

Research Article

Elevation gradient modulates the effects of herbaceous encroachment on the long-term growth trends and climate sensitivity of *Rhododendron aureum* in alpine tundra

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Abstract

As global warming drives plant upward migration, the alpine tundra of Changbai Mountain is experiencing encroachment by *Deyeuxia angustifolia* (Komarov) Y. L. Chang, a low-elevation herb. However, its impact on native shrubs such as *Rhododendron aureum* Georgi remains unclear. Here, we analyzed the radial growth trends and climate sensitivity of *R. aureum* across elevations and encroachment gradients using linear and mixed-effects model methods, and explored the mediating roles of soil properties and plant traits. Our study revealed that *R. aureum* exhibited stronger positive long-term growth trend at higher elevations compared to lower elevations. Mild and moderate encroachment of *D. angustifolia* enhanced the positive growth trend of *R. aureum*, especially at the low elevations. Moreover, *R. aureum* showed weak climate sensitivity at mid-elevation but stronger responses to winter temperatures at low elevation and to spring–summer temperatures and precipitation at high elevation. *D. angustifolia* encroachment further intensified this sensitivity, characterized by stronger negative responses to spring, autumn and winter temperatures but positive responses to summer temperatures and autumn precipitation. Overall, elevation primarily influenced *R.*

aureum growth and its sensitivity to precipitation through soil conditions and plant size traits, while soil conditions and leaf economic traits influence temperature sensitivity. These findings advance understanding of alpine vegetation dynamics and contribute to ecosystem conservation under climate change.

Keywords: climate change, dwarf evergreen shrubs, elevation, climate sensitivity, soil properties, plant functional traits

海拔梯度调控草本植物入侵对牛皮杜鹃长期生长和气候敏感性的影响

摘要：随着全球变暖驱动山地植物向上迁移，长白山苔原正经历低海拔草本植物大叶章(*Deyeuxia angustifolia* (Komarov) Y. L. Chang)的持续入侵。然而，目前学术界尚不清楚入侵植物对牛皮杜鹃(*Rhododendron aureum* Georgi)等原生灌木的影响。本研究基于线性模型和混合效应模型，分析了不同海拔梯度大叶章入侵对牛皮杜鹃径向生长趋势与气候敏感性的影响，并探讨了土壤理化性质与植物功能性状的调节作用。结果表明：1)与低海拔相比，高海拔区域牛皮杜鹃表现出更强的长期正向生长趋势；轻度和中度大叶章入侵增强了牛皮杜鹃的正向生长趋势，尤其在低海拔地区这一趋势更为明显。2)牛皮杜鹃在中海拔区域的气候敏感性较弱，而在低海拔对冬季温度、高海拔对春夏温度和降水的响应更强。大叶章入侵进一步增强了牛皮杜鹃气候敏感性，具体表现为对春、秋、冬季温度的负响应增强，而对夏季温度与秋季降水的正响应增强。3)海拔主要通过土壤条件和植物大小性状影响牛皮杜鹃的生长及其降水敏感性，而土壤条件与叶片经济性性状则主导其温度敏感性。本研究深化了对气候变化背景下高山苔原灌木生长动态及其气候敏感性调控机制的认识，为高山生态系统的保护与适应性管理提供了理论依据。

关键词：气候变化，常绿矮灌木，海拔，气候敏感性，土壤性质，植物功能性状

INTRODUCTION

Shrubs, dominant in tundra ecosystems, are highly sensitive to climate change (Elmendorf *et al.* 2012) and play critical roles in biodiversity conservation and carbon sequestration (Mekonnen *et al.* 2021). Climate warming has been shown to promote the growth of shrubs (McManus *et al.* 2012), increase their abundance (Sturm *et al.* 2001) and drive their range expansion in the arctic and alpine regions (Wang *et al.* 2024). However, warming may also accelerate the growth of herbaceous plants, potentially affecting native shrubs through interspecies competition (Zong *et al.* 2022). Shrub growth sensitivities to climatic drivers, including temperature and precipitation, exhibit substantial variation across elevational gradients and species interactions and are further shaped by site-specific factors such as snow cover dynamics, soil physicochemical properties and plant functional trait composition (Blok *et al.* 2011; Elmendorf *et al.* 2012; Francon *et al.* 2023; Zong *et al.* 2022). Despite this, the impacts of the encroachment of herbs on shrub growth and climate sensitivity across elevation gradients, as well as the regulatory roles of soil properties and plant functional traits, remain poorly understood.

Shrub growth and climate sensitivity are strongly influenced by elevation (Primicia *et al.* 2015) in the alpine environments. At the upper limit of species' distribution range, temperatures are a major limiting factor for plant growth. Consequently, alpine shrubs typically respond positively to higher summer temperatures (Francon *et al.* 2023; Hallinger *et al.* 2010), and this response tends to become more pronounced with increasing elevation (Myers-Smith *et al.* 2015). However, rising temperatures can also induce water deficits, constraining growth (Sigdel *et al.* 2018), with such effects being more pronounced at lower elevations (Gaire *et al.* 2023; García-Cervigón *et al.* 2018). Previous studies also underscore the critical role of moisture availability in shaping future shrub growth and distribution patterns (Lu *et al.* 2019; Wang *et al.* 2021). These conflicting results highlight the importance of investigating how elevation shapes shrubs' growth and their responses to climatic variability (Primicia *et al.* 2015).

Species interactions play a pivotal role in shaping resource utilization efficiency and survival strategies, thereby influencing shrub growth and their responses to climate change. Previous studies have shown that sparse herbaceous cover can

reduce shrub growth, while denser cover may threaten survival (Tao *et al.* 2011). On the Tibetan Plateau, competitive interactions have been found to diminish the growth benefits induced by warming in species at alpine treelines (Liang *et al.* 2016; Sigdel *et al.* 2020; Wang *et al.* 2016). Similarly, in the eastern Romanian Carpathians, elevated temperatures have reduced plant growth at lower elevations, particularly among individuals experiencing competitive pressure (Primicia *et al.* 2015). Facilitative interactions were also demonstrated (Chen *et al.* 2024; Nuche and Alados 2018), with evidence suggesting that increased tree cover can enhance the survival of shade-tolerant shrubs (Germany *et al.* 2021). While most previous studies have focused on trees, research on shrubs—which exhibit similar interaction patterns—remains relatively scarce. In particular, the long-term growth dynamics and climate–growth relationships of alpine shrubs under varying intensities of species interactions are still poorly understood (Pellizzari *et al.* 2016; Šenfeldr *et al.* 2021).

Elevation and species interactions shape plant growth and climate responses both directly and indirectly by altering soil properties and plant functional traits (Bauman *et al.* 2022; McGill *et al.* 2006; Wang *et al.* 2022). Higher elevations exhibit lower temperatures and shorter growing seasons, typically directly reducing growth but increasing climate sensitivity (Myers-Smith *et al.* 2015). These conditions also limit specific leaf area (LA), leaf nutrient content and soil fertility, further constraining photosynthesis and growth while amplifying climatic variability responses (Gazol *et al.* 2022; HilleRisLambers *et al.* 2013; Reich 2014; Wang *et al.* 2022). Species interaction directly affects plant growth and its climate sensitivity by modifying ecological niche or light availability (Tan *et al.* 2024) and also indirectly by changing soil nutrients through litter input (Tao *et al.* 2011). Understanding these mechanisms is key to predicting tundra vegetation dynamics under climate change.

