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RESEARCH

Decoupling of larch growth from temperature in the Central Eastern Alps is modulated by stand density

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Abstract

Tree growth in boreal regions and at high elevations, where low temperatures limit growth, has generally benefited from recent climate warming. However, since the late 20th century, a reduced sensitivity of tree growth to temperature has been observed, primarily at high-latitude forest sites in the Northern Hemisphere. This phenomenon, termed the divergence problem, has been linked to temperature-induced drought stress and increased competition for resources in densifying stands. Here, we investigate how stand density influences radial growth of European larch (*Larix decidua* Mill.) in subalpine larch grasslands of the Central-Eastern Alps. Increment cores from 140 larch trees across seven sites were analyzed. Each site comprised a pair of stands with comparable environmental conditions but contrasting management history and stand density: an abandoned larch grassland that developed into a closed stand and a continuously managed larch grassland that remained open. Response function analyses indicated that May-August temperature significantly promoted radial growth in both open and closed stands. However, after 2000, climate warming did not translate into increased basal area increment (BAI). Instead, BAI trends in both managed and abandoned larch grasslands became decoupled from temperature trends, likely reflecting increasing nutrient or water limitation, as suggested by stronger growth declines with increasing stand density. These findings highlight the role of traditional land-use practices by reducing competition among existing trees. We conclude that stand density is a key constraint on larch growth and should be explicitly considered in areas where land-use changes alter stand structure.

Keywords Basal area increment · Climate warming · Competition · Divergence problem · Land-use change · Larch grassland

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Introduction

The effects of climate warming on tree growth have been widely studied across the Northern Hemisphere. At high latitudes and elevations, warming generally enhances radial growth by alleviating temperature limitations (Jacoby and D'Arrigo 1997; Mäkinen et al. 2003; Nothdurft and Vospernik 2018). In contrast, at lower elevations and dry inner-Alpine sites, intensified drought stress has been associated with reduced growth (Obojes et al. 2018, 2024; Rozenberg et al. 2020; Schuster and Oberhuber 2013). Since the late 20th century, deviations from these established climate-growth relationships have been observed in boreal regions such as Alaska and Siberia. This phenomenon, known as the divergence problem (DP), describes a loss of climate sensitivity and/or a mismatch between recorded temperatures and tree-ring growth (D'Arrigo et al. 2008). Proposed explanations include increasing drought stress under warming, altered seasonality and phenology reducing temperature sensitivity, reduced solar radiation ("global dimming"), and methodological issues related to detrending that may attenuate low-frequency climate signals (Briffa et al. 1998; Barber et al. 2000; Büntgen et al. 2006; D'Arrigo et al. 2008; Kirdyanov et al. 2020; Loehle 2009; Melvin and Briffa 2008; Wilmking et al. 2004).

In the European Alps, Büntgen et al. (2008) found no evidence of the DP. However, Oberhuber et al. (2020) reported that recent warming no longer enhanced basal area increment (BAI) at subalpine sites in the Central European Alps, likely due to increased competition for resources such as light, nutrients, and water in dense stands. While the DP typically reflects large-scale shifts in tree ecophysiological responses to climate warming, stand density represents a local, non-climatic constraint associated with canopy structure. Consequently, temporal changes in stand structure, often driven by land-use change, may substantially shape long-term growth trends.

In the high montane and subalpine zones of the European Alps, tree densification has been particularly pronounced in larch grasslands (Fontana et al. 2014; Garbarino et al. 2011), a traditional agroforestry system combining fodder and timber production. European larch (*Larix decidua* Mill.), a light-demanding pioneer species, thrives on well-drained, disturbed soils and is periodically affected by nine-year outbreaks of the larch budmoth (*Zeiraphera diniana* Gn.), which temporarily reduces radial growth (Baltensweiler et al. 2008). In the subalpine zone, larch forms pure, open forests or coexists with Swiss stone pine (*Pinus cembra* L.) or Norway spruce (*Picea abies* [L.] Karst.) in mixed stands (Da Ronch et al. 2016). At lower elevations, pure larch grasslands have historically been maintained through mowing, grazing, and thinning, i.e., the selective removal of trees (Fontana et al. 2014; Schulze et al. 2007).

