). Leaf samples were dried at 65°C for 48
189 hours until a constant weight was achieved, ground into a fine powder, and



190 approximately 2 mg of the powder was weighed into tin capsules for analysis.
191 Phosphorus (P) content was determined by digesting leaf samples with concentrated
192 nitric acid (HNO₃) at 180°C for 30 minutes in a microwave digestion system. The
193 digested extracts were analyzed using the molybdenum-antimony anti-
194 spectrophotometric method, which involved forming a blue complex in an acidic
195 medium and measuring absorbance at 880 nm. Non-structural carbohydrate (NSC)
196 content was quantified using the anthrone-sulfuric acid method. Soluble sugars were
197 extracted by heating ground leaf samples in 80% ethanol at 80°C for 30 minutes,
198 followed by centrifugation to collect the supernatant. Starch was hydrolyzed from the
199 residual pellet using perchloric acid. Both sugar and starch concentrations were
200 determined by reacting the extracts with anthrone reagent at 100°C and measuring
201 absorbance at 620 nm, using glucose as a calibration standard. Stable isotope ratios
202 ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) were analyzed using a continuous-flow isotope ratio mass spectrometer
203 (Delta V Advantage, Thermo Fisher Scientific, Germany). Ground leaf samples were
204 loaded into tin or silver capsules, and isotope values were calibrated against the Vienna
205 Pee Dee Belemnite (VPDB) standard for $\delta^{13}\text{C}$ and the Vienna Standard Mean Ocean
206 Water (VSMOW) standard for $\delta^{18}\text{O}$. Laboratory standards were analyzed every 10
207 samples to ensure precision and accuracy.
208



Table 1. Classification of leaf functional traits and their parameters.

Categorization	Traits	Attributes	Calculation (units)
Structural	SLA	Specific leaf area	$\text{cm}^2 \cdot \text{g}^{-1}$
Traits	LDMC	Leaf dry matter content	$\text{mg} \cdot \text{g}^{-1}$
Nutrient Traits	NSC	Non-structural carbohydrate	%
	C	Carbon content	%
	N	Nitrogen content	$\text{mg} \cdot \text{kg}^{-1}$
	P	Phosphorus content	$\text{mg} \cdot \text{kg}^{-1}$
Photosynthetic	gs	Stomatal conductance	$\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
Traits	A	Net photosynthetic rate	$\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
	PNUE	Photosynthetic nitrogen use efficiency	$\mu\text{mol} \cdot (\text{g N})^{-1} \cdot \text{s}^{-1}$
	PPUE	Photosynthetic phosphorus utilization efficiency	$\mu\text{mol} \cdot (\text{g N})^{-1} \cdot \text{s}^{-1}$
Hydraulic	WUE	Water use efficiency	$\mu\text{mol} \cdot \text{mmol}^{-1}$
traits	$\delta^{18}\text{O}$	Oxygen isotope	‰
	$\delta^{13}\text{C}$	Carbon isotope	‰

2.4 Statistical analyses

All the data were tested for normality (Shapiro–Wilk) and homogeneity of variance (Levene’s test), and log-transformed to meet the statistical analysis requirements (Rog et al., 2021). One-way analysis of variance (ANOVA) was used to compare the interspecific differences between both species for each trait. Linear mixed models (LMMs) were used to analyze the responses to elevation, species and their interaction. Relationships among different traits were analyzed using principal component analysis (PCA). The quartile coefficient of dispersion (QCD) was calculated for each trait to assess the degree of intraspecific variation.

$$QCD = \left(\frac{Q3 - Q1}{2} \right) \div \left(\frac{Q3 + Q1}{2} \right)$$



QCD is a more robust measure method of discretization than the coefficient of variation. The latter is not suitable for datasets including isotope measurements (Brendel, 2014) or log-transformed data (Canchola et al., 2017). We calculated Pearson's correlation coefficients among the traits. Based them, we conducted trait network analysis (R software package igraph, Csardi & Nepusz, 2006) to examine the coordination among multiple traits of the two tree species, with each trait denoting a node and only edges with significance ($p < 0.05$) were shown. The overall and node parameters of the trait network were calculated. All the data processing and plotting were conducted using R 4.3.1.

