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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ABSTRACT

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

Keywords:

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

1. Introduction

45

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

132   dormant volcano and also is the highest mountain in Northeast China with its summit

133   at 2696 m a.s.l. The area has a temperate continental climate, with a mean temperature

134   of −7.3 to 4.9 °C in the growing season and annual precipitation of 800 to 1800 mm.

135   The volcanic eruption of 946 AD destroyed most of the vegetation and formed a

136   spectrum of vertical zones over a long period of succession. From top to bottom, the

137   vegetated landscapes are alpine tundra (>2,000 m a.s.l.), deciduous broad-leaved *B.*

138   *ermanii* forests (1,700–2,000 m a.s.l.), alpine coniferous spruce-fir forests (1,100–1,700

139   m a.s.l.), and mixed coniferous and broad-leaved forests (740–1,100 m a.s.l.). *B.*

140   *ermanii* is a treeline species. Although the elevation of the forest line is 2000 m, *B.*

141   *ermanii* can still be distributed upward to 2200 m, and *P. jezoensis* is the main

142   established species of the cloud fir forest. During the growing season, for every 100 m

143   of elevation gain, the mean annual atmospheric temperature in the understory of the

144   area decreased by approximately 0.68 °C and the mean annual atmospheric humidity

145   in the understory increased by approximately 0.93% (Reich et al., 1998).

146   **2.2 Experimental design and sampling**

147   We selected *B. ermanii* as a representative treeline species and *P. jezoensis* as a

148   non-treeline species for this study. This selection reflects the unique composition of the

149   treeline in the Changbai Mountain region, where *B. ermanii* predominates, constituting

150   over 90% of the treeline species population. In contrast, *P. jezoensis* is mainly

151   distributed along the lower boundary of the *B. ermanii* range, accounting for more than

152   70% of the tree species population in this zone. These distribution patterns make *P.*

153   *jezoensis* an ideal representative of non-treeline species. We set up experimental plots

154   comprising a total of 12 plots at 100 m intervals within the main distribution range of

155   the treeline species *B. ermanii* (1700–2200 m) and the non-treeline species *P. jezoensis*

156   (1300–1800 m). The plots were in the natural native forest far away from the highway,

157   with the trees in the sample plots in good growing conditions and with moderate spacing

158   between each other. We conducted on-site field measurements and tree sampling in

159   August 2023 (peak of the growing season). Our study focuses on the relative spatial

160   variations in leaf functional traits of the two species by analyzing data from vdifferent

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.

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 μmol mol^{-1},

172 photosynthetically active radiation at 1500 μmol m^{-2} 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 (HNO_3) 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   ($\delta^{13}C$ and $\delta^{18}O$) 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 $\delta^{13}C$ and the Vienna Standard Mean Ocean

206   Water (VSMOW) standard for $\delta^{18}O$. Laboratory standards were analyzed every 10

207   samples to ensure precision and accuracy.

208

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

210

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

211

212   **2.4 Statistical analyses**

213   All the data were tested for normality (Shapiro–Wilk) and homogeneity of

214   variance (Levene's test), and log-transformed to meet the statistical analysis

215   requirements (Rog et al., 2021). One-way analysis of variance (ANOVA) was used to

216   compare the interspecific differences between both species for each trait. Linear mixed

217   models (LMMs) were used to analyze the responses to elevation, species and their

218   interaction. Relationships among different traits were analyzed using principal

219   component analysis (PCA). The quartile coefficient of dispersion (QCD) was calculated

220   for each trait to assess the degree of intraspecific variation.

221
$$QCD = \left(\frac{Q3-Q1}{2}\right) \div \left(\frac{Q3+Q1}{2}\right)$$

222   QCD is a more robust measure method of discretization than the coefficient of

223 variation. The latter is not suitable for datasets including isotope measurements

224 (Brendel, 2014) or log-transformed data (Canchola et al., 2017). We calculated

225 Pearson's correlation coefficients among the traits. Based them, we conducted trait

226 network analysis (R software package igraph, Csardi & Nepusz, 2006) to examine the

227 coordination among multiple traits of the two tree species, with each trait denoting a

228 node and only edges with significance ($p<0.05$) were shown. The overall and node

229 parameters of the trait network were calculated. All the data processing and plotting

230 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**

235   The results of the PCA analysis showed that the first two principal components

236 explained 53.6% of the total variance in leaf functional traits of *B. ermanii* and 58.7%

237 of that of *jezoensis* (Figure 1).

238   For *B. ermanii*, the first axis explained 33.5% of the variance, which was positively

239 correlated with SLA, NSC, WUE, PPUE, and PNUE, and negatively correlated with C,

240 δ^{13}C, and gs. The second axis explained 20.1% and was negatively correlated with δ^{18}O.