Since the mid-20th century, socio-economic changes such as mechanized haymaking and increased agricultural productivity in valley meadows have led to widespread abandonment of these traditional and labor-intensive larch grasslands. Consequently, Norway spruce has increasingly invaded larch grasslands, transforming open larch stands into denser mixed forests (Garbarino et al. 2011). However, some larch grasslands remain traditionally managed, and conservation efforts aim to preserve their biodiversity and cultural value (Fontana et al. 2014; Nagler et al. 2015; Schulze et al. 2007). Building on the findings of Oberhuber et al. (2020), this study investigates the impact of stand density on larch radial growth to further examine evidence of the divergence problem in the European Alps. Specifically, we tested the following hypotheses (H):

H1 *The divergence between basal area increment (BAI) trends and climate warming is greater in closed, high-density stands than in open, low-density stands, reflecting the negative effects of increased competition and reduced resource availability on tree growth.*

H2 *In high-elevation larch grasslands, stand densification weakens temperature sensitivity of radial growth, reducing the relative importance of temperature as a growth driver.*

Materials and methods

Study design

Tree growth variability in mountain forests is influenced by multiple drivers, including climate, topography, and anthropogenic or biotic disturbances (Schurman et al. 2024; Holtmeier and Broll 2007). To assess these influences, we combined response function analyses (Zang and Biondi 2015) with generalized linear mixed-effects modeling (GLMM). Response function analyses were first conducted to identify the climate variables most strongly affecting growth. These variables were subsequently incorporated into a GLMM to quantify their relative importance alongside other environmental and stand-related drivers while accounting for the hierarchical structure of the data.

Study sites

Seven sites comprising a total of 14 stands were selected across the Central Eastern Alps. Six sites (12 stands) were located in North Tyrol, Austria (municipalities of Mieders, Neustift, Navis, and Obernberg), while one site (two stands)

