



Enhanced herbaceous encroachment due to niche overlap in alpine tundra of Northeast China

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ABSTRACT

The directional ecological filtering hypothesis posits that species in high-altitude environments typically exhibit broad environmental tolerance, influencing the colonization success of non-native species through niche overlap with natives. This study examines this hypothesis on Changbai Mountain, focusing on the encroachment of the herb *Deyeuxia angustifolia* from mountain birch forests into alpine tundra, where it competes with the endemic *Rhododendron aureum*. We established a permanent plot containing 10,000 continuous quadrats (2×2 m) in the summer of 2014, covering from treeline to the upper limit of alpine tundra. Each quadrat was divided into 40×40 cm resolution cells, totaling 250,000 cells. In 2014 we photographed and manually interpreted tundra plant species for all cells, assessing topographic and edaphic niche characteristics (the range of the factors) for both species. Findings reveal: (1) Over 50 % niche overlap between *D. angustifolia* and *R. aureum*, suggesting intense competition; (2) Broader niche width for *R. aureum* compared to *D. angustifolia*; and (3) The expansion of *D. angustifolia* is facilitated by available nitrogen, while *R. aureum* is uniquely adapted to low phosphorus levels at higher altitudes. These results demonstrate that ecological and environmental filtering jointly shape distribution patterns of *R. aureum* and *D. angustifolia*, supporting the idea that environmental filtering is critical in the colonization of invading plant species. Our research sheds light on the pivotal roles played by microenvironmental factors, notably topography and soil, in determining the composition and distribution of plant communities, and contributes valuable insights for understanding and forecasting future shifts in plant composition of alpine tundra.

1. Introduction

Over the past decades, global environmental changes have led to changes in species composition of alpine ecosystems with non-native plant species encroaching upwards (Alexander et al., 2016). This shift in vegetation is primarily attributed to climate change

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and nitrogen deposition. Climate change plays a pivotal role by improving growth conditions in these ecosystems, such as extending the growing season, which in turn reduces ecological barriers for low-altitude plants, facilitating their upward migration (Chen et al., 2011; Du et al., 2018). Increased atmospheric nitrogen (N) deposition, especially pronounced in high-altitude areas over the past decades (Phoenix et al., 2006) has profound impacts for plants in alpine regions traditionally limited by nitrogen (Fowler et al., 2013). The augmented nitrogen levels have been linked to the upward encroachment of herbaceous species from lower altitudes, a trend observed and discussed in various studies (Körner, 1995; Zong et al., 2016).

On the Changbai Mountain in northeastern China, a low-elevation herb *Deyeuxia angustifolia*, a small narrow-leaf reed, has expanded its distribution range upward into the alpine shrubby tundra ecosystem and has gradually replaced the shrub species *Rhododendron aureum*, which has mainly been regarded as a result of global warming since the 1980s (Jin et al., 2017), and increased atmospheric N deposition (Zong et al., 2016). However, the upward migration of *D. angustifolia* does not proceed neatly at the same rate, forming a mosaic landscape on the slope, which suggests that microsites might play an important role in determining the migration rate and success of *D. angustifolia*. Microtopography regulates not only microclimate (Chung and Yun, 2004) but also soil nutrients and water conditions including winter snow cover (Lembrechts et al., 2018; Li et al., 2022; Zong et al., 2022). The interplay between local tundra microtopography, soil properties, and external factors such as climate warming and nitrogen deposition could result in intricate and patchy changes in alpine tundra vegetation (Beckage et al., 2008).

Ecological niche characteristics refer to nutrient, water, and light requirements for plant growth. Species replacement occurs when the niche characteristics of endemic plants overlap with those of the encroaching plant species (Yuan et al., 2021). The size and arrangement of ecological niches are the fundamental factors determining future changes in alpine tundra vegetation. Alexander et al. (2011) proposed the directional ecological filtering hypothesis (DEFH) or the ecological filtering hypothesis (EFH) and suggested that (a) species growing in high-altitude areas often have a wide range of tolerance to environmental conditions, and (b) an important factor for successful colonization by non-native species is a tolerance range that overlaps that of native species. Therefore, it can be assumed that the encroaching species may have similar ecological niche characteristics to the endemic species if the successful plant