241 LDMC, N, P, and gs synergized and constrained each other with WUE and ^{18}O.

242 Meanwhile, the second axis delineated habitats that differed between high and low

243 elevations, with survival at higher elevations clustered in the positive direction of PC2

244 (Figure 1a).

245   For *P. jezoensis*, the first two principal components accounted for 58.7% of the

246 total variation, with the first axis explaining 33.7%, mostly related to photosynthetic

247 and nutrient traits. The first axis was positively related to A, PPUE, PNUE, and WUE,

248 and negatively related to N and P. The second axis explained 25%, mostly related to

249 structural and hydraulic traits, positively correlated with SLA and δ^{18}O, and negatively

250 correlated with δ^{13}C, and LDMC, δ^{13}C synergize with each other, constraining each

251   other with SLA. The distribution was clustered more across elevations, with no clear

252   elevational differentiation along the axis of variation (Figure 1b).
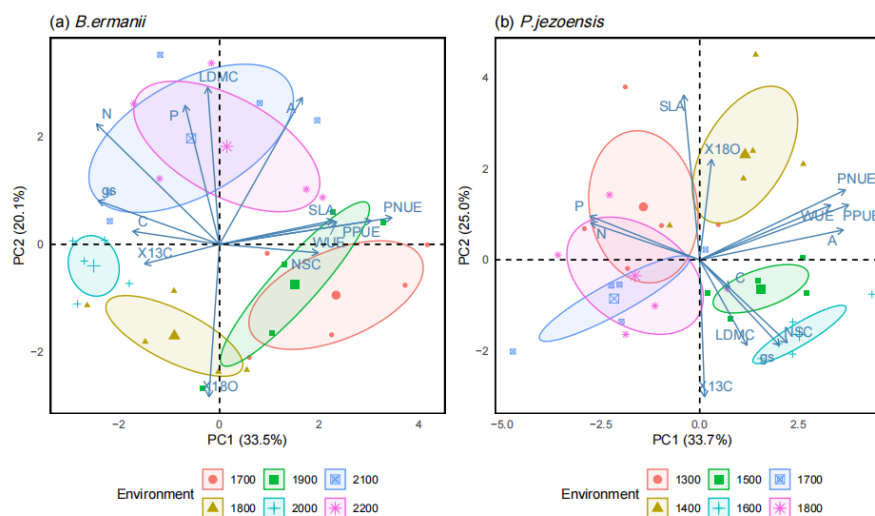
253

254   Figure 1. PCA analysis of 13 leaf functional traits of *B. ermanii* and *P. jezoensis*. The

255   parameter descriptions are provided in Table 1.

256   There were significant differences in most of the leaf functional traits between *B.*

257   *ermanii* and *P. jezoensis*, with higher SLA, NSC, N, A, PNUE, PPUE, WUE, and $\delta^{18}O$

258   of *B. ermanii* than that of *P. jezoensis*. Meanwhile, LDMC, and $\delta^{13}C$ were higher of *P.*

259   *jezoensis* than that of *B. ermanii* (Table 2, Figure 2). There were no significant

260   differences in leaf C and P contents and gs between the two species (Table 2).

261   Changes in leaf functional traits of the two species differed with elevation (Table

262   2). The LDMC, N, P, and gs of *B. ermanii* increased with elevation. Meanwhile, WUE

263   and $\delta^{18}O$ decreased in *B. ermanii* species. $\delta^{13}C$ increased but SLA decreased with