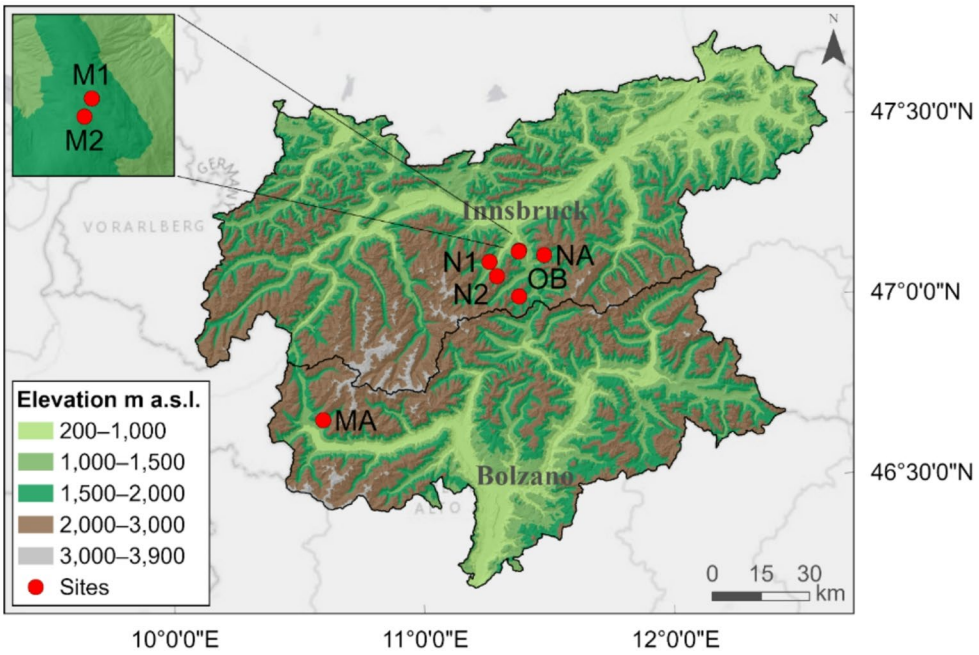


Fig. 1 The study area (Central Eastern Alps) with the seven selected larch sites. Site codes: M1, M2, Mieders; MA, Matsch/Mazia; N1, N2, Neustift; NA, Navis; OB, Obernberg (Brenner). All stands were located in the subalpine zone between 1600 and 1900 m a.s.l. Map lines demarcate North Tyrol (Austria) from South Tyrol (Italy). Data source: DTM 5 m North Tyrol (Land Tirol – data.tirol.gv.at) and DTM 2.5 m South Tyrol (Autonome Provinz Bozen – provinz.bz.it)

Table 1 Site characteristics of open (O) and closed (C) stands

Site	Lat	Lon	Elevation (m a.s.l.)		Aspect	Slope (°)
			Min	Max		Mean ± SD
M1O	11.421	47.152	1633	1694	SW	30.9 ± 2.2
M1C	11.422	47.152	1636	1694	SW	29.2 ± 3.0
M2O	11.418	47.150	1646	1698	NE	24.1 ± 5.3
M2C	11.421	47.148	1639	1681	NE	21.5 ± 3.4
MAO	10.609	46.695	1834	1887	SE	25.1 ± 4.0
MAC	10.610	46.695	1767	1823	SE	28.2 ± 3.6
N1O	11.296	47.122	1676	1721	S	23.5 ± 2.5
N1C	11.304	47.124	1633	1715	S	36.2 ± 5.0
N2O	11.329	47.084	1614	1691	E	34.4 ± 4.3
N2C	11.326	47.082	1705	1781	E	35.8 ± 1.8
NAO	11.520	47.137	1716	1764	SE	23.2 ± 5.0
NAC	11.526	47.137	1751	1797	SE	23.8 ± 5.7
OBO	11.415	47.025	1764	1804	SE	21.1 ± 3.7
OBC	11.418	47.024	1710	1760	S	25.0 ± 4.8

Site codes: M1, M2, Mieders; MA, Matsch/Mazia; N1, N2, Neustift; NA, Navis; OB, Obernberg (Brenner). Geographic coordinates (Lat, Latitude, Lon, Longitude) are given for the center of each stand

was situated in South Tyrol, Italy, at the LTSER site Matsch/Mazia (LTER_EU_IT_097), one of the driest valleys in the Alps (Fig. 1; Table 1). Mieders and Neustift (Stubai Valley) are part of the LTSER (Long-Term Socio-Ecological Research) platform Tyrolean Alps (Kerle and Tappeiner 2017). Each site provided a pair of larch stands, one open and one closed, resulting in 14 stands in total. Stands were classified as open if stand basal area (BA) ≤ 40 m^2 ha^{-1} and canopy cover (CC) ≤ 40%, and as closed if BA > 40 m^2 ha^{-1} and CC > 40%.

BA was derived within a 20 × 20 m plot (Fig. S1) by (i) measuring diameter at breast height (DBH) of all living trees with DBH > 5 cm using a diameter tape, (ii) calculating BA per tree ($BA = \pi \times (DBH/2)^2$), and (iii) scaling the summed BA of all trees to hectare level to obtain BA in m^2 ha^{-1}. CC was estimated as the proportion of ground area covered by the vertical projection of tree crowns. The thresholds for BA and CC were based on observations across our open and closed stands (maximum BA and CC in open stands: 35.8 m^2 ha^{-1} and 40%; minimum BA and CC in closed stands: 44.6 m^2 ha^{-1} and 65%; Table 2) and are consistent with Pretzsch (2009), who reported that stand competition for light-demanding species such as *Larix decidua* becomes strong at BA > 35–45 m^2 ha^{-1}.