The Changbai Mountain tundra is one of the only two alpine tundra areas in China and represents a unique landscape in the eastern temperate Eurasian continent. Over the past 63 years, the ecological environment of the Mt. Changbai tundra has undergone significant changes, with the average temperature during the growing season (June to September) increasing by 1.32 °C (Wu 2024). This rapid warming has triggered notable shifts in vegetation dynamics, including the upward

migration of the lower-elevation species *Deyeuxia angustifolia*, which poses a negative effect on the native shrub *Rhododendron aureum* (Tan *et al.* 2024), a crucial species for carbon sequestration and biodiversity conservation (Christiansen *et al.* 2018). The degradation of *R. aureum* shrublands would transform the tundra into a meadow, potentially shifting it from a carbon sink to a carbon source (Xing *et al.* 2024). While remote sensing and plot-level studies have detected shrub degradation (Tan *et al.* 2019; Zong *et al.* 2022), the long-term growth trends, climate sensitivity and the contributions of soil properties and plant functional traits to these dynamics across elevation and encroachment gradients remain poorly understood. This study provides the first comprehensive assessment of how elevation and *D. angustifolia* encroachment jointly influence *R. aureum* growth and its climate sensitivity on Mt. Changbai. Specifically, we aim to: (1) analyze the growth trends of *R. aureum* over time, (2) evaluate the climate sensitivity of its growth and (3) explore how soil properties and plant functional traits mediate the effects of elevation and *D. angustifolia* encroachment on *R. aureum* growth and its climate responses.

MATERIALS AND METHODS

Study site

This study was conducted in the alpine tundra on the west-facing slope of Mt. Changbai (41°58′–41°59′ N, 127°59′–28°01′ E). From 1961 to 2023, the region experienced a mean annual temperature of −7.1 °C and an average annual precipitation of approximately 1355.9 mm, with 981.5 mm falling during the growing season (Wu 2024). During the period 2001–2023, the average temperature in the growing season was 6.5 °C (Wu 2024). Long-term variations in temperature and precipitation in the Changbai Mountain tundra are presented in [Supplementary Figs S1–S4](#). The tundra soil, 10–20 cm thick, is formed on a weathered alkaline trachyte, rich in organic matter (20%–30%) but less in available nutrients (Li *et al.* 2023). The shrubby-moss lichen tundra is dominated by *R. aureum*, *Vaccinium uliginosum* L., *Dryas octopetala* L. and *Carex pseudolongerostrata* Y.L.Chang and Y.L.Yang (Jin *et al.* 2016). In recent years, climate warming has driven the upward migration of the herbaceous species *D. angustifolia*, previously

confined to lower elevations below the treeline, into the alpine tundra, impacting the growth and distribution of the native shrub *R. aureum* (Zong *et al.* 2014).

Experimental design

On 25 July 2022, we selected three elevations on the western slope of Changbai Mountain's tundra zone, representing the low (L, 2050 m a.s.l.), middle (M, 2200 m a.s.l.) and high (H, 2350 m a.s.l.) elevation distribution of *D. angustifolia* encroachment into *R. aureum* communities. The degree of *D. angustifolia* encroachment was classified into four categories: unencroached pure *R. aureum* communities (E0), mildly encroached mixed communities (30% cover, E1), moderately encroached mixed communities (60% cover, E2) and severely encroached mixed communities (90% cover, E3) (Fig. 1).

All study sites were located within a nature reserve, free from human disturbance. At each elevation, 1 m × 1 m plots were carefully selected to ensure similar micro-habitat conditions (e.g. slope, aspect and flat terrain position) and exclude potential

confounding factors, as no signs of herbivory, animal trampling or plant diseases were observed. At low elevation, plots from all four encroachment stages were sampled (LE0, LE1, LE2, LE3); at middle elevation, three encroachment stages were observed and selected (ME0, ME1, ME2) and at high elevation, only pure *R. aureum* plots (HE0) were present. Each treatment was replicated three times, resulting in a total of 24 plots across the three elevations. Plots were spaced at least 10 m apart to minimize spatial autocorrelation and ensure sampling independence.

Data collection and preparation

Tree-ring data collection and preparation

Three *R. aureum* individuals were sampled per plot, resulting in a total of 72 plants. For each individual, intact plants were collected, and three cross-sections were obtained from the roots, stems and shoots using the continuous sectioning method (Kolishchuk 1990) (Supplementary Fig. S5), after which they were preserved in formalin–acetic acid–alcohol solution.

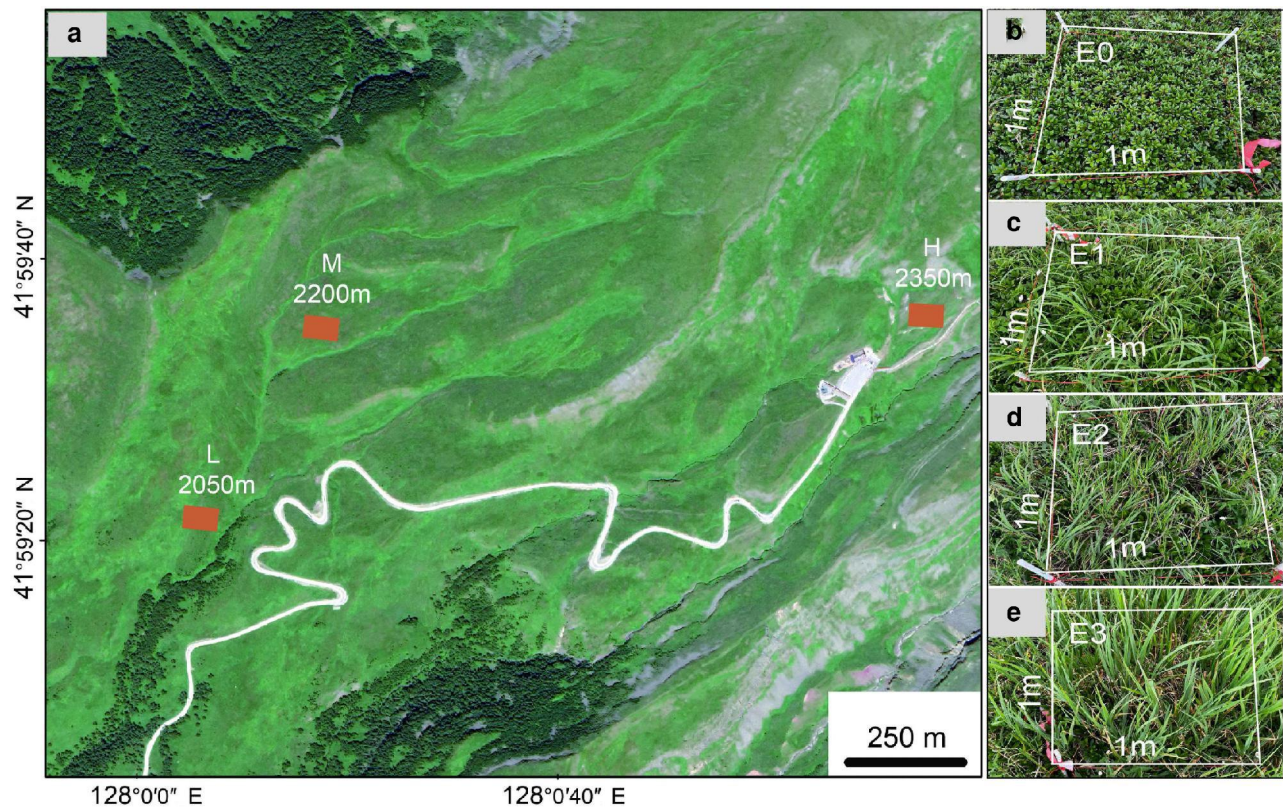


Figure 1: The location of the study sites (a) and four encroachment levels of *Deyeuxia angustifolia* in study plots for (b) unencroached pure *Rhododendron aureum* communities (E0), (c) mildly encroached mixed communities (30% cover, E1), (d) moderately encroached mixed communities (60% cover, E2) and (e) severely encroached mixed communities (90% cover, E3).

Cross-sections were sectioned into 20 μm slices using a rotary microtome, stained with fuchsia and solid green dyes and mounted on microscope slides. High-resolution images were captured with an Olympus BX53 microscope equipped with an EP50 micro-digital camera and analyzed using Olympus EPview 1.2 software.

Soil properties data collection and preparation

In the field, soil temperature was recorded every 30 min from 1 September 2022 to 31 August 2023 using ONSET HOBO loggers (21-002, ONSET Computer Corporation, USA). Soil samples were collected from a depth of 0–10 cm using a 3 cm stainless steel soil drill at five locations within each plot and then pooled. The samples were transported to the laboratory within 2 days, air-dried and ground for soil properties analysis.