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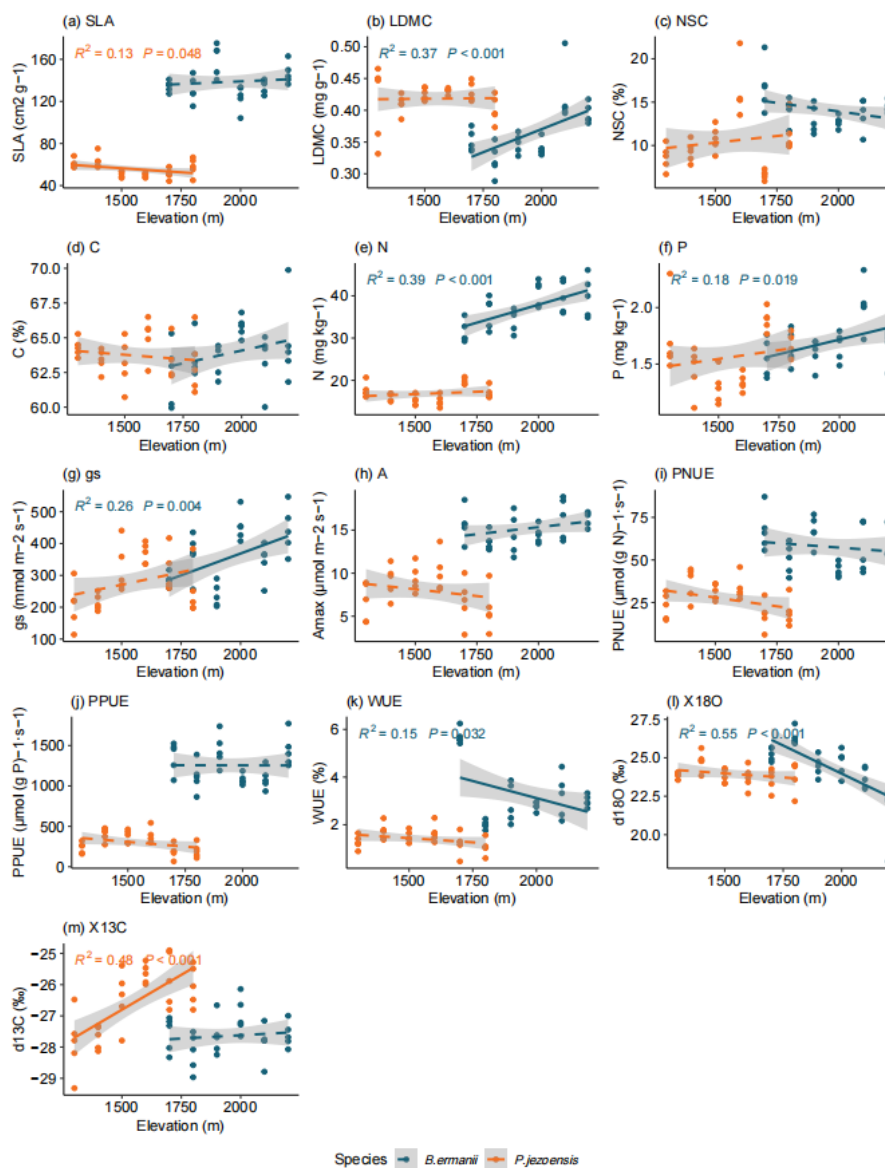
Figure 2. Linear regression relationship of 13 leaf functional traits of *B. ermanii* and *P. jezoensis* with elevation. The parameter descriptions are provided in Table 1.

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
^{18}O	6.12	**<0.05**	28.87	**<0.01**	17.95	**<0.01**
^{13}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 δ^{13}C, C, and δ^{18}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, δ^{18}O, LDMC, and δ^{13}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).
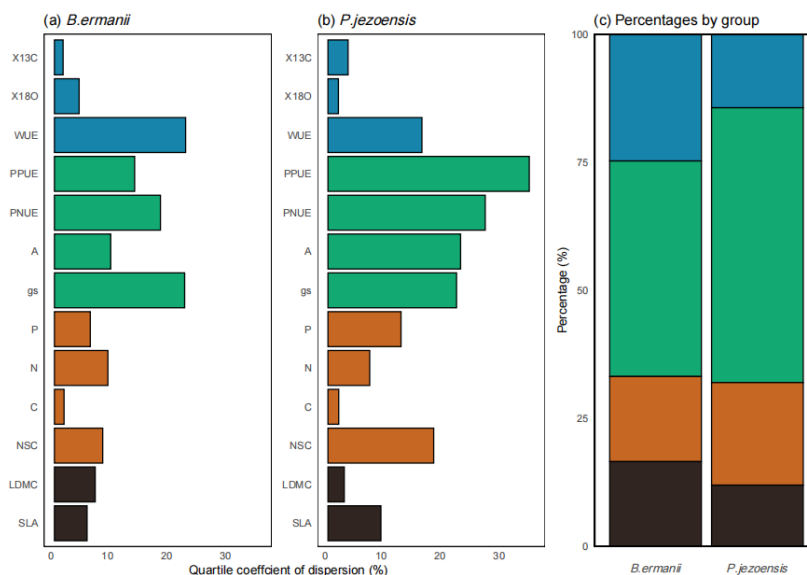
Figure 3. QCD of 13 leaf functional traits of *B. ermanii* and *P. jezoensis*, and the percentage of QCD for each grouped trait, Black: Structural Traits; Red: Nutrient Traits; Green: Photosynthetic Traits; Blue: Hydraulic traits. The parameter descriptions are provided in Table 1.