Table 2 Stand characteristics of open (O) and closed (C) stands

Site	Cambial age (years)	BA (m^2 ha^{-1})	Canopy cover (%)	Stand height (m)	DBH (cm)
	Mean ± SD				Mean ± SD
M1O	159 ± 44	35.8	40	20	65.1 ± 6.4
M1C	216 ± 69	50.5	70	21	61.4 ± 11.9
M2O	155 ± 42	23.9	30	21	57.9 ± 10.4
M2C	140 ± 44	46.6	70	22	58.7 ± 9.5
MAO	104 ± 10	16.9	20	21	60.2 ± 3.5
MAC	111 ± 22	55.1	70	23	64.3 ± 7.3
N1O	130 ± 17	20.3	20	21	62.2 ± 7.2
N1C	116 ± 47	44.8	65	21	63.4 ± 6.8
N2O	154 ± 44	10.1	5	17	75.2 ± 12.2
N2C	139 ± 49	44.6	65	21	66.5 ± 11.6
NAO	144 ± 66	21.7	25	20	63.9 ± 8.1
NAC	157 ± 83	44.8	65	21	60.6 ± 9.7
OBO	111 ± 37	15.8	15	19	60.5 ± 8.8
OBC	179 ± 64	44.8	65	21	64.3 ± 10.7

M1, M2, Mieders; MA, Matsch/Mazia; N1, N2, Neustift; NA, Navis; OB, Obernberg (Brenner). Cambial age was determined at breast height (1.3 m). BA, stand basal area; DBH, diameter at breast height; SD, standard deviation

Open stands corresponded to managed larch grasslands, whereas closed stands had been formerly managed but were later abandoned or afforested (between 1950 and 1980), allowing them to develop into denser mixed larch-spruce stands (Fig. S1). Because each pair of stands appeared similar in the oldest available aerial photographs (1970–1974) in terms of BA and CC, we assumed that they had been historically managed in a comparable way until one stand was abandoned. Using GIS software, 1-ha stands were delineated based on historical and current aerial photographs, ensuring similar elevation, slope, aspect, and siliceous bedrock at each site to minimize microsite effects on tree growth (Table 1).

Field sampling and preparation of increment cores

Field sampling was conducted between June and August 2023. For each stand, BA, CC, and stand height were recorded (Table 2). BA was calculated within a selected 20 × 20 m plot (Fig. S1) by measuring all living trees with a DBH > 5 cm. Tree height was measured using a laser rangefinder (Nikon Forestry Pro), and soil depth was recorded at 10 distributed points within each stand. Increment cores were sampled from 10 larch trees per stand (Fig. S1), selecting those with the largest DBH to obtain long-term growth histories representative of each stand. All sampled trees were free of major stem or crown anomalies and had straight, untwisted stems. One increment core per tree was extracted at breast height (BH; 1–1.3 m) and parallel to the slope. Stem diameter and bark thickness were measured at BH, and GPS coordinates and photographs were recorded for each sampled tree.

In the laboratory, increment cores were air-dried, mounted on wooden holders, and their surfaces were prepared using a sharp industrial blade until annual rings became clearly visible (Pilcher 1990). White chalk powder was applied to enhance the contrast of tree-ring boundaries. Total ring width (TRW) was measured at a resolution of 1 µm using a stereomicroscope with up to 45× magnification (Olympus SZ61, Olympus GmbH, Hamburg, Germany) coupled with a LINTAB™ 6 measuring system (Rinntech, Heidelberg, Germany). Measurements were processed using TSAP-Win™ software (version 1.24, Rinntech, Heidelberg, Germany). Accurate dating of the time series was validated both visually and statistically with COFECHA (Holmes 1983), and year assignments were cross-checked against regional larch chronologies (Oberhuber et al. 2020). Missing annual rings that occurred sporadically were manually inserted with a TRW value of zero. When the pith was missed during coring, the number of absent rings was estimated based on DBH or the curvature of the innermost rings.