In the laboratory, soil pH was measured in a 1:2.5 soil-to-water suspension using a pH meter. Soil water content (SWC) was determined by oven-drying 10 g of fresh soil at 105 °C for 4 h. Total soil carbon (TC) and nitrogen (TN) were analyzed using an elemental analyzer (Elementar, Vario Max CN, Germany), while total phosphorus (TP) was extracted with a HNO_3 -HF- HClO_4 solution and measured using molybdenum-antimony colorimetry. Soil N:P, C:N and C:P ratios were calculated from TC, TN and TP values. Dissolved organic carbon (DOC) was extracted with Milli-Q water and quantified using a TOC analyzer (Elementar vario TOC, Elementar Co., Germany). Ammonium nitrogen (NH_4^+ -N) and nitrate nitrogen (NO_3^- -N) were extracted with KCl solution and measured using a San⁺⁺ continuous flow analyzer (Skalar, Breda, GA, USA). Available phosphorus (AP) was extracted with NH_4F -HCl solution and determined using molybdenum blue colorimetry (Bao 2005). All abbreviations and units of soil properties are listed in [Supplementary Table S1](#).

Plant functional traits data collection and preparation

In each plot, five individuals of *R. aureum* were randomly selected for plant height (H) measurement, taken from the base of the stem to the tip of the terminal branch using a measuring tape. Additionally, 15 mature and healthy leaves were collected from each plot, promptly stored in a cooler with ice packs and transported to the laboratory for analysis of leaf functional traits.

In the laboratory, LA was measured using a portable LA meter (Yaxin-1241, Yaxin Inc., Beijing, China). Leaf thickness (LT) was determined with a vernier caliper (accuracy: 0.01 mm). Leaves were weighed fresh and then oven-dried at 70 °C for 48 h to obtain their dry weight. Specific leaf area (SLA) was calculated as LA divided by dry weight, and leaf dry matter content (LDMC) was determined as dry weight divided by fresh weight. Dried leaf samples were ground and sieved through a 60-mesh screen for chemical analysis. Leaf carbon (LC) and nitrogen (LN) contents were measured using an elemental analyzer (Elementar, Vario Max CN, Germany). Leaf phosphorus (LP) was extracted with HNO_3 - HClO_4 solution and quantified using molybdenum-antimony colorimetry. All abbreviations and units of plant functional traits are listed in [Supplementary Table S2](#).

Ring-width chronologies

Shrubs often exhibit wedge-shaped, missing or eccentric growth rings due to their growth form, age, environmental factors and disturbances, complicating cross-dating efforts. Following the methodology of [Francon et al. \(2017\)](#), we conducted cross-dating in three steps: (1) cross-dating all growth curves at least two directions within a cross section, (2) cross-dating mean growth curves across all sections for each individual and (3) cross-dating mean growth curves across individuals within each plot using visual comparisons of pointer years. Cross-dating accuracy was statistically validated using COFECHA ([Holmes 1994](#)).

To remove non-climatic growth trends, a spline detrending approach with a 50% frequency cut-off was applied using ARSTAN ([Bunn 2008](#)), resulting in eight chronologies across different encroachment intensities and elevations ([Supplementary Fig. S6](#)). Chronologies were evaluated for variance explained by the expressed population signal (EPS), mean inter-series correlation (R_{bar}) and mean sensitivity (MS) ([Table 1](#)).

Statistical analysis

Growth trend analysis

We quantified radial growth of *R. aureum* based on basal area increment (BAI). For each individual, annual BAI was calculated from raw ring-width measurements according to the equation:

Table 1: Characteristics of ring-width chronologies of *Rhododendron aureum* at 2050, 2200 and 2350 m a.s.l

Chronology	L			M			H	
	E0	E1	E2	E3	E0	E1	E2	E0
Mean RW	0.998	0.990	0.988	1.003	1.036	1.005	1.002	0.106
Span	1990–2021	1975–2021	1981–2021	1964–2021	1990–2021	1987–2021	1991–2021	1979–2021
NSD	21	21	20	20	14	15	12	17
NI	8	9	9	7	6	8	6	8
Rbar	0.30	0.28	0.33	0.36	0.26	0.31	0.28	0.28
EPS	0.786	0.79	0.786	0.786	0.786	0.786	0.786	0.786
MS	0.16	0.14	0.16	0.17	0.18	0.19	0.14	0.16
Mean RW (mean ring width), Span (chronology length), NI (number of individuals), Rbar (mean inter-series correlation), EPS (expressed population signal) and MS (mean sensitivity). Values refer to chronologies after detrending.								

$$BAI_t = \pi(R_t^2 - R_{t-1}^2) \tag{1}$$
where R_t and R_{t-1} are the radial radius at year t and $t-1$ (Monserud and Sterba 1996). BAI_t represents radial growth for year t . For each individual, we then averaged BAI across the three sections (root, stem, shoot) to obtain an individual-level BAI series. Based on these individual-level series, we further calculated mean BAI at the plot level and subsequently at the environment level by averaging across all individuals within each plot and environment. To assess long-term growth trends, we fitted linear regressions of annual BAI against calendar year within each environment. In addition, to evaluate recent growth performance, we calculated the mean BAI over the most recent 5 years (2017–2021). Statistical analyses were performed in R version 4.3.0.

Climate sensitivity analysis

We applied linear mixed models to evaluate climate sensitivity (Ropars et al. 2017). Meteorological data were obtained from the Tianchi National Weather Station (42°10" N, 128°50" E; 2623 m a.s.l.), located 6.2 km from the study site and accessed via the China Meteorological Data Service Center (<http://data.cma.cn/>). Monthly temperature and precipitation were used as the fixed effects, with year as a random effect and mean standardized ring width as the response variable. We calculated three climate sensitivity indices: (1) ΔAIC, the difference in Akaike Information Criterion between the best climate model and a null model (Table 2), (2) R^2 for the best climate model and (3) the absolute slope of the growth–climate relationship. These indices were evaluated across elevation and encroachment gradients (Supplementary Table S3).

Pathways and effects analysis

We used the principal component analysis (PCA) to reduce a multidimensional soil and trait space to its first two principal component axes (soil PC1 and PC2 and trait PC1 and PC2). Based on the results of PCA analyses, we further used structural equation models (SEMs) to investigate the pathways and sizes of the effects of elevation and *D. angustifolia* encroachment on the growth and climate sensitivity of *R. aureum*. In the models, elevation and *D. angustifolia* encroachment were the exogenous variables, and the PC1 and PC2 of the soil properties and the plant functional traits were the endogenous

Table 2: The structure of the mixed effect models in this study

Mixed effect models	Response variables	Fixed effect	Random effect	Akaike's information criterion
The clim model	Standardized ring-width indices	Monthly climatic variables	Year	AIC _{clim}
The null model	Standardized ring-width indices	1	Year	AIC _{null}

Climate sensitivity = $\pm 1 \times |AIC_{clim} - AIC_{null}|$. The plus and minus signs are consistent with the plus and minus signs of the slopes of the climate models.

variables predicting the response and are predicted by the exogenous variables. The mean BAI, temperature sensitivity, maximum temperature sensitivity and precipitation sensitivity were the response variables, with temperature and precipitation sensitivities being the mean differences of Akaike's information criterion (AIC) of the climate model and of the null model, the maximum temperature sensitivity being the number of months in that environment in which growth responded significantly to maximum temperature. We additionally analyzed the pathways to maximum temperature sensitivity because growth responses to mean and minimum temperatures could only be explained by elevation, encroachment, soil conditions and plant traits up to 10%, whereas the response to maximum temperature could be explained up to 26%. The adequacy of the models was assessed via chi-square (χ^2) tests, AIC, comparative fit index (CFI) and root mean square error of approximation (RMSEA). Adequate model fits are indicated by non-significant χ^2 tests ($P > 0.05$), a low AIC, RMSEA and a high CFI (CFI > 0.95) (Arbuckle 2010; Grace 2006). The SEMs were performed using Amos 24.0 (IBM SPSS Inc., Chicago, IL, USA).