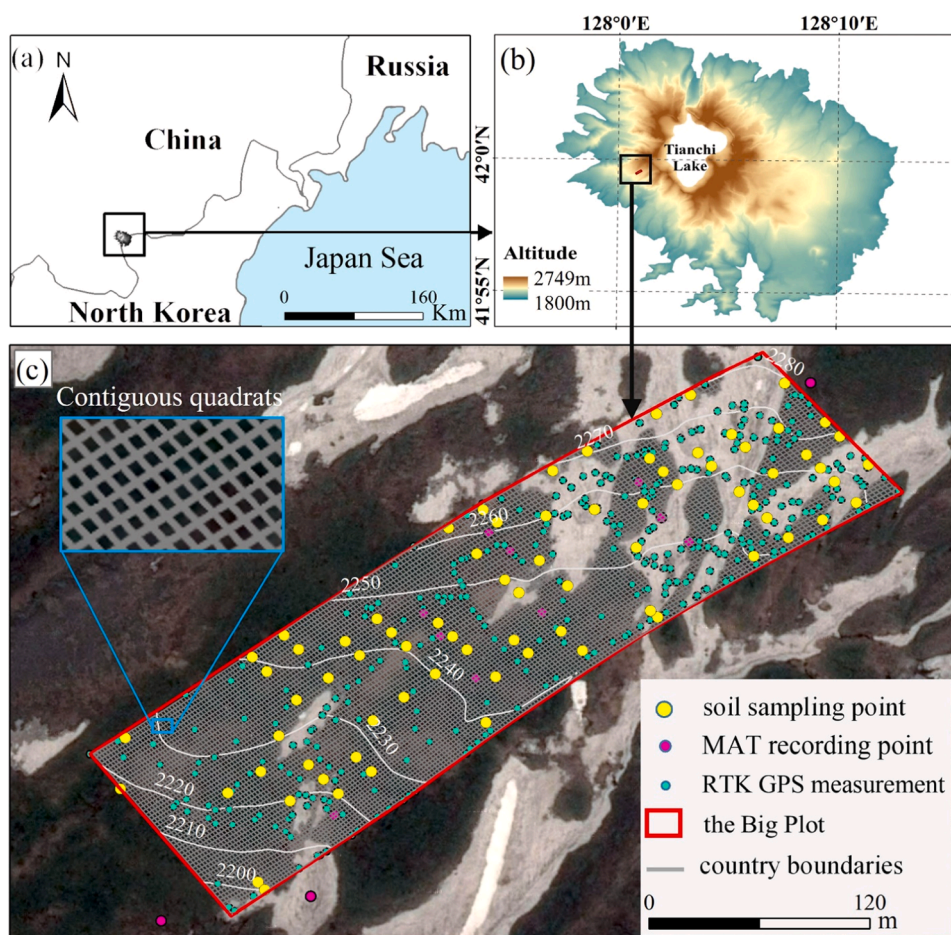


Fig. 1. Geographical location of the study area. (a) location of Changbai Mountain in Northeast China. (b) The alpine tundra in the study region, extending from 1800 m to the summit at 2749 m. (c) The satellite image shows locations of the Big Plot, soil samples, soil temperature measurements (derived mean annual temperature, MAT), and elevation measurements (real-time kinematic, RTK), and 10,000 contiguous quadrats.

encroachment is driven by the ecological filtering mechanism (Diez et al., 2008). This will lead to large niche overlap of encroaching and endemic species, thus resulting in a competitive relationship (Rodríguez, 2006).

Competition involves different aspects of niche characteristics of plants. The match of niche characteristics of the encroaching species and the local environments determines whether the plants can successfully encroach. In high-altitude areas, variations in microclimate and microtopography create suitable habitats that facilitate the encroachment of low-altitude plants (Lembrechts et al., 2018). Encroaching species usually have higher resource acquisition ability and higher resource utilization efficiency than endemic species. Hence, after colonization under specific environmental conditions, an encroaching species can gradually gain the dominant position in the community through its strong competitiveness. This can ultimately threaten the survival of endemic plants (Rodríguez, 2006).

The effects of microsites on encroachment and species replacement of *D. angustifolia* in the alpine tundra of Changbai Mountain have never been investigated. Therefore, we conducted the present study to understand better the upward migration processes and mechanisms of *D. angustifolia*. Our aim is to determine whether the topographical and edaphic niche overlap of plant species drives the upward migration of *D. angustifolia*. We hypothesize that: (1) the niche characteristics of the encroaching herbaceous species *D. angustifolia* and the endemic species *R. aureum* overlap to a certain degree, forming a competitive relationship (Hypothesis 1); and (2) microtopography-related soil factors play a more important role in determining the potential encroachment of *D. angustifolia* (Hypothesis 2).

2. Materials and methods

2.1. Study area

The Changbai Mountain (41°41'49" to 42°25'18"N and 127°42'55" to 128°16'48"E) is located in Northeast China (Fig. 1a). Five distinct vertical vegetation zones occur from 500 m to 2691 m above sea level (a.s.l.) on that Mountain: deciduous broadleaf forests (below 500 m a.s.l.), mixed Korean pine-broadleaf forests (500–1100 m a.s.l.), spruce (*Picea asperata*) and Korean pine (*Pinus koraiensis*) forests (1100–1700 m a.s.l.), mountain birch (*Betula ermanii*) forests (1700–2000 m a.s.l.), and alpine tundra beyond 2000 m a.s.l. (Zong et al., 2016). The alpine tundra is typically covered by snow for most of the year, and the brief growing season lasts from June to September. The annual precipitation ranges from 559 to 1554 mm (mean precipitation is 1056 mm). The precipitation data was collected from an automatic weather station (41°59'34"N, 128°1'4"E) set up at an elevation gradient of 2246 m in the alpine tundra on the western slope of Changbai Mountain.

The alpine tundra we investigated is located on the west-facing slope of the Changbai Mountain (Fig. 1b). The tundra is dominated by dwarf shrubs including rhododendron (*Rhododendron aureum*), blueberry (*Vaccinium uliginosum*), and mountain avens (*Dryas octopetala* var. *asiatica*), with some scattered distributed perennial herbs such as *Sanguisorba sitchensis* (*Sanguisorba stipulata*), *Sanguisorba parviflora* (*Sanguisorba tenuifolia*), hawkweed (*Hieracium coreanum* Nakai), *Ligularia fischeri* (*Ligularia jamesii* (Hemsl.) Kom.), and monkshood (*Aconitum tschangbaischanense*).

Deyeuxia angustifolia is native to the Changbai Mountains but was not recorded in alpine tundra until the 1990s. Early records indicated that *D. angustifolia* was more typical of the low-altitude montane birch forest but not of alpine tundra (Qian, 1979). Therefore, it is described as an encroaching species in previous studies (Zong et al., 2016). *D. angustifolia* is a perennial herb characterized by rapid growth, clonal and sexual reproduction, short juvenile period and high seed production (Williamson and Fitter, 1996). These traits enable it to thrive in the harsh conditions of the alpine tundra (Quiroz et al., 2009). Over the past three decades, *D. angustifolia* has progressively encroached upon the alpine tundra. By 2019, less than 5 % of the tundra zone on the western slope remained unaffected by the encroachment of *D. angustifolia*, while over 40 % of the area had an herbaceous cover exceeding 70 % (Zong et al., 2013b). The expansion of *D. angustifolia* has caused a significant decline in the abundance of the alpine tundra shrubs.