231

232 3. Results

233 3.1 Differences in leaf functional traits of *B. ermanii* and *P. jezoensis* along 234 elevational gradients

The results of the PCA analysis showed that the first two principal components explained 53.6% of the total variance in leaf functional traits of *B. ermanii* and 58.7% of that of *jezoensis* (Figure 1).

For *B. ermanii*, the first axis explained 33.5% of the variance, which was positively correlated with SLA, NSC, WUE, PPUE, and PNUE, and negatively correlated with C, $\delta^{13}\text{C}$, and gs. The second axis explained 20.1% and was negatively correlated with $\delta^{18}\text{O}$. LDMC, N, P, and gs synergized and constrained each other with WUE and ^{18}O . Meanwhile, the second axis delineated habitats that differed between high and low elevations, with survival at higher elevations clustered in the positive direction of PC2 (Figure 1a).

For *P. jezoensis*, the first two principal components accounted for 58.7% of the total variation, with the first axis explaining 33.7%, mostly related to photosynthetic and nutrient traits. The first axis was positively related to A, PPUE, PNUE, and WUE, and negatively related to N and P. The second axis explained 25%, mostly related to structural and hydraulic traits, positively correlated with SLA and $\delta^{18}\text{O}$, and negatively correlated with $\delta^{13}\text{C}$, and LDMC, $\delta^{13}\text{C}$ synergize with each other, constraining each



other with SLA. The distribution was clustered more across elevations, with no clear elevational differentiation along the axis of variation (Figure 1b).

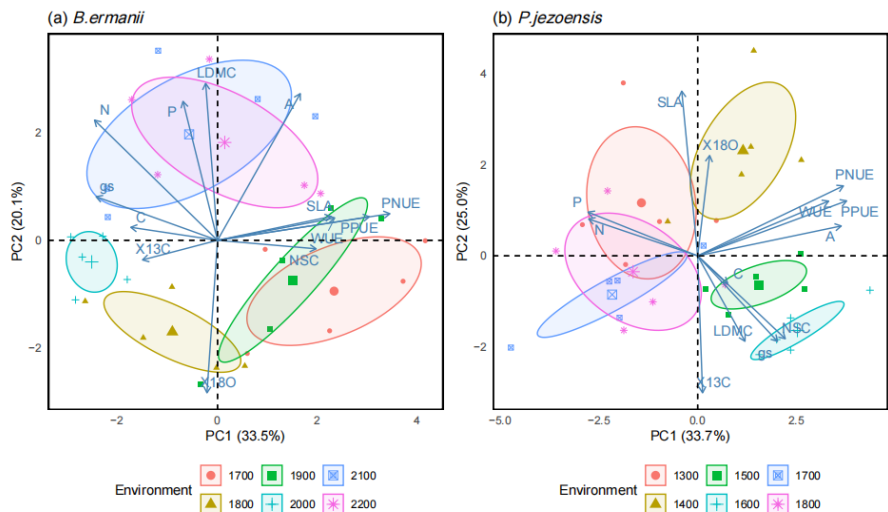


Figure 1. PCA analysis of 13 leaf functional traits of *B. ermanii* and *P. jezoensis*. The parameter descriptions are provided in Table 1.

There were significant differences in most of the leaf functional traits between *B. ermanii* and *P. jezoensis*, with higher SLA, NSC, N, A, PNUE, PPUE, WUE, and $\delta^{18}\text{O}$ of *B. ermanii* than that of *P. jezoensis*. Meanwhile, LDMC, and $\delta^{13}\text{C}$ were higher of *P. jezoensis* than that of *B. ermanii* (Table 2, Figure 2). There were no significant differences in leaf C and P contents and gs between the two species (Table 2).

Changes in leaf functional traits of the two species differed with elevation (Table 2). The LDMC, N, P, and gs of *B. ermanii* increased with elevation. Meanwhile, WUE and $\delta^{18}\text{O}$ decreased in *B. ermanii* species. $\delta^{13}\text{C}$ increased but SLA decreased with increasing in *P. jezoensis* (Figure 2).