RESULTS

Growth trends of *R. aureum*

At 2050 m, *R. aureum* growth showed a significant increasing trend of 0.0256 cm² per year at LE1 and 0.0343 cm² per year at LE2 environments but no trend at LE0 and LE3 environments (Fig. 2a). LE1 significantly enhanced the mean BAI over the past 5 years (Fig. 2b). At 2200 m, *R. aureum* growth only displayed a significant increasing trend of 0.0227 cm² per year at ME2 environment but no trend at ME0 and ME1 environments (Fig. 2a). At 2350 m, *R. aureum* growth exhibited a significant increasing trend of 0.0189 cm² per year at ME0 environment (Fig. 2a).

Overall, *R. aureum* exhibited a stronger positive long-term growth trend at higher elevations compared to lower elevations in the absence of *D. angustifolia* encroachment (Fig. 2a). Moreover, mild and moderate encroachment of *D. angustifolia* enhanced the positive growth trend of *R. aureum*, especially at the low elevations (Fig. 2a).

Climate sensitivity of *R. aureum*

At 2050 m, growth was suppressed by winter (February) warming but enhanced by September precipitation at LE0 environment (Fig. 3). Moderate encroachment (LE1–LE2) shifted sensitivity toward negative effects of autumn (previous October) warming and positive responses to summer (July and August) temperatures (Fig. 3a–c). At LE3 environment, growth declined with winter (previous December) and spring (April) warming but increased with August warmth and September precipitation (Fig. 3).

At 2200 m, *R. aureum* growth did not exhibit a significant climate response at ME0 environment (Fig. 3) but showed negative responses to autumn (previous November) warming at ME1 environment and to winter (February) warming at ME2 environment (Fig. 3a–c). A positive association with previous November precipitation was also observed at ME2 environment (Fig. 3d).

At 2350 m, *R. aureum* growth at the HE0 environment was promoted by early-summer (June) warmth and March, August and September precipitation but suppressed by April warming (Fig. 3).

Overall, *R. aureum* showed stronger climate sensitivity at higher elevations, characterized by reduced responses to winter temperatures but enhanced responses to spring–summer temperatures and precipitation. *D. angustifolia* encroachment further intensified this sensitivity, characterized by stronger responses to spring, summer and autumn temperatures and autumn precipitation (Fig. 3).

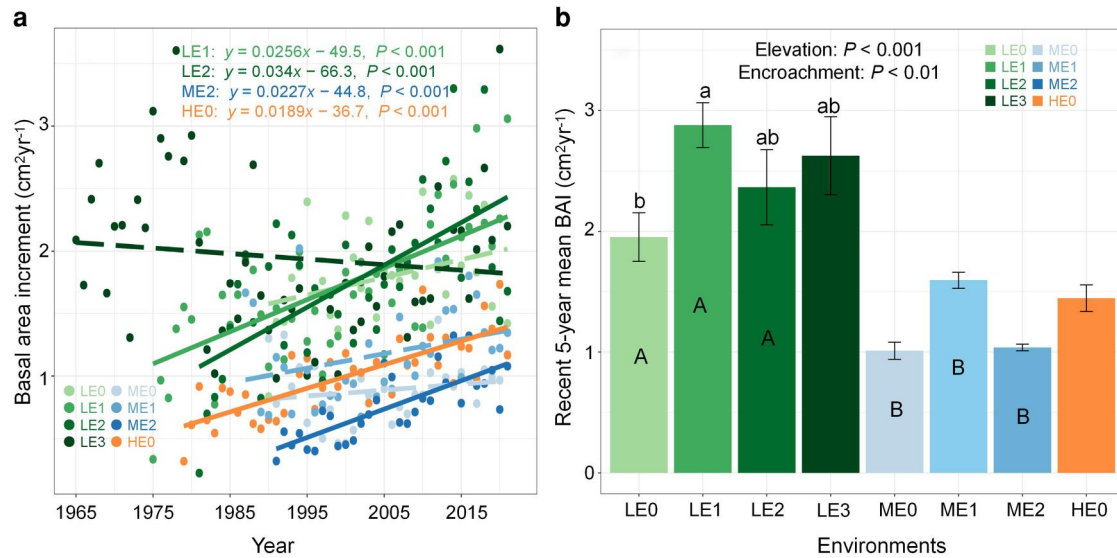


Figure 2: Effects of elevation and *Deyeuxia angustifolia* encroachment on the growth of *Rhododendron aureum*. (a) Long-term basal area increment (BAI) trends across elevation and encroachment gradients in recent decades; significant ($P < 0.05$) trends are shown as solid lines and non-significant ($P > 0.05$) trends as dashed lines. (b) Mean BAI ($\pm$ SE) across elevation and encroachment gradients from 2017 to 2021. Different uppercase and lowercase letters indicate significant differences ($P < 0.05$) among elevations within each encroachment level and among encroachment levels within each elevation, respectively. Statistical results for the main and interaction effects are provided. For both panels, L, M and H represent low-, mid- and high-elevation sites, respectively; E0, E1, E2 and E3 denote no, mild, moderate and severe levels of *D. angustifolia* encroachment, respectively.

Soil properties and plant functional traits

Both elevation and *D. angustifolia* encroachment significantly affected soil properties and plant functional traits (Supplementary Figs S7 and S8). For soil properties, C:N, N:P and C:P ratios, DOC, NH₄⁺-N, AP and pH all declined significantly with increasing elevation. At 2050 m, N:P and C:P ratios increased initially and then declined with increasing encroachment, while TP showed the opposite pattern. At 2200 m, N:P and C:P ratios decreased significantly, whereas TP increased under encroachment (Supplementary Fig. S7). For plant traits, LN increased with elevation, while H, LA, LDMC and LC decreased. At both elevations, *D. angustifolia* encroachment significantly increased SLA, LN and LP but decreased LT and LDMC (Supplementary Fig. S8).

The PCA further revealed distinct multivariate patterns in soil properties and plant functional traits (Fig. 4). For soil properties, the first two principal components explained 44.07% and 29.14% of total variation, respectively. PC1 was associated with temperature variables, available nutrients and nutrient ratios (e.g. AP, NH₄⁺-N, NO₃⁻-N and C:N ratio). PC2 was mainly driven by TC, TN, TP, C:P and N:P ratios and SWC (Fig. 4a). For plant

functional traits, PC1 accounted for 41.74% of the variation and was strongly associated with resource economic traits such as LDMC, SLA and LN, suggesting a trade-off between resource acquisition and conservation strategies across environmental conditions. PC2 (20.86%) was primarily linked to size traits, including LA, H and BD (Fig. 4b). These patterns were further supported by the loading scores (Tables 3 and 4).

Impact pathways and effects

The SEMs showed good model fit, explaining 72% of the variation in mean BAI over the past 5 years, 9% in temperature sensitivity, 26% in maximum temperature sensitivity and 21% in precipitation sensitivity (Fig. 5a–d). *Rhododendron aureum* growth was mainly constrained by the increased elevation (standardized total effect (STE) = -0.56), indirectly mediated through Soil PC1 (temperature and nutrient availability, 1.04) and Trait PC2 (size traits, 0.78) (Figs 5a and 6a). *Deyeuxia angustifolia* encroachment had a negligible effect on *R. aureum* growth (Fig. 5a).