In 2014, we established a 100 m (width) × 400 m (length) Big Plot in the alpine tundra, ranging from 2190 to 2300 m a.s.l., on the west-facing slope of the Changbai Mountain (Fig. 1b). The plot covers an environmental gradient ranging from areas where *D. angustifolia* has already established dominance to areas where it has yet to encroach. Due to the large area of the plot and significant environmental heterogeneity within the alpine tundra (Wu et al., 2018), diverse environmental gradients are encompassed within the Big Plot. The Big Plot is located on the upper slopes of a volcanic cone of Changbai Mountain. The topography of the Big Plot includes snow erosion depressions and gully valleys due to the alternating effects of weathering and freeze-thaw action. The slope within the plot ranges from 0 to 73°, resulting in significant topographical variation. The primary soil type within the Big Plot is mountain tundra soil. The soil has developed upon volcanic ejecta, with tuff and quartz trachyte serving as the primary parent materials. This development has resulted in a brief pedogenesis period, a low degree of development, and thin soil layers (Meng, 1982). The soil is predominantly acidic, with pH ranging from 3.9 to 4.9. The content of available nitrogen and phosphorus in the soil is low, with levels ranging from 0.52 to 0.76 g/kg and 0.6 to 1.1 g/kg, respectively. Within the plot, we recorded topographic, vegetation, and edaphic data.

2.2. Topographic data

We measured the topographic data using a difference global positioning system (DGPS) (Hua Xing A10 GPS RTK; A10 GNSS RTK, Zhong Haida, China), which has a vertical resolution of 5 cm and a horizontal resolution of 2.5 cm. Given the significant topographical variation, we carefully selected key terrain positions, including ridges, slopes, valleys, and flat areas, to represent a range of topographical conditions. The measurement points were uniformly distributed and placed at key terrain positions (Fig. 1c). At each point,

geographic coordinates and elevation were recorded, from which spatial interpolations were conducted to generate a digital elevation model (DEM) at 1 m resolution. This approach ensures a comprehensive assessment of the spatial variations in topography. We further derived slope, aspect, curvature, and topographic roughness from the DEM using ArcGIS (10.7).

2.3. Vegetation data

The Big Plot was arranged into a rectangular area consisting of 50 × 200 contiguous 2 × 2 m quadrats. In the growing season (July and August) in 2014, each quadrat was sequentially photographed with a camera (CANON EW-82, CANON INC., Japan). The camera was kept at a height of 1.5 m above the ground surface to ensure a clear and complete picture of the plants throughout the quadrat, and the photos were numbered according to its geographical coordinates.

Each quadrat was further divided into 25 continuous grid cells (40 × 40 cm each) and a total of 250,000 grid cells. We used a unified method to interpret visually all 250,000 grid cells and we recorded abundance information by species (Fig. 2). We created a shapefile based on quadrat spatial information to contain boundaries of each of the 250,000 grid cells (Fig. 2). Because of the difference between the plane quadrat and the 3D terrain on the ground, control points were selected to rectify the shapefile of the grid cells for the DEM. In this manner, we created a final ArcGIS grid such that the spatial distribution of any recorded plant species can be generated across the entire plot. Some anomalous data points were identified in the final mosaic of species spatial distribution data, which were usually isolated and scattered. These anomalies were likely from misinterpretation of plant species by the interpreters. We carefully reviewed and re-interpreted these anomalous points to minimize additional errors introduced during the visual interpretation process. For this study, the spatial distribution data for *R. aureum* and *D. angustifolia* with coverage greater than 0 % were extracted. The entire interpretation and error correction processes lasted from 2014 to 2020.

2.4. Edaphic data

Within the Big Plot, we collected 226 soil samples (0–10 cm) distributed among *D. angustifolia* and *R. aureum* community patches for subsequent analysis (Fig. 1c). Specifically, the soil surface layer (0–5 cm) includes the litter leaching transition layer and the humus layer, while soil deeper than 5 cm is mostly composed of the humus gravel layer and volcanic ejecta layer (Zhang, 2023). The soil samples were air-dried and transported to the laboratory, and the oven-dried soils were ground with a ball mill. After the pre-treatments, the soil physical and chemical properties were analyzed, including soil organic carbon (SOC), total nitrogen (TN), available nitrogen (AN), total phosphorus (TP) and pH value. The pH value was determined through potentiometric measurement with an acidometer (Sheldrick and Wang, 1993) by testing a mixture with a soil-to-water ratio of 1:5 (10 g soil; 50 mL water). Concentrations of SOC and TN were measured and obtained at the same time with an elemental analyzer (Elementar Analyzer System, EA3000, Italy). AN was tested using the alkaline hydrolyzation diffusion method (Cong et al., 2012). TP was digested with HNO₃-HF-HClO₄ in a microwave system; the volume was fixed after the acid was digested, and its value was obtained using the Mo-Sb anti-colorimetric method by measuring the digestion solution (Fen et al., 2015).

The soil temperature was monitored in the field continuously from August 2014 through August 2015. In 2014 the monitoring points were set up within the permanent plot with the geographical location information recorded (Fig. 1c). We have established a