**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, δ^{18}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 δ^{13}C was negatively correlated with δ^{18}O. Meanwhile, gs of

308   *P. jezoensis* was positively correlated with A, PNUE, and PPUE, and δ^{13}C was

309   positively correlated with δ^{18}O.

310
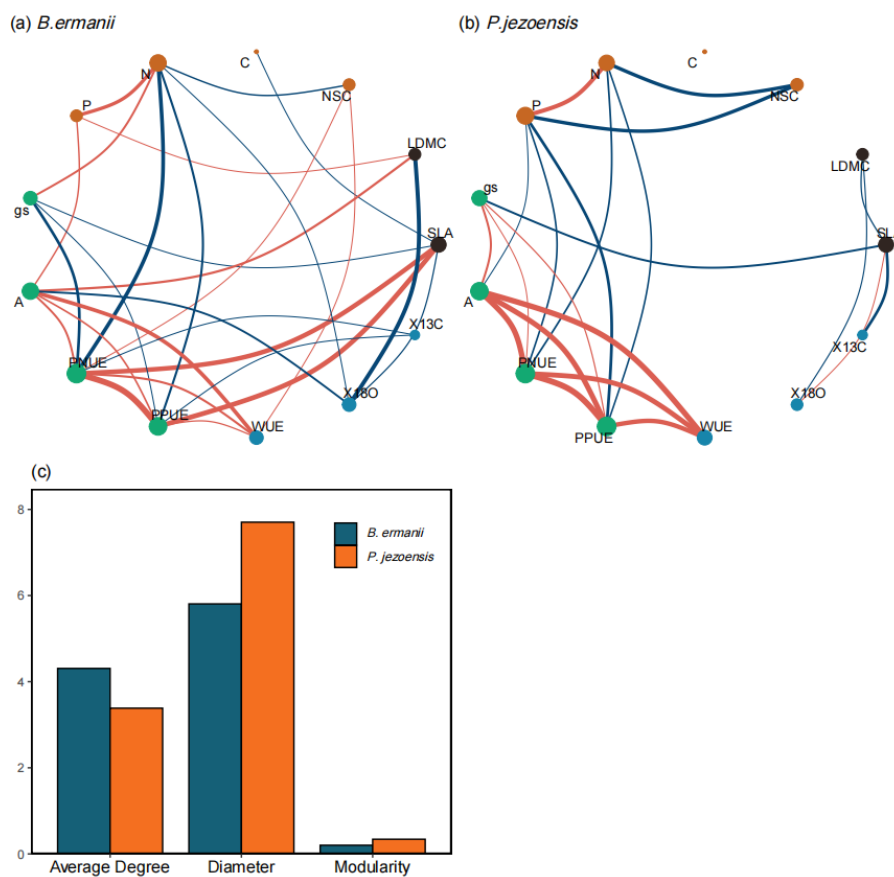
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312   Figure 4. Network of leaf functional traits of (a) *B. ermanii* and (b) *P. jezoensis*, with

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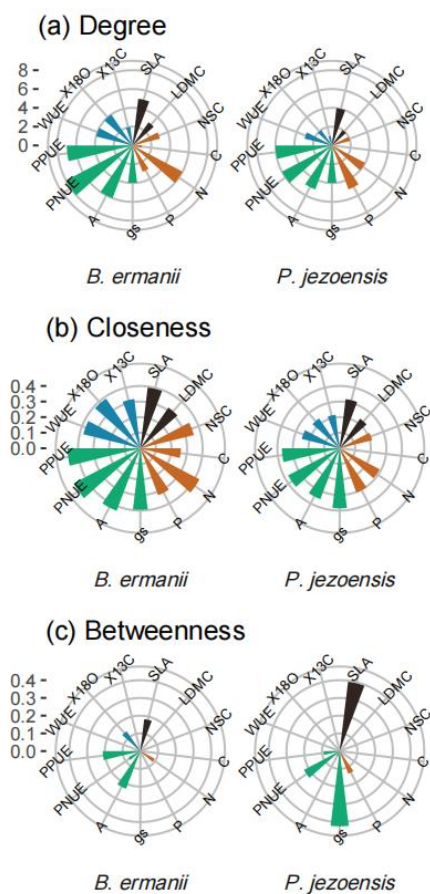
Figure 5. Node parameters of the networks of leaf functional traits of *B. ermanii* and *P. jezoensis*. The parameter descriptions are provided in Table S2.

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 gs enhanced CO_2 uptake (Wang et al. 2022), which supported high

329   photosynthetic capacity (Collins et al., 2016). The gs 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 $\delta^{13}C$ and $\delta^{18}O$ 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 $\delta^{13}C$ and $\delta^{18}O$ 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

20

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

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

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

469   paper.

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