Temperature sensitivity was influenced minimally by elevation (± 0.03), acting through direct positive effects and indirect effects via decreased Soil PC1 and Trait PC2. *Deyeuxia angustifolia* encroachment

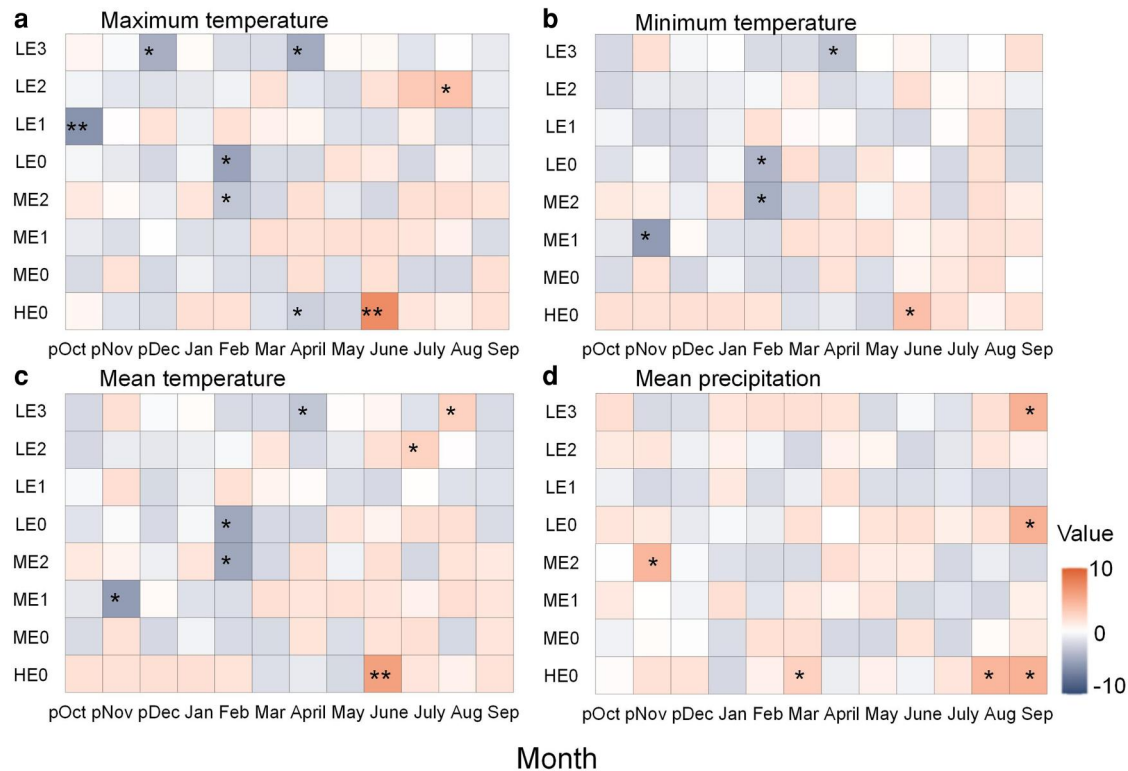


Figure 3: Climate sensitivity of *Rhododendron aureum* to (a) maximum, (b) minimum, (c) mean temperature and (d) mean precipitation under different *Deyeuxia angustifolia* encroachment levels across three elevations (from the previous October to the current September). Sensitivity indices represent the differences in AIC values between climate models and null models, adjusted by regression slopes. Statistical significance is indicated as: * $P < 0.05$, ** $P < 0.01$. pOct, pNov and pDec refer to the previous year's October, November and December, respectively, while Jan–Sep denotes the months from January to September of the current year. For the figure, L, M and H represent low-, mid- and high-elevation sites, respectively; E0, E1, E2 and E3 denote no, mild, moderate and severe levels of *D. angustifolia* encroachment, respectively.

had a negligible net effect (0.00) by balancing direct and indirect effects (Figs 5 and 6b, c).

Elevation had a strong net positive effect on precipitation sensitivity ($STE = 0.34$), which reflects the combined influence of a positive direct pathway, a positive indirect pathway via reduced Soil PC1 and Trait PC1 and negative indirect pathways via Trait PC2. In contrast, *D. angustifolia* encroachment had a minor net effect ($STE = -0.14$), as opposing indirect pathways through Trait PC1 and PC2 largely canceled each other out (Figs 5d and 6d).

DISCUSSION

Growth trends of *R. aureum*

Rhododendron aureum exhibited a stronger positive long-term growth trend at the higher elevation than at lower elevations in non-encroached plots. This aligns with remote sensing observations of upward shifts in *R. aureum* distribution within the Mt.

Changbai tundra (Zong *et al.* 2022). The pronounced positive growth trend of *R. aureum* at the higher elevation also corresponds with findings from the Alps, where warming has accelerated shrub and tree growth (Šenfeldr *et al.* 2021). This may be attributed to stronger increases in growing season temperatures (Körner 2012; Myers-Smith *et al.* 2015), reduced intraspecific competition, specific microclimatic advantages and faster juvenile growth in widely distributed shrubs at a higher elevation (Francon *et al.* 2023; Primicia *et al.* 2015). At lower elevations, no significant growth trend was observed under unencroached conditions, potentially due to the impact of snowpack distribution. Snow insulation plays a vital role in plant survival during winter (Zong *et al.* 2022). Climate warming may accelerate snowmelt, exposing plants to freezing conditions in winter and increasing the risk of drought in the subsequent growing season (Berner *et al.* 2020), which could counteract the positive effects of warming and limit growth at lower elevations.

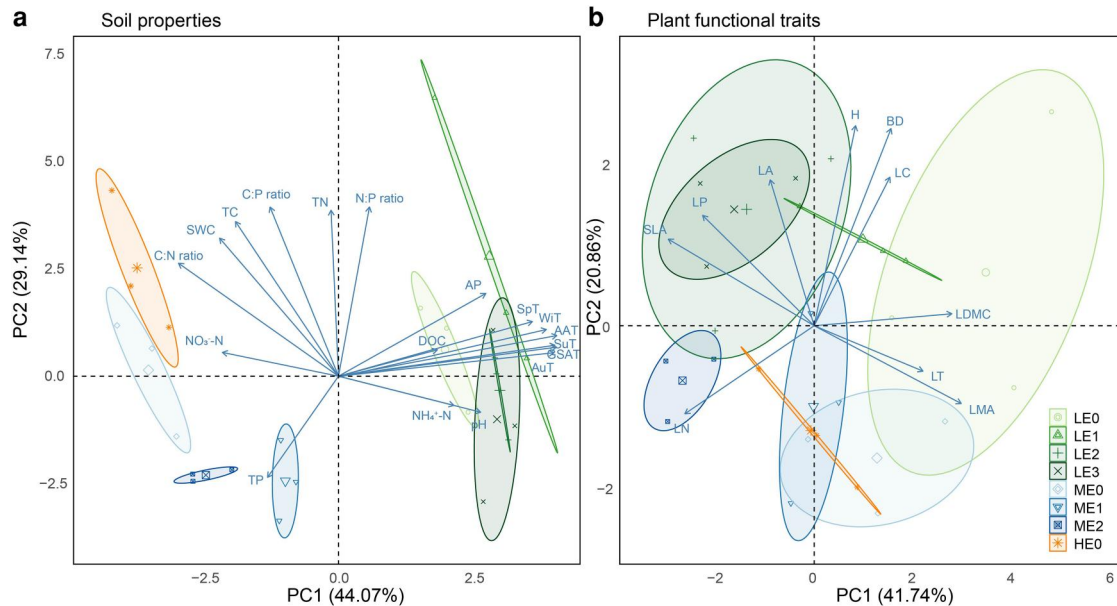


Figure 4: Principal component analysis (PCA) of (a) soil properties and (b) plant functional traits across different elevations and encroachment levels. Arrows indicate variable loadings on the first two principal components (PC1 and PC2), and their directions reflect the strength and orientation of correlations among variables. Each ellipse represents the 95% confidence region for the trait distribution within a given elevation and encroachment combination (LE0–LE3, ME0–ME2, HE0). For the figure, L, M and H represent low-, mid- and high-elevation sites, respectively; E0, E1, E2 and E3 denote no, mild, moderate and severe levels of *Deyeuxia angustifolia* encroachment, respectively.