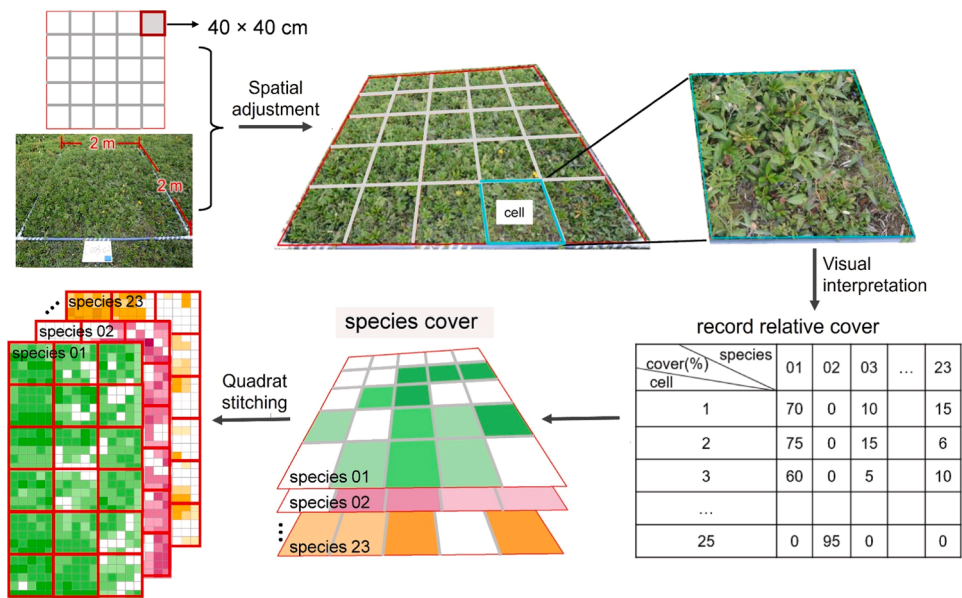


Fig. 2. Acquisition process of plant distribution information over the Big Plot.

total of 13 monitoring points for measuring mean annual temperature (MAT) within and surround the Big Plot. These monitoring points are distributed relatively evenly and randomly, which can adequately reflect the spatial variations in soil temperature within the Big Plot. The vertical and horizontal distances between sites monitored on the slope were 100 m (the average elevation difference was 25–30 m) and 25 m, respectively. The temperature recorder (Tidbit@Tv2) was set at a soil depth of 5 cm. The instrument has a resolution of 0.02 °C, and data were collected every 30 minutes to provide a long-term data sequence. As the temperature recorders remained buried throughout the study, soil temperature data were consistently recorded from the same cells. The climate in the Changbai Mountain alpine tundra zone is characterized by cold temperatures. Consequently, plants must complete their growth and reproduction within the short growing season (June to September) (Zong et al., 2013a). Therefore, in addition to the mean annual soil temperature (MAT), we specifically calculated the mean soil temperature during the growing season (GSMT) to capture the critical period for plant growth and reproduction from June to September 2015. The mean soil temperature during the growing season (GSMT) (June–September) and the mean annual temperature (MAT) were extrapolated spatially to all grid cells using Kriging interpolation based on the soil maps. Although the soil temperature varies annually, the relative spatial differences in soil temperature generally remain stable (Gubler et al., 2011). Therefore, the soil temperature data from one year are sufficient to reflect the relative spatial variations in soil temperature within the Big Plot.

We obtained 13 environmental variables from the soil data and topographic data (Table 1). The sample points were spatially calibrated and matched to the topographic data of the DEM, and the values of all environmental factors corresponding to the sample points were extracted using spatial analysis tools. All data analyses were conducted in ArcGIS (10.7) and R (3.6.1).

2.5. Determination of the topographical and edaphic niche characteristics of *D. angustifolia* and *R. aureum*

We assumed that the topographical and edaphic niche characteristics of *R. aureum* and *D. angustifolia* could be derived from the identified environmental factors (Table 1). Based on these factors, we used 18 sample points as *D. angustifolia* dominated sites (labeled DA-points), 44 as *R. aureum* dominated sites (labeled RA-points) and 14 points were *D. angustifolia* and *R. aureum* mixture (labeled MIX-points). DA-points specifically refer to sites that are exclusively occupied by *D. angustifolia*, no mixing with other species. Similarly, RA-points dominated sites refer to sites that are exclusively occupied by *R. aureum*. Within the Big Plot, these sample points represent the most suitable environmental conditions of *D. angustifolia* and *R. aureum* communities, respectively. Hurlbert (1978) defined ecological niche overlap as the frequency of encounters of two species in the same resource state. Therefore, the mean and range (standard deviation) of each environmental factor within the DA-points and RA-points reflect the niche characteristics of these two species. Our primary aim was to assess the niche characteristics of topography and soil for the two species. The niche overlap we quantified refers to the probability of both species co-occurring under the same topographic and soil conditions. This overlap can be reflected in the DA-points and the RA-points. The topographical and edaphic niche overlap between them can be verified by the environmental factors from the MIX-points (Abrams, 1980; Colwell and Futuyma, 1971).

We applied the random forest statistical method (Blanche et al., 2001; Kursu and Rudnicki, 2010) to select the main environment variables which dominate the spatial distribution of *R. aureum* and *D. angustifolia* for the DA-points and RA-points. We also selected MAT (mean annual temperature), TWI (topographic wetness index) and SOC (soil organic carbon) as other important variables to classify the niche characteristics, because they play important ecological roles in alpine tundra ecosystems.

In high-altitude areas, temperature is an especially important factor restricting plant growth (McCarty, 2001; Walther et al., 2002). MAT of the *D. angustifolia* and *R. aureum* communities was used to describe the soil temperature of their micro-habitats. Soil moisture is also an important factor affecting the distribution of plants. Studies have shown that in the growing season, the soil moisture content at the same soil depth significantly varies among microtopography (Wang et al., 2019). Thus, TWI (topographic wetness index) was

Table 1
Environmental variables.

Factor	Variable	Abbr.	Ecological Relevance	Method
Soil physicochemical properties	Soil organic carbon	SOC	Soil fertility level	Lab analysis
	Total nitrogen	TN	Soil fertility level	Lab analysis
	Total phosphorus	TP	Soil fertility level	Lab analysis
	Available nitrogen	AN	Soil fertility level	Lab analysis
	pH	–	Soil fertility level	Lab analysis
Soil temperature	Mean annual temperature	MAT	Annual mean temperature of surface soil	Kriging interpolation
	Growing season mean temperature	GSMT	Growing season mean temperature of surface soil	Kriging interpolation
Topographic variables	Elevation	ELE	Indicator of microclimate	DEM
	Slope	Slope	Soil moisture and solar radiation	Calculated from DEM
	Curvature	Curvature	The degree of deformation at a point on the surface	Calculated from DEM
	Topographic wetness index	TWI	Soil moisture content under different topographic conditions	$\ln\left(\frac{x}{\tan y}\right)$ (x is the ratio of catchment area to runoff width, y is slope)
	Roughness	Roughness	Indicator of surface morphology	$\frac{1}{\cos(\text{slope of DEM} \times \pi \div 180)}$
	Relief	Relief	Topographical relief	$ \text{DEM}_{\max} - \text{DEM}_{\min} $

important in analyzing the similarities and differences in the surface soil moisture conditions between the *D. angustifolia* and *R. aureum* communities. Additionally, encroachment by *D. angustifolia* reduces the total biomass of alpine tundra plants (Tan et al., 2019) and changes the soil organic carbon storage in endemic plants communities (Ni et al., 2022). Therefore, we analyzed differences in the soil organic carbon content of the *D. angustifolia* and *R. aureum* communities.