Basal area increment

To investigate long-term growth trends, TRW was converted into basal area increment (BAI), which provides a more direct quantitative proxy of woody biomass production and reduces age- and size-related growth effects (Babst et al. 2014; Biondi and Qeadan 2008). BAI series were generated using the *bai.out* function of the *dplR* package (Bunn 2008) in R (R Core Team 2023), converting ring-width series (mm) into ring-area series (mm^2) based on stem diameter (bark excluded). The conversion accounts for the progressive decrease in ring radius toward the pith, assuming circular stem growth (Biondi 1999):

$$\mathrm{BAI} = \pi \left(r^2_n - r^2_{n-1}\right)$$

where *r* is the radius inside the bark and *n* is the year of ring formation. Stand-specific BAI trends were derived by calculating annual mean BAI values across all sampled trees within each stand. For comparative analyses, mean BAI series were aggregated for seven open and seven closed stands. The annual difference in growth between stand types (ΔBAI) was calculated as:

$$\Delta\,\mathrm{BAI} = \mathrm{BAI}_{\mathrm{open}} - \mathrm{BAI}_{\mathrm{closed}}$$

For the period 2000–2022, differences in annual mean BAI between open and closed stands were tested using an independent-samples t-test, with homogeneity of variances assessed using Levene's test.

Table 3 Growth metrics of tree ring series of open (O) and closed (C) stands

Site	IntCorr (*r*)	AR1	EPS	SNR
M1O	0.60	0.71	0.88	7.2
M1C	0.57	0.79	0.88	7.2
M2O	0.63	0.77	0.92	11.5
M2C	0.65	0.74	0.90	9.2
MAO	0.68	0.72	0.95	20.6
MAC	0.63	0.71	0.92	12.0
N1O	0.60	0.61	0.89	8.1
N1C	0.53	0.58	0.87	6.9
N2O	0.54	0.63	0.83	4.9
N2C	0.61	0.62	0.86	6.4
NAO	0.62	0.65	0.91	10.0
NAC	0.61	0.68	0.92	11.1
OBO	0.52	0.61	0.82	4.4
OBC	0.61	0.73	0.89	8.4

Site codes: M1, M2, Mieders; MA, Matsch/Mazia; N1, N2, Neustift; NA, Navis; OB, Obernberg (Brenner). IntCorr, inter-series correlation; AR1, first order autocorrelation; EPS, expressed population signal; SNR, signal-to-noise ratio

Climate data and climate-growth analyses

Two climate variables were analyzed: mean air temperature and total precipitation. Climate data for the period 1920–2022 were obtained from the Europe-wide E-OBS v28.0e daily gridded dataset (Cornes et al. 2018). Daily mean temperature and daily precipitation totals were aggregated to monthly values to match the requirements of the response function analyses. Temperature data were downscaled to the mean elevation of the study sites using the standard lapse rate of 0.65 °C per 100 m (Barry and Chorley 2003).

Static and moving monthly climate-growth analyses were conducted for 1920–2022 to (i) identify the climate variables most strongly influencing tree growth for inclusion in the subsequent generalized linear mixed model, and (ii) assess the temporal stability of climate-growth relationships, with particular emphasis on potential effects of stand densification and divergence phenomena. Bootstrapped response functions (1000 replications) were calculated using the *dcc* function of the *treeclim* package (Zang and Biondi 2015), with significance set at $\alpha = 0.05$. For static analyses, annual BAI series were correlated with monthly climate data from September of the previous year to September of the current year. For the moving response function analysis, the months showing the strongest correlations with growth were selected, and a 50-year moving window was applied to evaluate temporal changes in climate sensitivity.