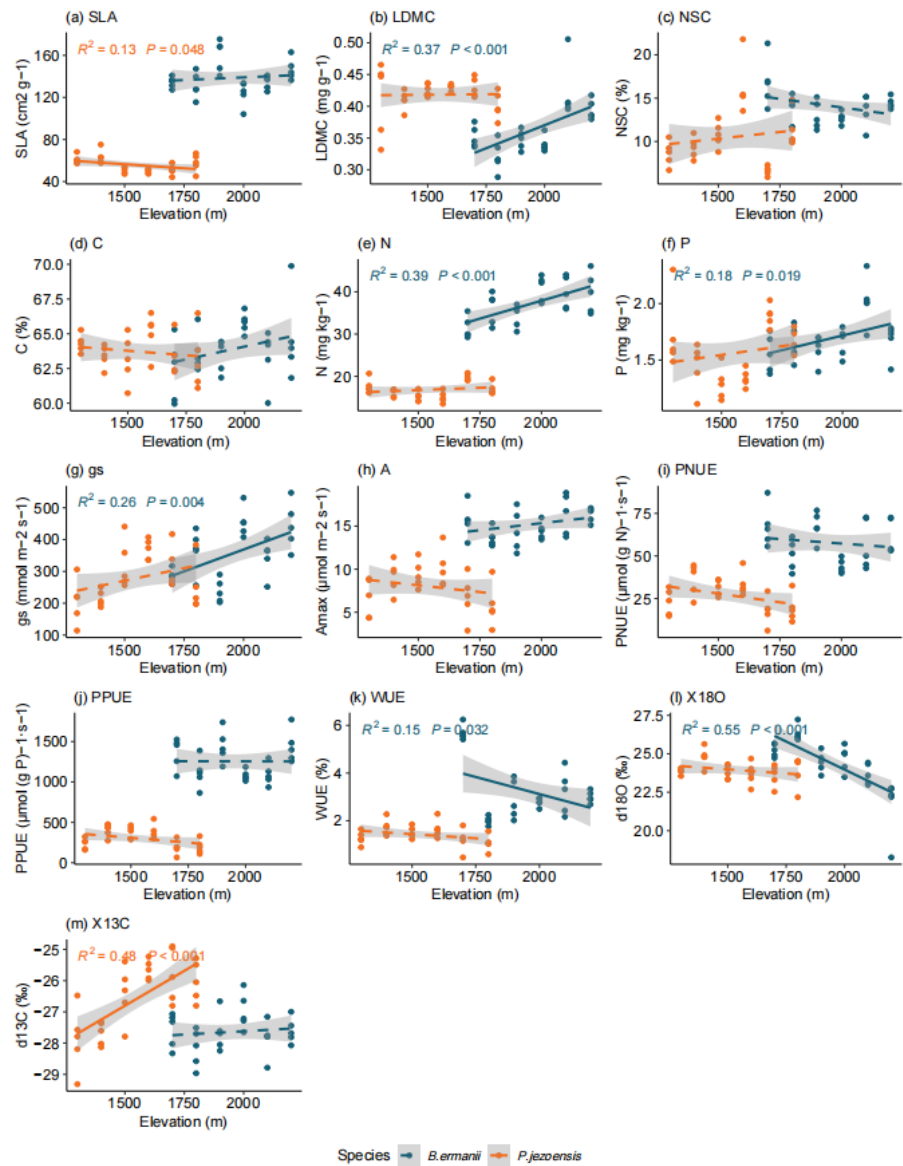


Figure 2. Linear regression relationship of 13 leaf functional traits of *B. ermanii* and *P. jezoensis* with elevation. The parameter descriptions are provided in Table 1.



Table 2. Differences in leaf functional traits of *B. ermanii* and *P. jezoensis* at different elevations analyzed using linear mixed models.