2.6. Data analysis

We analyzed the topographical and edaphic niche characteristics of the DA-points and RA-points and verified the overlap of topographical and edaphic niche characteristics with the MIX-points. We used a t-test to analyze the significance of differences of topographical and edaphic niche characteristics in terms of topographic and edaphic variables for the DA-points and RA-points ($p < 0.05$). The analysis was performed using SPSS software (SPSS, Chicago, USA). All data were tested using Shapiro–Wilk in SPSS for normality before applying the t-test. Results showed that most of the variables passed the test ($p > 0.05$). If data of any variable did not pass the test, we transformed the data to make it suitable for t-test.

3. Results

3.1. Differences and overlaps of niche characteristics between *D. angustifolia* and *R. aureum*

The frequency distribution of the two species varied among variables of soil, topography, and temperature. *D. angustifolia* showed a notable preference for areas characterized by higher available nitrogen (AN) and total phosphorus (TP), and lower soil organic carbon (SOC) compared to *R. aureum* (Fig. 3a, b and d). Moreover, the frequency distributions of *D. angustifolia* in AN, TN, SOC, and pH showed greater concentrations than those of *R. aureum* (Fig. 3a, c-e). Additionally, the frequency distribution of *D. angustifolia* exhibited higher concentrations in roughness, topographic wetness index (TWI), slope, curvature, relief, and elevation (ELE) compared to *R. aureum* (Fig. 3f-k). *D. angustifolia* demonstrated a preference for areas with higher mean annual temperature (MAT) and growing season mean temperature (GSMT) compared to *R. aureum* (Fig. 3l, m).

The analysis of the random forest revealed that the variables AN, TN, TP, slope, and roughness were more influential in determining the distribution of *D. angustifolia* and *R. aureum* than the other environmental factors analyzed (Fig. S1). AN was found to have the

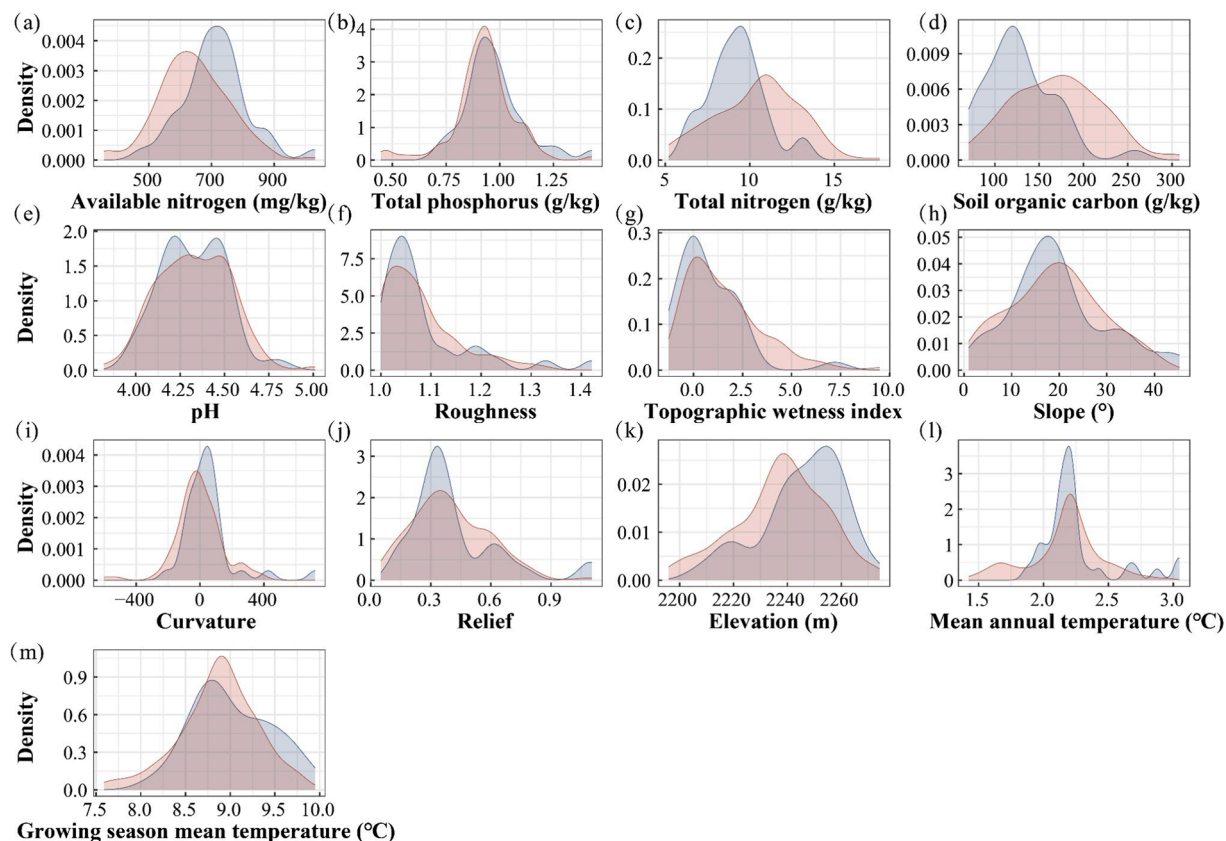


Fig. 3. The frequency distribution of *D. angustifolia* (blue) and *R. aureum* (red) along environmental gradient.

strongest effect on the distribution of *D. angustifolia* and *R. aureum* (Fig. S1).