Generalized linear mixed model

A generalized linear mixed model (GLMM) was used to quantify the relationship between BAI of individual trees over the period 1920–2022 ($n = 11{,}651$) and site, stand, land-use, climate, and growth disturbance variables across open and closed stands. A gamma distribution with a natural logarithm link function was applied. The gamma distribution is flexible and well suited for modeling non-negative, heteroscedastic data (Venables and Ripley 2010). Variable and interaction selection was performed using a stepwise procedure, removing predictors and interactions with p values > 0.05 and addressing multicollinearity by excluding variables with Pearson correlation coefficients ≥ 0.6. To account for the longitudinal nature of the data, a one-year lag of the dependent

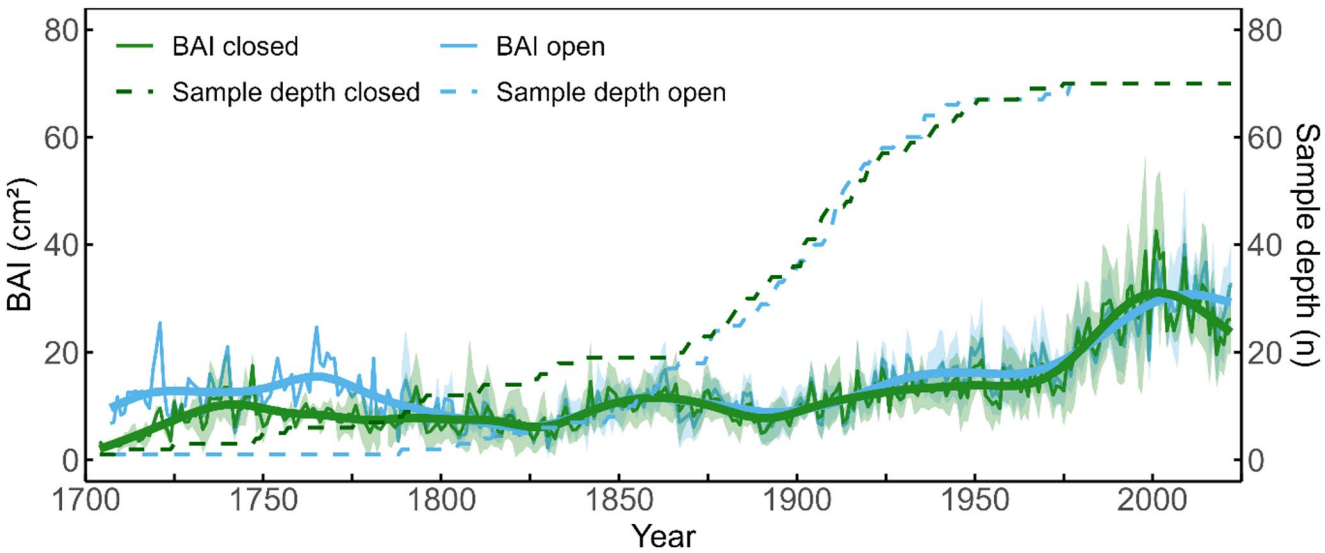


Fig. 2 Time series of basal area increments (BAI) in open (blue) and closed stands (green) from 1704 to 2022. Thirty-year smoothed trend lines are shown in thicker lines, with shaded areas representing the standard deviation (blue for open, green for closed). Dashed lines indicate sample depth, i.e., the number of trees measured per year, for open (blue) and closed stands (green)