	Elevation		Species		Elevation *Species	
	F	p	F	p	F	p
SLA	399.28	<0.01	304.42	<0.01	1.93	0.18
LDMC	10.13	<0.01	47.283	<0.01	9.13	<0.01
NSC	13.42	<0.01	11.46	<0.01	2.69	0.11
C	0.67	0.42	0.16	0.69	4.27	<0.05
N	506.38	<0.01	186.42	<0.01	10.46	<0.01
P	9.71	<0.01	0.14	0.71	0.38	0.54
gs	25.77	<0.01	0.10	0.76	0.92	0.35
A	90.55	<0.01	65.19	<0.01	3.57	0.07
PNUE	46.67	<0.01	67.39	<0.01	0.33	0.57
PPUE	221.25	<0.01	191.71	<0.01	0.69	0.41
WUE	19.85	<0.01	53.40	<0.01	2.61	0.12
$\delta^{18}\text{O}$	6.12	<0.05	28.87	<0.01	17.95	<0.01
$\delta^{13}\text{C}$	6.67	<0.05	47.39	<0.01	15.80	<0.01

3.2 Intraspecific variation in leaf functional traits of *B. ermanii* and *P. jezoensis*

The intraspecific variation in functional traits of *B. ermanii* was lower than that of *P. jezoensis*. The four traits with the greatest intraspecific variation of *B. ermanii* were gs, WUE, PNUE, and PPUE. The traits with the least intraspecific variation were $\delta^{13}\text{C}$, C, and $\delta^{18}\text{O}$ (Figure 3a). The top four traits with high intraspecific variation of *P. jezoensis* were PPUE, PNUE, A, and gs. Meanwhile, the traits with low intraspecific variation were C, $\delta^{18}\text{O}$, LDMC, and $\delta^{13}\text{C}$ (Figure 3b). Regarding the intraspecific variation in different traits of both species, the traits combination with the highest intraspecific variation of both species was photosynthetic traits, and the traits combination with the second-highest intraspecific variation was hydraulic traits in *B. ermanii* and nutrient traits in *P. jezoensis*, and the intraspecific variation in structural traits of both species was small (Figure 3c).

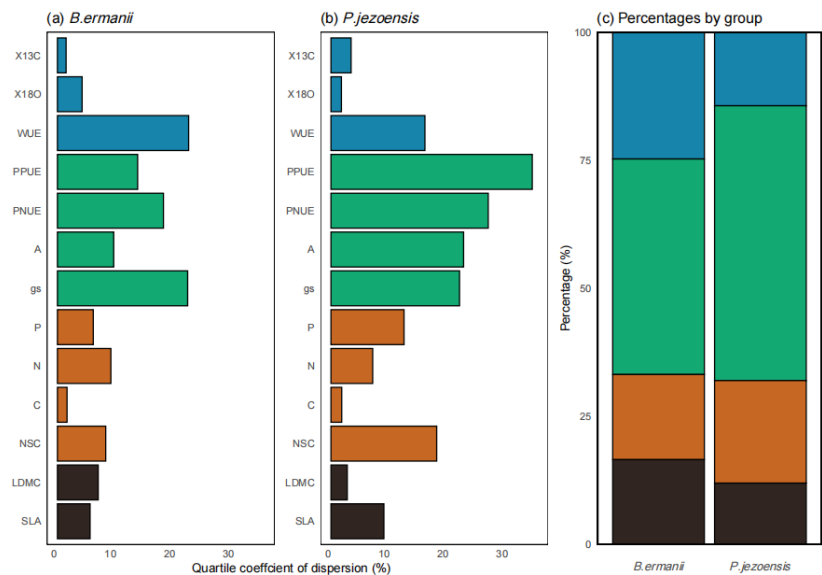


Figure 3. QCD of 13 leaf functional traits of *B. ermanii* and *P. jezoensis*, and the percentage of QCD for each grouped trait, Black: Structural Traits; Red: Nutrient Traits; Green: Photosynthetic Traits; Blue: Hydraulic traits. The parameter descriptions are provided in Table 1.