The niche characteristics of *D. angustifolia* and *R. aureum* showed significant differences in terms of AN, TN, TP, and roughness (all $p < 0.05$; Fig. 4a-d). The AN niche of *D. angustifolia* and *R. aureum* did not overlap at all (Fig. 4a). *D. angustifolia* had a relatively high AN requirement, with a tolerable minimum AN of 0.68 g/kg, which is almost the upper limit for *R. aureum* (Fig. 4a). *R. aureum* can survive at AN value below 0.52 g/kg (Fig. 4a). The TN niche differed significantly between *D. angustifolia* and *R. aureum* ($p < 0.05$; Fig. 4c), and *R. aureum* requires less TN than *D. angustifolia*. *D. angustifolia* has a higher TP requirement than *R. aureum* ($p < 0.05$; Fig. 4b). *R. aureum* can grow in rougher topography (highest value = 1.14) ($p < 0.05$; Fig. 4d). In contrast, the niches of *D. angustifolia* and *R. aureum* did not significantly differ in terms of SOC, slope, TWI, and MAT ($p > 0.05$). The SOC and slope niche of *R. aureum* completely included that of *D. angustifolia*, and the TWI niche of *D. angustifolia* completely included that of *R. aureum*. In addition, other niche characteristics of *D. angustifolia* and *R. aureum* in terms of edaphic factors also have different degrees of overlap (Fig. S2), and the niche characteristics of *R. aureum* were wider than those of *D. angustifolia* in terms of almost all edaphic factors (Fig. 4a-h; Fig. S2).

3.2. Verification of niche overlap of *D. angustifolia* and *R. aureum*

More than 50 % of the MIX-points fell within the overlapping range of the niche characteristics for the two species, except for AN (Fig. 5a), and more than 50 % of the MIX-points were distributed in the respective niche ranges of *D. angustifolia* and *R. aureum* (Fig. 5b). For AN, the verification data (MIX-points) of *R. aureum* were distributed in a range higher than its niche, and the lowest value was the lower limit of the niche range of *D. angustifolia*. At the same time, the verification data of *D. angustifolia* were all distributed in a lower range than its niche (Fig. 5b), indicating that *R. aureum* has a certain tolerance for high AN condition, and *D. angustifolia* also has a certain tolerance for low AN condition. In terms of TN, TP, roughness, MAT, TWI, SOC, and slope, more than 50 % of the verification data of *D. angustifolia* and *R. aureum* were distributed in their respective niche ranges (Fig. 5b).

4. Discussion

4.1. Niche overlap of the two species

We discovered niche overlap between the endemic and encroaching species in most niche characteristics, consistent with our first hypothesis. This finding suggests that the two species have the potential to coexist in many scenarios while they will compete for the same resources. Many studies have concentrated on climatic factors, underscoring the significance of climate in determining plant distribution (Atwater et al., 2018). However, our study reveals that the microenvironment, particularly in terms of topography and soil, plays a crucial role in regulating the distribution of encroaching plants and endemic plants.

Our results indicated that the overlap rate for certain niche characteristics between *D. angustifolia* and *R. aureum* reached 90 %. For example, their requirements for topography and soil conditions were highly similar (Fig. 4), indicating a potential competitive relationship between the two species. This competitive relationship is evident in the ability of *D. angustifolia* to rapidly occupy areas

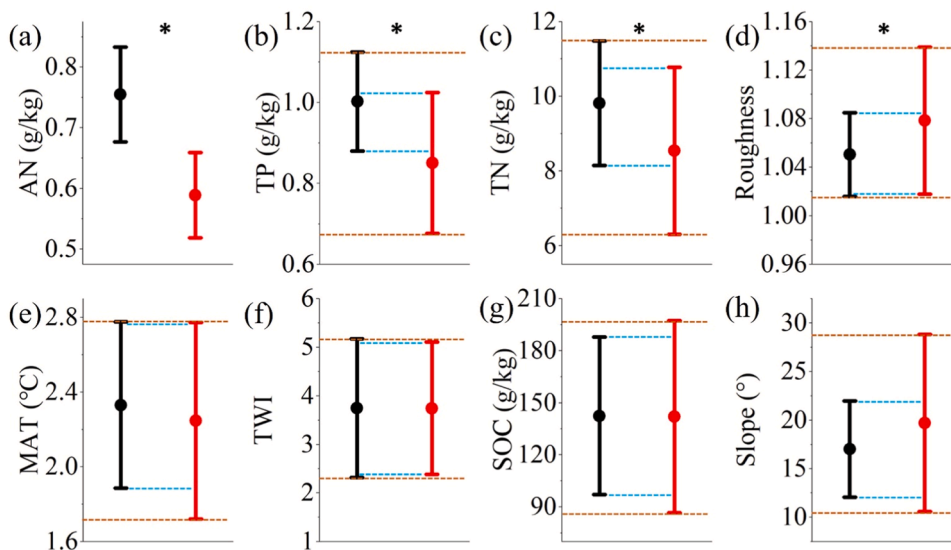


Fig. 4. Panel shows the niche characteristics (mean ± 1 SD) of *D. angustifolia* (black) and *R. aureum* (red). The range between the two blue dashed lines is the overlapping range of the niche characteristics of *D. angustifolia* and *R. aureum*. The range between the two orange dashed lines is the maximum range of the two plants' niche characteristics. The ratio of the range of blue (i.e. overlapping range) to the range of orange dashed lines (i.e. maximum range) is the niche overlapping rate of *D. angustifolia* and *R. aureum*. The symbol “*” indicates significant difference in niche characteristics between *D. angustifolia* and *R. aureum* ($p < 0.05$).