At the lower and middle elevations, mild and moderate encroachment of *D. angustifolia* enhanced the positive growth trend of *R. aureum*, while severe encroachment resulted in a nonsignificant negative growth trend. Species interactions are known to modulate resource acquisition and growth dynamics (Lantz *et al.* 2009). Previous studies have shown that species interactions can slow warming-induced upward shifts of tree lines on the Tibetan Plateau (Liang *et al.* 2016), while a study also showed that facilitation and competition dominated in sparse versus dense vegetation scenarios, respectively (Zheng *et al.* 2024). In our study, moderate encroachment increased the LA and crown size of *R. aureum*. This, combined with the stems of *D. angustifolia*, may improve snow retention, insulate the soil and raise winter temperatures, potentially alleviating cold stress and early summer drought (Sturm *et al.* 2005). In addition, *D. angustifolia* encroachment can improve litter quality (Zhang *et al.* 2022), which, together with increased soil temperatures, may stimulate microbial and enzymatic activity and increase soil available nutrients (Jin *et al.* 2019), finally promoting growth and its long-term positive trends. However, severe encroachment may cause light limitation, thus impairing photosynthesis and carbon fixation in

R. aureum (Zhao *et al.* 2020), ultimately hindering the growth of *R. aureum*.

Climate sensitivities of *R. aureum*

Rhododendron aureum exhibited stronger climate sensitivity at higher elevations, characterized by reduced responses to winter temperatures but enhanced responses to spring–summer temperatures and precipitation, showing a shift in growth limitation from winter frost risk to the availability of heat and moisture during the growing season with the elevation. The research conducted in the Pyrenees (Francon *et al.* 2023) showed that the growth of *Rhododendron ferrugineum* depends on persistent snowpacks for protection against frost, drought and radiation (Gracia *et al.* 2007; Larcher and Wagner 2004). In alpine environments, snowpack depth and the timing of snowmelt vary with elevation, with higher elevations generally experiencing deeper and more persistent snow cover. In our study, shrub height decreased with increasing elevation (Table 5), suggesting that taller individuals are more common at lower elevations where snowpacks are relatively shallow. These taller shrubs are more likely to protrude above the snow surface, making them vulnerable to frost damage or

Table 3: Loadings of different soil properties on the first and second principal component axes of the PCA analysis for soil properties

Soil properties	PC1_loading	PC2_loading
AAT	0.96182130519008	0.225713798224768
GSAT	0.960174474462756	0.16110153811546
SummerT	0.953426203582695	0.17180426115673
AutumnT	0.94920464041663	0.130530688878356
SpringT	0.915555211473145	0.25921147962397
WinterT	0.854060557105514	0.303342444416729
Soil C:N ratio	−0.704745176	0.627109844859292
AP	0.64885943606972	0.459304272527466
pH	0.626241774543022	−0.199880473
SWC	−0.523753613	0.766599288104829
NO ₃ [−] -N	−0.51147122	0.132070301006924
NH ₄ ⁺ -N	0.508316458207495	−0.16192677
TC	−0.453702061	0.858628089809314
DOC	0.435433759564575	0.146543170043265
TP	−0.312490844	−0.561477599
Soil C:P ratio	−0.301422882	0.93894510706063
Soil N:P ratio	0.136435107351379	0.939591378293656
TN	−0.032872415	0.921363270243937

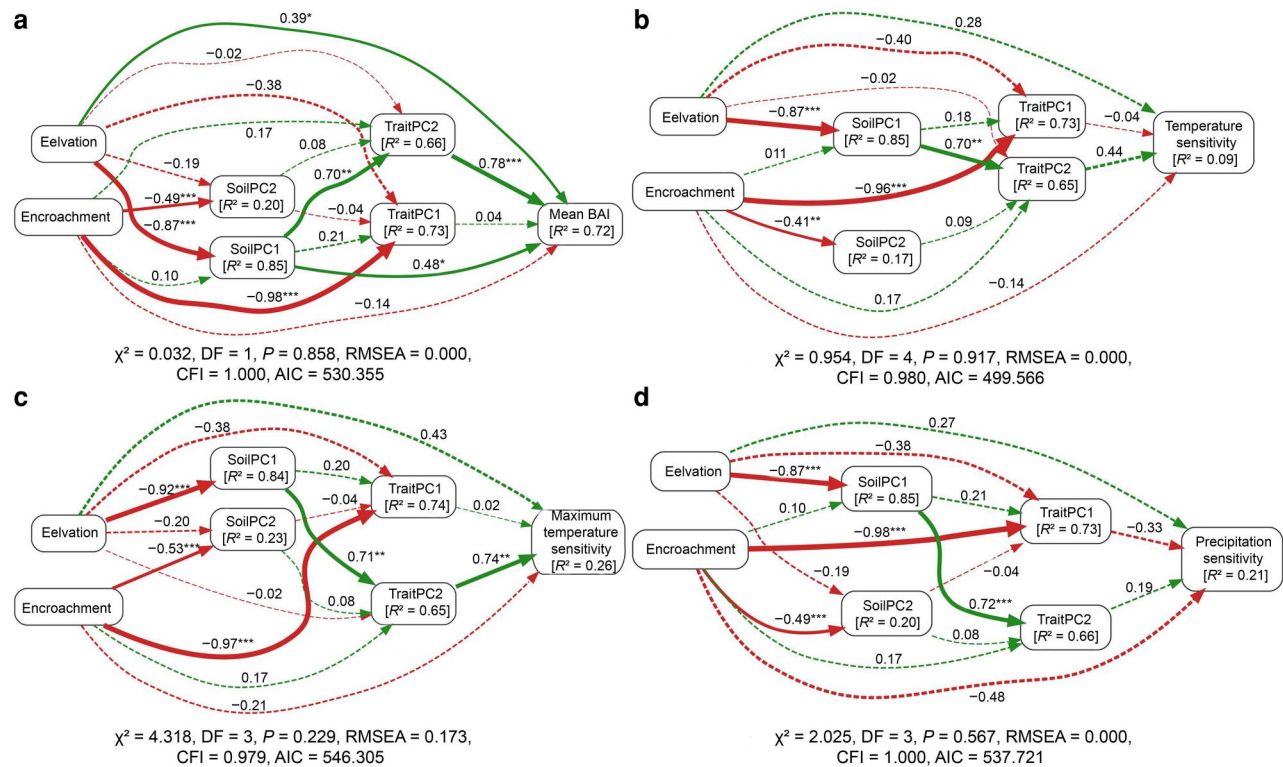
earlier exposure caused by premature snowmelt (Domine *et al.* 2016; Hallinger *et al.* 2010). In contrast, at higher elevations, the snowpack is deeper and more persistent, and the shorter stature of *R. aureum* allows most individuals to remain buried and thus buffered from direct winter temperature fluctuations. However, spring (April) warming at high elevations may accelerate snowmelt, leaving soils frozen and plants susceptible to late frost events or drought stress during the following growing season (Berner *et al.* 2020; Francon *et al.* 2020; Zong *et al.* 2022). Warmer summer temperatures enhanced *R. aureum* growth at 2350 m, consistent with shrub responses across the circumpolar north (Myers-Smith *et al.* 2015) and other alpine regions (Francon *et al.* 2021; Hallinger *et al.* 2010; Liang *et al.* 2012), with the strong June temperature signal underscoring the importance of early-summer warmth for photosynthesis and carbohydrate accumulation in initiating the growing season (Hallinger *et al.* 2010). Because radial growth usually ceases by September, the positive response

to September precipitation at both elevations is unlikely to reflect direct cambial activity. Rather, late-season moisture may prolong photosynthetic activity and enhance carbohydrate storage, or improve soil water recharge before freezing, thereby mitigating subsequent frost and drought risks and supporting growth in the following year (Liang *et al.* 2015; Pandey *et al.* 2020). At 2350 m, consistently positive responses to precipitation in March and August further support this shift in limiting factors under climate change (Francon *et al.* 2020; Rodriguez-Caton *et al.* 2021).