3.3 Coordination of leaf functional traits in *B. ermanii* and *P. jezoensis*

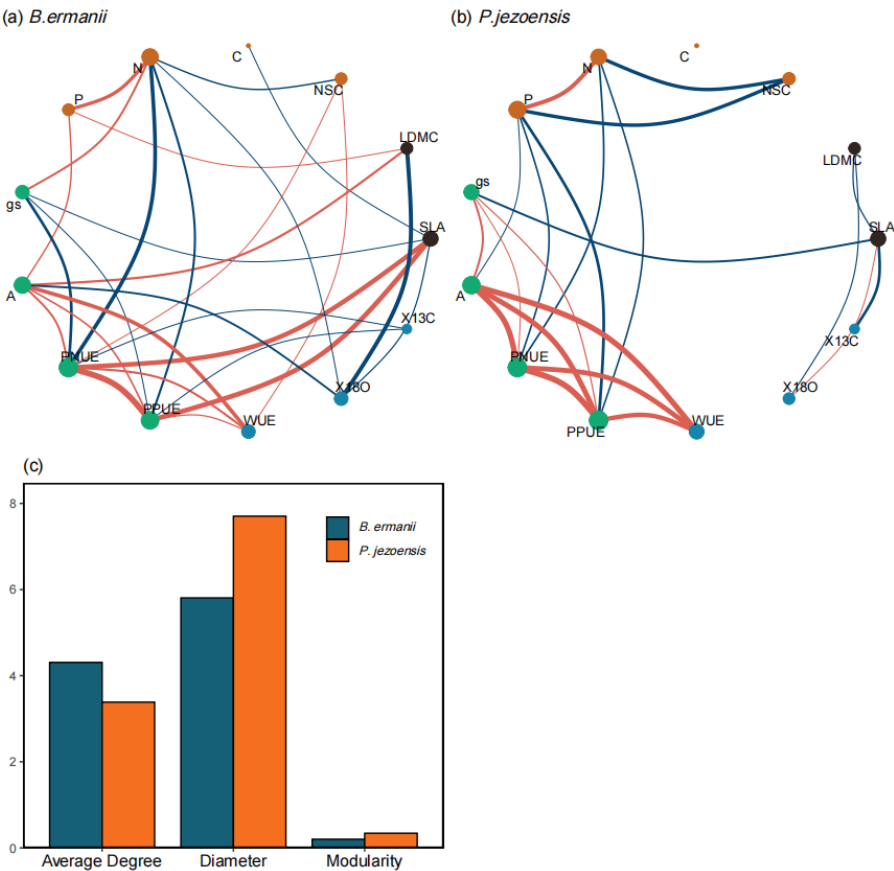
The trait networks of *B. ermanii* and *P. jezoensis* differed. Traits were more tightly linked within the trait network of *B. ermanii*, while traits were more loosely linked within the trait network of *P. jezoensis* (Figure 4a and 4b). The average degree of the trait network of *B. ermanii* and the number of edges connecting the central trait to other traits were higher than that of *P. jezoensis*. The trait network of *P. jezoensis* had a larger diameter and shorter distance between any two traits, and a higher modularity than that of *B. ermanii* (Figure 4c). For the hub traits of the trait network, the traits with highest degrees for both *B. ermanii* and *P. jezoensis* were the photosynthetic traits, especially PNUE and PPUE (Figure 5a). The closeness of each trait was similar with the degrees (Figure 5b). The traits with the highest betweenness were PPUE, A, $\delta^{18}\text{O}$ for *B. ermanii* and gs, PNUE, and SLA for *P. jezoensis* (Figure 5c).

There are some common points in the mutual synergy of traits between *B. ermanii* and *P. jezoensis*, such as a strong link between photosynthetic and nutrient traits and a



304 strong link between structural and hydraulic traits. However, photosynthetic traits were
305 also closely linked to structural and hydraulic traits for *B. ermanii*, which were not as
306 closely linked for *P. jezoensis*. The *gs* of *B. ermanii* was mostly negatively correlated
307 with PNUE and PPUE, and $\delta^{13}\text{C}$ was negatively correlated with $\delta^{18}\text{O}$. Meanwhile, *gs* of
308 *P. jezoensis* was positively correlated with A, PNUE, and PPUE, and $\delta^{13}\text{C}$ was
309 positively correlated with $\delta^{18}\text{O}$.