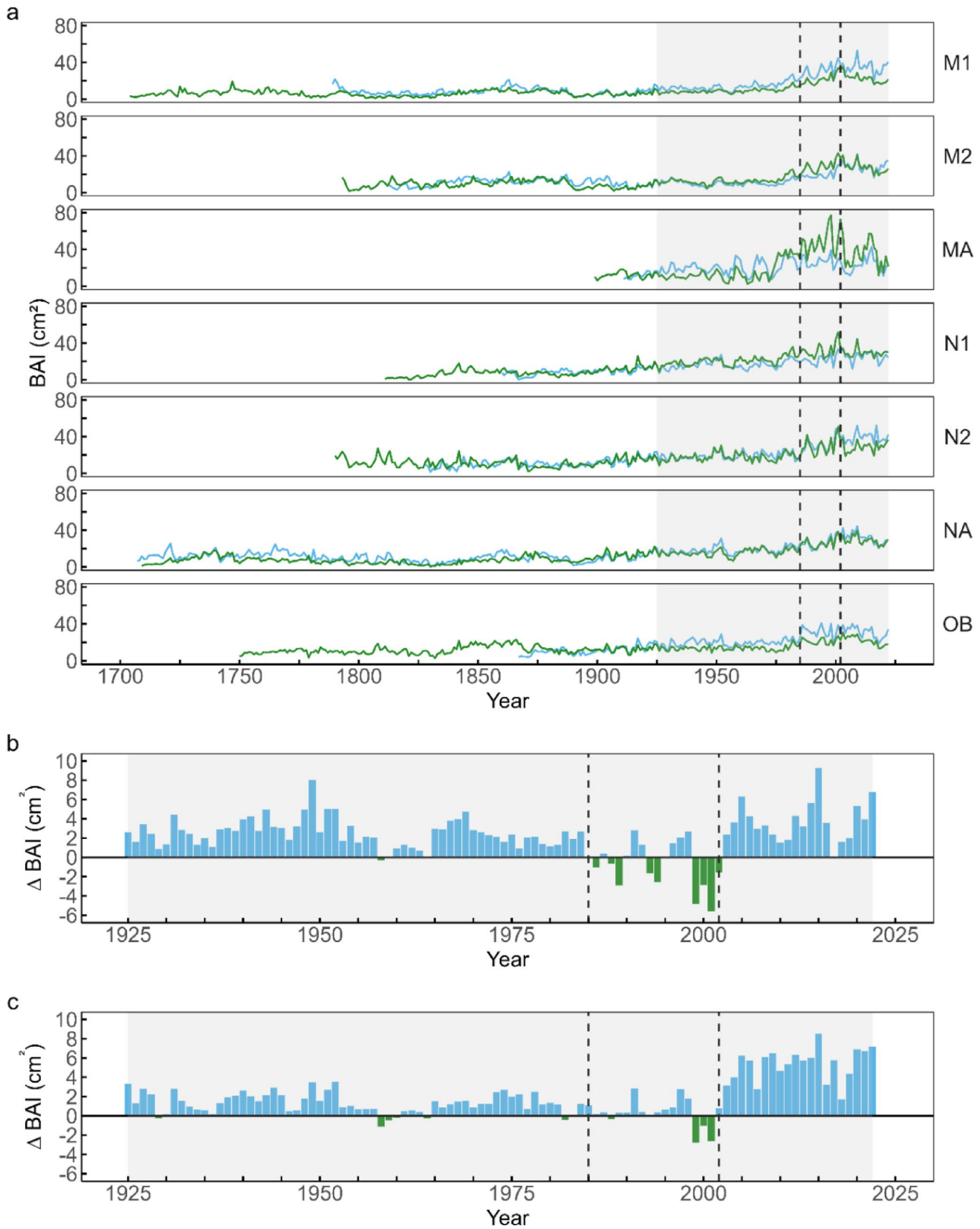

a
BAI (cm²)
M1
M2
MA
N1
N2
NA
OB
Year
b
Δ BAI (cm²)
Year
c
Δ BAI (cm²)
Year

Fig. 3 **a** Time series of basal area increments (BAI) in open (blue) and closed stands (green). Site codes: M1, M2, Mieders; MA, Matsch/Mazia; N1, N2, Neustift; NA, Navis; OB, Obernberg. **b** Yearly difference in BAI (ΔBAI) between open and closed stands for the period 1925–2022 (gray shading; sample depth ≥ 57). Positive values (blue bars) indicate higher growth in open stands, whereas negative values (green bars) indicate higher growth in closed stands. Grey dashed lines mark the period 1985–2002, when BAI in closed stands was considerably higher than in open stands. **c** Yearly difference in BAI (ΔBAI) for the same period as in (b), excluding the MA stands