Deyeuxia angustifolia encroachment increased the climate sensitivity of *R. aureum* growth, particularly by amplifying its negative responses to spring, autumn and winter temperatures, as well as its positive responses to summer temperatures and autumn precipitation. However, the specific effects varied with elevation. At 2050 m, *D. angustifolia* encroachment weakened the negative effect of winter (February) temperatures but amplified the negative effect of spring (April) warming. The

Table 4: Loadings of different plant functional traits on the first and second principal component axes of the PCA analysis for functional traits of *Rhododendron aureum*

Plant traits	PC1_loading	PC2_loading
LMA	0.873939239100353	-0.282840461
SLA	-0.866993283	0.314768047789533
LDMC	0.818447955683593	0.0435736400208952
LN	-0.768461408	-0.320138945
LP	-0.662732801	0.401101619897314
LT	0.646875376517987	-0.165112846
BD	0.456953109238544	0.716523543192048
LC	0.45020203046611	0.539712957892043
LA	-0.26117677	0.530246341571303
H	0.246382347849359	0.727045225773732

**Figure 5:** Structural equation models (SEMs) showing the direct and indirect effects of elevation and *Deyeuxia angustifolia* encroachment on (a) mean basal area increment (Mean BAI), (b) temperature sensitivity, (c) maximum temperature sensitivity and (d) precipitation sensitivity. Arrows indicate standardized causal paths, with arrow thickness proportional to effect strength. Path coefficients are shown along each arrow, and their sign indicates whether the effect is positive or negative. Solid lines denote significant pathways ($P < 0.05$), while dashed lines denote non-significant pathways ($P > 0.05$). R^2 values beside response variables represent the proportion of variance explained. Model fit indices are given below each panel; overall, all models showed satisfactory fit (non-significant χ^2 , $RMSEA \approx 0$, $CFI > 0.95$ and low AIC values). The loadings of soil and plant trait variables on the first two principal components (PC1 and PC2) are provided in Tables 3 and 4.

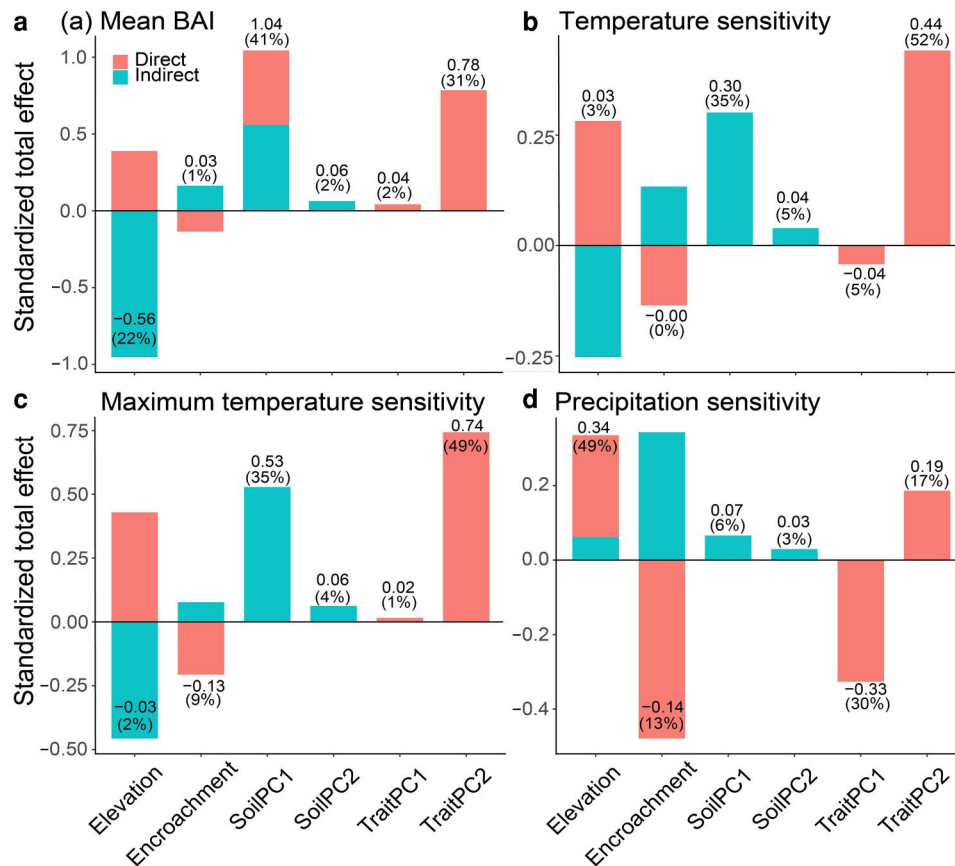


Figure 6: Standardized total effects (STE) of elevation, *Deyeuxia angustifolia* encroachment, soil properties and plant functional traits on (a) mean basal area increment (Mean BAI), (b) temperature sensitivity, (c) maximum temperature sensitivity and (d) precipitation sensitivity. For each predictor, STEs are partitioned into standardized direct effects (SDE; red) and standardized indirect effects (SIE; blue). The percentages indicate the relative contribution of each component to the total effect. Positive and negative values denote enhancing and suppressing influences, respectively. The loadings of individual soil properties and plant functional traits on the first two principal components (Soil PC1–2 and Trait PC1–2) are listed in Tables 3 and 4.

reduced shrub height of *R. aureum* under encroachment (Table 1) likely allowed individuals to remain better covered by the already shallow snowpack, thereby potentially reducing their risk of frost damage in winter (Gracia *et al.* 2007; Larcher and Wagner 2004). In contrast, April represents a critical period for budburst and the onset of growth; during this stage, competition from *D. angustifolia* for water and nutrients can exacerbate the adverse effects of warming. At 2200 m, encroachment enhanced negative responses of *R. aureum* growth to autumn and winter (previous November and current February) warming. This is because shading may reduce light availability, thereby limiting photosynthesis, carbon fixation and carbohydrate storage during the growing season (Zhao *et al.* 2020), while warmer conditions in autumn and winter can increase respiration and depleted stored reserves (Sperling *et al.* 2015). Conversely, encroachment

strengthened positive responses to summer (June) warming and autumn (November) precipitation. Under shaded conditions, summer warmth may partially offset low-temperature limitations, enhance carbon fixation efficiency under low light, promote non-structural carbohydrate accumulation and extend the active growing period. Similarly, November precipitation, which falls primarily as snow, can be intercepted by the stems of *R. aureum* and *D. angustifolia*. This snow cover may then insulate the soil, conserve moisture and supply water at the onset of the next growing season—thereby enhancing overwinter survival and supporting subsequent plant growth.

Regulation effects of soil properties and plant functional traits

The growth of *R. aureum* was primarily constrained by elevation, both directly and indirectly through its

Table 5: Height and basal stem diameter of *Rhododendron aureum* and *Deyeuxia angustifolia* located at different sites

Elevation	Encroachment	H _R	BD _R	H _D	BD _D
L	E0	29.07 ± 4.52	6.38 ± 0.98		
	E1	23.74 ± 3.32	5.08 ± 0.36	71.6 ± 4.62	1.89 ± 0.12
	E2	17.73 ± 2.6	5.11 ± 0.21	61.41 ± 2.86	2.16 ± 0.02
	E3	28.33 ± 1.4	5.68 ± 0.42	65.47 ± 7.37	1.98 ± 0.11
M	E0	26.13 ± 4.4	5.36 ± 0.39		
	E1	27.53 ± 1.05	5.65 ± 0.94	62.83 ± 3.8	1.78 ± 0.22
	E2	22.99 ± 1.31	4.25 ± 0.06	85 ± 5.11	2.13 ± 0.03
H	E0	26.13 ± 2.14	6.2 ± 0.67		

H_R, BD_R, H_D and BD_D represent the height and basal stem diameter of *R. chrysanthum* and *D. angustifolia*, respectively. Data are shown as means ± 1 standard error.

effects on soil temperature, nutrient availability and plant size traits. In contrast, *D. angustifolia* encroachment exerted only a negligible net effect. In alpine tundra ecosystems, temperature and nutrient availability are widely recognized as key limiting factors (Körner 2021), with extensive evidence supporting their positive influence on plant growth (Gazol *et al.* 2022; HilleRisLambers *et al.* 2013; McManus *et al.* 2012). Our findings suggest that soil temperature and nutrient variability were more pronounced along elevational gradients than along encroachment gradients, resulting in stronger elevational effects on *R. aureum* growth. With increasing elevation, reductions in soil temperature, nutrient supply and growing season length collectively limited plant height and LA development, thereby decreasing photosynthetic carbon assimilation and ultimately reducing radial growth. The negligible total effect of *D. angustifolia* encroachment reflected an offset between its positive and negative pathways. On one hand, the more decomposable mixed shrub-herb litter compared with *R. aureum* litter enhanced nutrient cycling (Li *et al.* 2023), producing nutrient-enriched soils (e.g. higher DOC and available phosphorus). These changes could directly promote *R. aureum* growth and indirectly favor traits associated with acquisitive strategies, such as greater plant height, larger SLA and higher nutrient contents, which indicate larger canopies and more efficient photosynthesis. On the other hand, shading from *D. angustifolia* encroachment may directly reduce carbon assimilation and radial growth in *R. aureum* (Zhao *et al.* 2020), while simultaneously driving a shift toward acquisitive leaf traits (e.g. thinner

leaves and lower dry matter content). Although such trait changes may initially enhance photosynthetic efficiency, they may compromise stress resistance and ultimately limit growth. The non-significant growth-promoting effect under severe encroachment may support our hypothesis.