310



311

312 Figure 4. Network of leaf functional traits of (a) *B. ermanii* and (b) *P. jezoensis*, with
313 red line indicating positive correlation and blue line indicating negative correlation,
314 showing only edges with significant correlation ($p<0.05$), (c) Overall parameters of
315 both leaf functional trait network. The parameter descriptions are provided in Table S2.

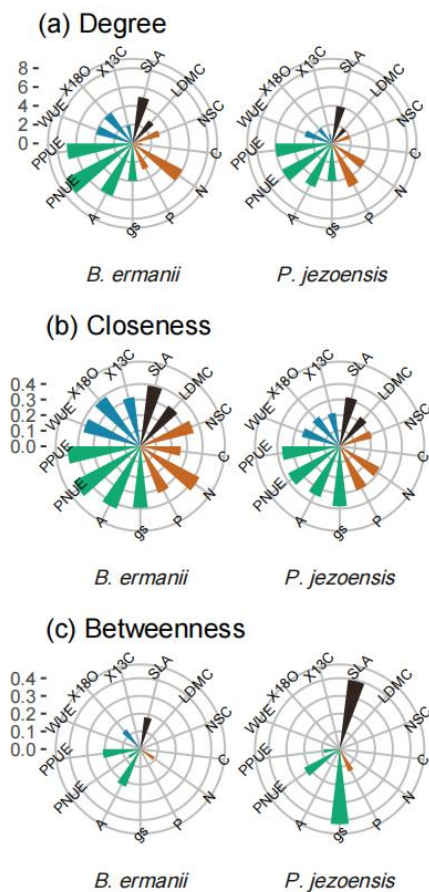


Figure 5. Node parameters of the networks of leaf functional traits of *B. ermanii* and *P. jezoensis*. The parameter descriptions are provided in Table S2.

4. Discussion

4.1 Differences in leaf functional traits between *B. ermanii* and *P. jezoensis*

The traits of the treeline species *B. ermanii*, which varied with elevation, reflected that although *B. ermanii* had a smaller intraspecific variation than *P. jezoensis* in the face of stronger stresses, it used an effective resource acquisition strategy and a radical water use strategy. Leaf N and P content increased with elevation. Leaf N is invested in the construction of photosynthesis-related enzymes, while leaf P influences membrane solubility, ATP, and NADPH production (Walker et al., 2014; Taiz et al., 2015). An



328 increase in g_s enhanced CO_2 uptake (Wang et al. 2022), which supported high
 329 photosynthetic capacity (Collins et al., 2016). The g_s of *B. ermanii* increases and WUE
 330 decreases with increasing elevation, which is also a radical water use strategy (Moreno-
 331 Gutiérrez et al., 2012). For species that use the "fast-aggressive" trait strategy grow
 332 better and are more dominant in resource-rich growing environments (Reich, 2014).
 333 This "fast-aggressive" trait strategy may have enabled *B. ermanii* to mobilize resources
 334 as aggressively as possible under harsher environmental conditions, and to be better
 335 equipped to cope with coercion, thus occupying treeline positions during succession.
 336 As the climate warms, this strategy will be more favorable to the expansion of *B.*
 337 *ermanii* and the upward shift of the treeline, because the "fast-aggressive" trait strategy
 338 allows the plant to respond rapidly to environmental changes and adapt to new
 339 environments (Liao et al., 2021). These findings suggest that *B. ermanii* exhibits greater
 340 adaptability to climate warming than *P. jezoensis*.