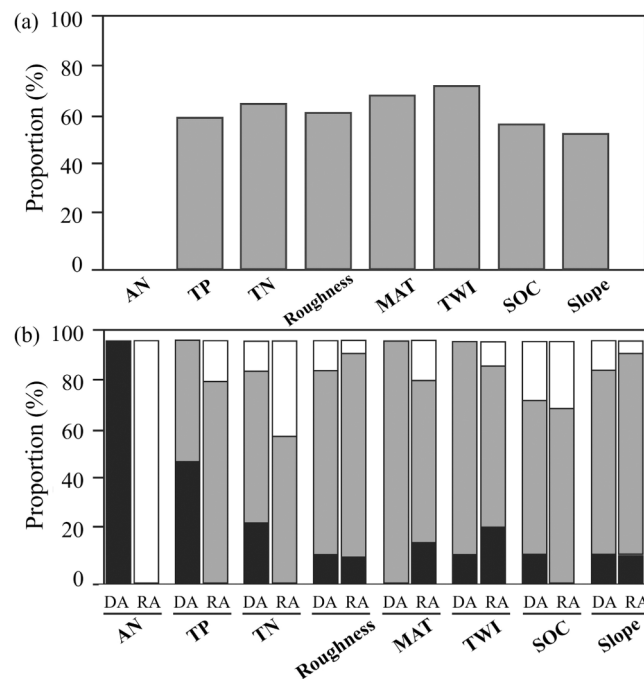


Fig. 5. Plots showing (a) the proportion of verification points (MIX-points) falling in the *D. angustifolia* and *R. aureum* niche overlap range, and (b) verification points of *D. angustifolia* (DA) and *R. aureum* (RA) falling above (white), within (gray), and below (black) their respective niche ranges.

with suitable growth conditions, thereby restricting the growth of the endemic plant *R. aureum*. Previous studies have demonstrated that species with similar niches often cannot coexist over extended periods (Shmida and Ellner, 1984). If coexistence does occur, it inevitably leads to niche differentiation, resulting in distinct niche spaces among the coexisting species (Gause, 1934; Whittaker, 1965). Therefore, the competition between the encroaching herbaceous plant and the endemic species may yield one of two outcomes: either one species perishes, or both species manage to coexist through the process of niche differentiation (de Back et al., 2007). Species might continually evolve through niche differentiation, coupled with ongoing intense interspecific and intraspecific competition, until a certain dynamic equilibrium is achieved in the interspecies relationship (Grime, 2006). Consequently, it can be inferred that encroaching herbs and endemic shrubs have the potential to coexist under stable environmental conditions (for example, in the absence of significant climate change), while maintaining a dynamic equilibrium.

4.2. Soil niche divergence between the two species

The results confirmed our second hypothesis that microtopography related soil conditions, play an important role in determining the potential encroachment of *D. angustifolia* into the alpine tundra. The results underscored the critical role of nitrogen availability in the expansion of *D. angustifolia*. This encroaching herb requires significantly more nitrogen than the endemic plant *R. aureum*, with the soil available nitrogen (AN) content in *D. angustifolia*'s distribution areas being markedly higher than in areas with the endemic plants (Fig. 4). As a fast-growing, perennial herbaceous plant, *D. angustifolia* has a high nitrogen demand to support its life cycle, surpassing the nitrogen utilization capabilities of *R. aureum* (Zong et al., 2016).

In contrast, the alpine tundra shrub *R. aureum* plants is adapted to harsh environments characterized by low nutrient availability and low temperatures. Consequently, its efficiency in utilizing external nutrients, such as nitrogen, is lower compared to the needs of *D. angustifolia* (Zong et al., 2016). Ehrenfeld (2003) observed that encroaching plants can rapidly increase their biomass while enhancing nitrogen utilization efficiency. Similarly, Aerts and Caluwe (1994) noted distinct differences in nitrogen absorption between perennial herb plants and evergreen shrubs. This suggests that with changes in community structure, perennial herb plants may gradually supplant evergreen shrubs.

Zong (2016) also explored the relative impacts of increasing temperature and nitrogen application, finding that nitrogen addition had a more pronounced effect than temperature increases. Furthermore, they discovered that the nitrogen utilization efficiency of *D. angustifolia* was higher than that of *R. aureum*. Our findings regarding the encroachment of *D. angustifolia* align with these previous studies, confirming the significant influence of nitrogen dynamics in this ecological process.

Rhododendron aureum demonstrates a higher tolerance for low-phosphorus conditions compared to *D. angustifolia* (Fig. 4). The lowest amount of phosphorus is typically found in very old soils under warm climates, as noted by Wardle et al. (2004). However, in the alpine tundra of Changbai Mountain, soil phosphorus primarily derives from the weathering of volcanic ejecta and remains relatively unaffected by external environmental changes in the short term (Childers et al., 2011). In such high-altitude environments,

the combination of low temperatures and sparse vegetation cover slows the weathering rate of volcanic materials, resulting in lower soil phosphorus content. Consequently, in the high-altitude areas of the Changbai Mountain tundra, soil phosphorus often serves as a major limiting nutrient, with the degree of limitation varying significantly under different topographic conditions (Turner et al., 2004). While many inorganic and organic phosphorus compounds in soil are insoluble, phosphate (PO_4^{3-}) is the primary form available to plants. However, under low pH conditions, phosphate can react with iron oxide and aluminum to form insoluble precipitates, rendering it inaccessible to plants (Chapin et al., 2011). The acidic soil of the Changbai Mountain alpine tundra severely limits phosphorus availability (Yang et al., 2016).