The temperature sensitivity of *R. aureum* was not significantly influenced by either elevation or *D. angustifolia* encroachment (total effects ≈ 0), whereas the maximum temperature sensitivity was significantly reduced under encroachment, with only minor elevational effects. In terms of mechanisms, encroachment triggered opposing pathways: on the one hand, nutrient enrichment and acquisitive trait expression may slightly enhance photosynthetic efficiency and temperature sensitivity. On the other hand, shading may suppress carbon assimilation, moderate leaf temperature and water loss and lower photorespiration, thereby reducing *R. aureum*'s response to temperature—especially extreme heat—and ultimately causing the negative effects to outweigh potential benefits. By contrast, elevation also exerted offsetting influences. Higher elevations reduced soil temperature and nutrient supply, which would theoretically increase the temperature sensitivity. However, in our study, this pathway may be counterbalanced by other effects—most notably the insulating role of snowpack at high elevations, which buffers extreme soil temperature fluctuations and mitigates thermal stress (Williams *et al.* 1996). Consequently, elevation showed no significant net effect on mean or maximum temperature sensitivity.

Elevation increases the precipitation sensitivity of *R. aureum* growth both directly and indirectly by reducing soil temperature and available nutrients. In contrast, the overall effect of *D. angustifolia* encroachment was negligible. Typically, lower elevations experience higher temperatures but lower precipitation and soil moisture, making plant growth more dependent on precipitation variability (Gea-Izquierdo *et al.* 2012; Olson *et al.* 2018). However, in our study, the elevation gradient was relatively short, and moisture availability was not a primary limiting factor. Instead, non-growing season precipitation mainly occurred as snowfall, suggesting that growth sensitivity to precipitation was largely driven by snowpack accumulation. At higher elevations, lower temperatures and nutrient limitations amplified the effects of snowpack, which provides thermal insulation and enhances nutrient cycling (Williams *et al.* 1996), leading to greater precipitation sensitivity. Although elevation also reduces precipitation sensitivity by affecting plant traits (reducing plant size), the effects are much smaller than those of elevation, elevated soil temperatures and nutrient changes. In contrast, *D. angustifolia* encroachment had a minimal effect on precipitation sensitivity, likely because snowfall influences soil conditions through changes in snow cover, moisture availability and snowmelt processes, which varied more across elevation gradients than encroachment levels. Thus, *R. aureum* growth's response to precipitation was primarily governed by elevation-driven soil and microclimatic factors rather than by *D. angustifolia* encroachment.

While our findings highlight elevation-specific and encroachment-dependent shifts in growth and climate sensitivity, we acknowledge that other ecological factors—such as herbivory, pathogen pressure and disturbance regimes—may also influence shrub growth and its sensitivity to climate. In our study, however, these potential confounding influences were carefully minimized: the sites were located within a nature reserve with no human disturbance, plots were selected under comparable micro-habitat conditions (slope, aspect, flat terrain), and no signs of herbivory, trampling or plant diseases were observed. We are therefore confident that the observed growth differences primarily reflect environmental factors, including elevation, climate and interspecific interactions. Nonetheless, these additional ecological processes remain important in shaping alpine shrub dynamics and warrant further investigation in future studies to

provide a more comprehensive understanding of shrub–climate interactions.

CONCLUSIONS

Our study reveals that *R. aureum* exhibits a positive radial growth trend over time, which is further enhanced at higher elevations (2350 m). Mild and moderate encroachment of *D. angustifolia* enhanced the positive growth trend of *R. aureum*, especially at the low elevations. Growth responses to climate vary with elevation, showing negative effects of spring temperature and positive effects of autumn precipitation at 2050 and 2350 m and positive effects of summer temperatures at 2350 m. *Deyeuxia angustifolia* encroachment increased the climate sensitivity of *R. aureum* growth, particularly by enhancing its negative responses to spring, autumn and winter temperatures, as well as its positive responses to summer temperatures and autumn precipitation. Overall, the growth of *R. aureum* and its precipitation sensitivity are more influenced by elevation, co-regulated by soil conditions and plant size traits; Soil conditions and leaf economic traits influence temperature sensitivity. These findings shed light on the variations and mechanisms driving the growth trends and climate sensitivity of *R. aureum* across elevation and encroachment gradients, contributing to a better understanding of tundra vegetation dynamics under global change and offering valuable insights for conservation and ecosystem management. Future controlled experiments could further enhance our understanding of the mechanisms driving shrub growth under diverse environmental conditions.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Selected soil properties in this study.

Table S2: Selected functional traits of *Rhododendron aureum* in this study.

Table S3: Significant climate (maximum, minimum, mean temperature and precipitation) sensitivity of *Rhododendron aureum* under different levels of *Deyeuxia angustifolia* encroachment at three elevations from the previous October to the current September.

Figure S1: Temporal trends in mean annual temperature (°C) and precipitation (mm) from 1990 to 2020.

Figure S2: Monthly variations in maximum, mean and minimum temperatures (°C) and precipitation (mm).

Figure S3: Trends in (a) maximum, (b) minimum, (c) mean air temperatures (°C) and (d) mean precipitation (mm) from 1960 to 2020.

Figure S4: Mann–Kendall (M–K) trend test statistics for (a) maximum, (b) minimum, (c) mean air temperatures and (d) mean precipitation from 1950 to 2020.

Figure S5: (a) Schematic of *Rhododendron aureum*, showing cross-sections with annual rings: ‘1’ marks the root stem disk, ‘2’ the stem and ‘3’ the shoot.

Figure S6: Detrended ring-width chronologies of *Rhododendron aureum* under no (a), mild (b), moderate (c), severe (d) encroachment of *Deyeuxia angustifolia* at 2050 m, and under no (e), mild (f), moderate (g) encroachment of *Deyeuxia angustifolia* at 2200 m and no (h) encroachment of *Deyeuxia angustifolia* at 2350 m.

Figure S7: (a–p) The soil properties in different environments, with significant differences among elevation and encroachment gradients indicated by distinct uppercase and lowercase letters ($P < 0.05$).

Figure S8: (a–h) The functional traits of *Rhododendron aureum* in different environments, with significant differences among elevation and encroachment gradients indicated by distinct uppercase and lowercase letters ($P < 0.05$).

Authors' Contributions

Na Li (Conceptualization, Investigation, Validation, Writing—original draft), Suke Hou (Conceptualization, Formal analysis, Investigation, Writing—original draft), Mai-He Li (Conceptualization, Methodology, Writing—review and editing), Xi Qi (Writing—review and editing), Liangjun Zhu (Writing—review and editing), Jitang Li (Writing—review and editing), Paolo Cherubini (Writing—review and editing), Zhaoyong Hu (Writing—review and editing), Zhengfang Wu (Conceptualization, Funding acquisition), Renkai Dong (Writing—review and editing), Lei Wang (Funding acquisition, Writing—review and editing), Youwen Wang (Writing—review and editing), Danyang Yuan (Writing—review and editing) and Haibo Du (Conceptualization, Funding acquisition, Resources, Writing—review and editing)

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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