341 Non-treeline species grow in environments that differ significantly from those of
 342 treeline species. This distinction leads to variations in their leaf functional trait
 343 adaptations to elevation, which are not driven by differences in functional types (Dong
 344 et al., 2025). The non-treeline species *P. jezoensis* used a more conservative resource
 345 use strategy and water use strategy in the face of cold stress. For *P. jezoensis*, and SLA
 346 decreased with elevation, suggesting that *P. jezoensis* increased leaf thickness,
 347 improved defense, extended leaf longevity, and optimized water use efficiency at higher
 348 elevations to ensure stable and efficient photosynthesis, which is a conservative
 349 resource use strategy (Khan et al., 2022). The increase in $\delta^{13}C$ at high elevation suggests
 350 an increase in water use efficiency of *P. jezoensis*, a more conservative water use
 351 strategy (Moreno-Gutiérrez et al., 2012). Perhaps this conservative resource and water
 352 strategy causes *P. jezoensis* to rise less than the treeline during succession. As the
 353 climate warms, the upper elevation limits of *P. jezoensis* will expand substantially
 354 slower than the treeline species *B. ermanii*, because in addition to competition with *B.*
 355 *ermanii*, this conservative trait strategy also limits *P. jezoensis* to expand (Liao et al.,
 356 2021).



4.2 Differences in intraspecific variation in leaf functional traits between *B. ermanii* and *P. jezoensis*

In line with our H1, we found that the intraspecific variation in the functional traits of the treeline species *B. ermanii* was smaller than that of the non-treeline species *P. jezoensis*, potentially because *B. ermanii* is distributed at higher elevations with harsher environments. In harsh environments, the construction costs of plant traits increase (Auld et al., 2010; Solé-Medina et al., 2022), resulting in smaller intraspecific variation. Previous studies also indicated that trait variation decreased as climatic conditions became more extreme, or climate filtering (Vicente et al., 2022; González De Andrés et al., 2024). Solé-Medina et al. (2022) found that *Q. faginea* showed lower plasticity in drier and colder environments (Solé-Medina et al., 2022). While higher intraspecific variation means more capability to cope with changes in environmental conditions, it also implies a higher investment of resources. Therefore, in resource-limited environments, there is a need for trade-offs between increased resilience through reduced trait variation and the strategic allocation of resources (Power et al., 2019).

The types of traits with the highest intraspecific variation of both *B. ermanii* and *P. jezoensis* were photosynthetic traits. The traits with the lowest intraspecific variation were structural traits. This is consistent with the traditional view of a "plasticity hierarchy", where physiological traits are the most plastic, while some anisotropic traits or structural traits are less plastic (Bonaparte et al., 1975; Sadras et al., 2012). This is because different types of traits have different construction costs, and physiological traits are less expensive to build and are reversible. Therefore, they are more likely to change with the environment (Li et al., 2018). However, construction costs of structural traits are higher and irreversible, so they are less likely to change (Stotz et al., 2021). The traits with the second-highest variation of the treeline species *B. ermanii* were hydraulic traits and of *P. jezoensis* were nutrient traits. This is because conifers have a higher margin of hydraulic security than broadleaf trees to better cope with variable moisture conditions (Choat et al., 2012). While broadleaf trees are inherently deficient in hydraulic security and can only increase intraspecific variation by changing their



386 traits to adapt to changes in the water status in the environment (Carnicer et al., 2013).
 387 The status of intraspecific variation between the treeline species *B. ermanii* and the non-
 388 treeline species *P. jezoensis* was influenced by the environment in which they grew,
 389 favoring their adaptation to environmental changes.

390 **4.3 Differences in coordination of leaf functional traits between *B. ermanii* and *P.*** 391 ***jezoensis***