Furthermore, previous studies have indicated a significant positive correlation between soil phosphorus content and phosphatase activity (Yang et al., 2016). As altitude increases in the alpine tundra zone of Changbai Mountain, soil phosphorus content initially rises from the alpine treeline at 2000 m a.s.l., then decreases beyond 2400 m. Correspondingly, with the decrease in soil phosphatase activity, available phosphorus also diminishes. Consequently, while *D. angustifolia* may expand rapidly at lower altitudes in the alpine tundra zone, its expansion is likely to be constrained by low-phosphorus conditions at higher altitudes in the alpine tundra zone. In contrast, *R. aureum*'s tolerance to low-phosphorus environments enables it to survive in high-altitude, phosphorus-deficient conditions. These findings indicate that, at least over a relatively short period, the encroaching herb *D. angustifolia* is unlikely to completely supplant *R. aureum* in the alpine tundra.

4.3. Topographic niche divergence between the two species

Rhododendron aureum exhibits a broader range of topographic niche characteristics compared to *D. angustifolia*. It is capable of thriving in steeper and more rugged topography, whereas *D. angustifolia* is limited to areas with relatively flat topography (Fig. 4). In high-altitude regions characterized by complex and heterogeneous topography, suitable conditions for *D. angustifolia* are typically found in low-lying lands and on leeward slopes, where the topography is relatively flat. These flat areas, compared to their surrounding environments, undergo more moderate temperature fluctuations (Lindkvist et al., 2000) and are less exposed to strong winds. As a result, such areas provide favorable habitats for encroaching plant species (Dobrowski, 2011).

In addition to soil factors, topography and climate significantly impact the encroachment of *D. angustifolia*. Rising temperatures can increase the photosynthetic rate and net primary productivity of *D. angustifolia*, thereby promoting the transition from alpine tundra to alpine meadow. Complex topography creates diverse habitats that provide favorable conditions for the encroachment of *D. angustifolia* (Wu et al., 2018). However, soil nutrient conditions directly affect plant growth, survival, and reproduction (Knauf et al., 2021), having a decisive influence on the encroachment of *D. angustifolia*. Therefore, while topography and climate may affect the distribution of *D. angustifolia* on a larger scale, at finer scales, microtopography-related soil factors play a more direct and significant role by regulating soil nutrient distribution and influencing the encroachment of *D. angustifolia*.

Other biotic factors such as competition with native species may also play crucial roles in the encroachment of *D. angustifolia* (Jin et al., 2013). For instance, strong competitors may limit the spread of *D. angustifolia*, whereas weak competitors or facilitative species may enhance its upward. Additionally, disturbances such as typhoons may create conditions where trees are removed and favor the development of *D. angustifolia* and consequently abundant *D. angustifolia* seed sources for encroachment (Jin et al., 2013). These various hypotheses underscore the complexity of ecological interactions. Future research should consider these alternative factors to develop a more comprehensive understanding of the encroachment dynamics of *D. angustifolia*.

Furthermore, previous studies have shown that the changes in vegetation patterns in the alpine tundra of Changbai Mountain over the past 30 years have been primarily due to the encroachment of low-altitude herbaceous plants. The insights obtained from examining the niche characteristics of these species not only help to clarify the observed trends of *R. aureum* and *D. angustifolia* in the past but also aid in predicting future changes in the Changbai Mountain alpine tundra.

4.4. Limitations and outlook

In the Changbai Mountain tundra, the herb *Deyeuxia angustifolia* has encroached from the understory of lower montane birch forests to tundra due to rising temperatures and nitrogen deposition (Zong et al., 2014). *D. angustifolia* exhibits a patchy, discrete spatial distribution, indicating selective habitat colonization influenced by soil and topography. However, as the plants encroach, they also alter the soil, creating a mutual feedback loop. Research has shown that encroaching plants can influence soil nutrient levels (Zhang et al., 2022). Specifically, unlike evergreen shrub *Rhododendron aureum*, *D. angustifolia* drops all its above-ground parts at the end of the growing season, thereby increasing soil organic carbon (SOC) in the tundra (Li et al., 2023). With a shorter lifespan, *D. angustifolia* invests more in growth rather than defense (Liao et al., 2008), resulting in higher plant nitrogen concentrations, which subsequently decompose and further increase soil available nitrogen (AN) (Wei et al., 2007). Conversely, total phosphorus (TP) in the tundra soil, originating from the release of parent rock, shows no significant change due to the encroachment of *D. angustifolia* (Liu et al., 2018). This complex interaction creates a dynamic environment in which feedback effects likely influence the observed patterns of plant distribution.

Additionally, our Big Plot (400 m by 100 m) is intended for long-term monitoring of tundra plant community change, particularly the process of *Deyeuxia angustifolia* encroachment. The Plot was first established in 2014 when drone technologies were not widely available. Our field crew took 10,000 photos using hand-held camera to cover the entire Plot (Fig. 1). Visual interpretation, field verification, and error correction of the 10,000 photos took 5–6 years to complete. We have flown drones in the intermediate years with the drone photos still in the process of interpretation. Thus, this is the very first product of this long-term monitoring program with which the following research will be referenced on. We expect comparison of changes from multi-stage photos to fully analyze the

phenomenon of herbaceous plant encroachment in the tundra of Changbai Mountain.

5. Conclusion

In our study, we performed analyses of the niche characteristics of *R. aureum* and *D. angustifolia* within the alpine tundra of Changbai Mountain. Our results demonstrated a significant overlap in most niche characteristics between these two species, highlighting competition as a crucial factor in shaping the dynamics of this community. Significantly, *R. aureum* displayed a wider range of adaptability in terms of topographic and soil niche characteristics compared to *D. angustifolia*. This finding implies that a complete displacement of *R. aureum* by *D. angustifolia* in the alpine tundra is unlikely. Our research sheds light on the pivotal roles played by environmental filtering, notably topography and soil, in determining the composition and distribution of plant communities. This conclusion can be further validated through our long-term monitoring work in the Big Plot.

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Declaration of Competing Interest

The authors declared that they have no conflicts of interest to this work.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03157](https://doi.org/10.1016/j.gecco.2024.e03157).

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