392 Inconsistent with our H2, the traits in the trait networks of the treeline species *B.*
 393 *ermanii* grown at higher elevations in harsher environments were more strongly
 394 internally connected. Meanwhile, those of the non-treeline species *P. jezoensis* were
 395 less internally connected and had a higher modularity. This reflects the different
 396 covariation and coordination of traits between *B. ermanii* and *P. jezoensis* in different
 397 habitats (He et al., 2020). As a treeline species, *B. ermanii*, by better coordinating
 398 different physiological and ecological functions through enhanced connectivity among
 399 internal traits (Wang et al., 2023). Therefore, photosynthetic traits in *B. ermanii* are
 400 strongly linked to structural and hydraulic traits. Efficient resource use, that is,
 401 photosynthesis and water regulation, is essential for survival and reproduction during
 402 the short growing season (Reich, 2014). In contrast, the non-treeline species, *P.*
 403 *jezoensis*, does not require tight internal trait coordination to cope with environmental
 404 stresses (He et al., 2020). Therefore, trait networks of *P. jezoensis* may exhibit a higher
 405 degree of modularity, suggesting greater independence among traits. Each module may
 406 focus on dealing with specific environmental or physiological problems rather than
 407 forming highly connected networks (Messier et al., 2017), which facilitates flexibility
 408 in less extreme environmental adaptations to a variety of different ecological niches (Li
 409 et al., 2015). Meanwhile, modularity optimization allows *P. jezoensis* to rapidly adapt
 410 and adjust its growth strategy in the face of diverse competitive and shaded
 411 environments (Westerband et al., 2021). This was consistent with the high intraspecific
 412 variability we found in *P. jezoensis*. PCA analyses showed more significant divisions at
 413 different elevations in *B. ermanii*, suggesting that elevation plays a dominant role in the
 414 variation of leaf functional traits of *B. ermanii*. However, in addition to cold



415 temperature, *P. jezoensis* may also be influenced by other factors, such as competition
 416 (Scherrer et al., 2020).

417 The central traits for both species are the photosynthetic traits, such as PNUE and
 418 PPUE. This suggests that the most central issue in the growth of both treeline and non-
 419 treeline species is how to use nutrient resources more efficiently to increase
 420 photosynthetic capacity to cope with harsh alpine growing environments (Funk, 2008)..
 421 Stomatal conductance of *B. ermanii* was negatively correlated with PNUE and PPUE,
 422 This indicated that as stomatal opening increased, photosynthetic nutrient use efficiency
 423 decreased and the nutrient requirement for photosynthesis greatly increased. The same
 424 negative correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ also reflected the complex stomatal
 425 regulation of *B. ermanii*, showing a independent regulation of water and carbon
 426 exchange through different mechanisms. It is clear that the synergistic approach among
 427 these traits in *B. ermanii* is a more radical regulatory strategy. The positive correlation
 428 between stomatal conductance and photosynthetic traits in *P. jezoensis* suggests that
 429 maintaining stomatal openness helps maximize photosynthesis in its growing
 430 environment, and the positive correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggests that in more
 431 resource-rich environments, the increase in stomatal conductance is synchronized with
 432 the enhancement of photosynthesis, thus optimizing carbon assimilation and water use,
 433 both of which are more conservative resource use strategies. The differences in leaf
 434 functional trait coordination between the two species are driven by their contrasting
 435 growth environments. These variations result from the distinct conditions of treeline
 436 and non-treeline habitats, rather than the distinction between evergreen conifers and
 437 deciduous broad-leaved trees (Dong et al., 2025).

438 5. Conclusion

439 Consistent with our hypotheses, we found that the treeline species *B. ermanii* had
 440 lower intraspecific variations in leaf functional traits but a stronger linkage among these
 441 traits than the non-treeline species *P. jezoensis*. This suggests that *B. ermanii*, occupying
 442 the alpine treeline position, has adopted a resource acquisition strategy and may
 443 continue to expand to higher elevations in the future. In contrast, the non-treeline



444 species *P. jezoensis* has adopted a resource-conserving strategy and showed less
445 possibility to expand its distribution range in the future. Our study provides new
446 insights into the responses of both treeline and non-treeline species to future climate
447 change, contributing to reveal current adaptation strategies of treeline and non-treeline
448 trees, and predict future dynamics of subalpine forests.

449

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458

459 **Author's contributions**

460 Renkai Dong, Hong S. He, and Mai-He Li conceived and designed the experiment.
461 Renkai Dong and Na Li performed the experiments. Renkai Dong analyzed the data,
462 prepared figures, and wrote original draft preparation. Hong S. He, Mai-He Li, Na Li,
463 Haibo Du and Yu Cong, revised the manuscript. All authors contributed to the work,
464 and they have read and agreed to the submitted version of the manuscript.

465

466 **Declaration of competing interest**

467 The authors declare that they have no known competing financial interests or
468 personal relationships that could have appeared to influence the work reported in this
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