variable was included as a robustness check, alongside site and land-use variables. Consequently, the first year of observations was excluded from the analysis. All covariates were z-standardized to avoid issues with excessively high eigenvalues. All significant two-way interactions were assessed post-hoc by analyzing simple effects, i.e., the effect of one factor at specific levels of the other. Random intercepts for site and individual trees were included to account for the nested structure of the data, where observations within the same site or tree are likely more similar than those from different sites or trees. Region was initially included as a random factor but removed in the final model due to negligible variance. The final model was selected based on the lowest Akaike Information Criterion (AIC) following the stepwise procedure (Akaike 1998). Model validation included checking for outliers, overdispersion, residual patterns, influential observations, and overall fit. The Intraclass Correlation Coefficient (ICC) was calculated to quantify the proportion of variance attributable to each random effect, and Likelihood Ratio Tests (LRTs) were performed to evaluate whether including random effects significantly improved model fit.

For the final model, we report: (i) R^2, degrees of freedom (*df*), and *p* values for tests of conditional and marginal model significance; (ii) log-likelihood, AIC, deviance, and residual *df*; (iii) the Chi-square/*df* ratio as an indicator of overdispersion; (iv) parameter estimates (standardized coefficients and odds ratios) for fixed and marginal effects. All GLMM analyses were conducted in Jamovi (The jamovi project 2024) using the *GAMLj3* package (Gallucci 2025). Additional details on model fitting are provided in the Supplementary Material (Fig. S2 and Tables S2–S4).

The following variables were included in the GLMM:

Site variables: *elevation* (m a.s.l.), *slope* (°), and *southerness* (°).

Land-use variables: *mowing/grazing* (true/false), *thinning* (true/false), and *afforestation* (true/false). Stand-specific land-use information was collected through personal communication with landowners (Table S1). Mowing/grazing and thinning were applied in open stands to maintain larch dominance and prevent natural succession toward denser larch–spruce stands. In closed stands, thinning was applied until land-use abandonment (1950–1980). Due to a high correlation between mowing/grazing and thinning ($r = 0.995$; $p = < 0.001$), only mowing/grazing was retained as a predictor in the final model. Two stands, MAC and N1C, were afforested in 1980. The afforestation variable was retained until 2022 to capture its ongoing effect on stand development and tree growth.

Stand variables: *stand basal area* ($m^2\ ha^{-1}$). Stand basal are (BA) was used to capture changes in tree density over time. In open, continuously managed stands, individual trees increased in diameter, but regular thinning likely compensated for increases in basal area, so it was assumed to remain constant. In abandoned, currently closed stands, BA prior to abandonment was assumed to be comparable to that of the corresponding open stand. Following abandonment or afforestation (1950–1980), BA increased due to progressive tree densification. To reconstruct stand-specific trajectories, the BA of the open stand at the year of abandonment and the measured BA in 2022 were used as boundary conditions, and BA was linearly interpolated between these years to represent gradual densification over time.

Climate variables: *previous year's October temperature*, *current year's summer temperature* (May-August), *current year's March precipitation*, and *current year's July precipitation.* These variables were selected based on significance in the static climate-growth analysis.

Growth disturbance variables: Mass outbreaks of the *larch budmoth* were included as growth-disturbance events (true/false). Outbreak years were identified based on growth reductions in measured tree-ring chronologies and corroborated with budmoth population data from the European Alps (Wermelinger et al. 2018). The years considered as outbreaks were: 1948/49, 1957/58, 1965/66, 1975/76, 1984/85, 1991/92, 1999/2000, 2006/07, and 2016/17.

Results

All statistics quantifying agreement in the year-to-year variation of ring-width series (i.e., inter-series correlation, expressed population signal, and signal-to-noise ratio) were high across all stands, regardless of stand density (Table 3). This indicates a homogeneous response of cambial activity to environmental drivers. Ring-width series also exhibited high autocorrelation, reflecting carryover effects of growth from the previous year.

Trends in basal area increment

Radial growth trends in both open and closed stands were similar until around 2000, with BAI increasing markedly between 1970 and 2000. From 2000 onwards, growth trajectories began to diverge: BAI declined in closed stands, whereas in open stands it showed only a slight decrease a few years later (Fig. 2).

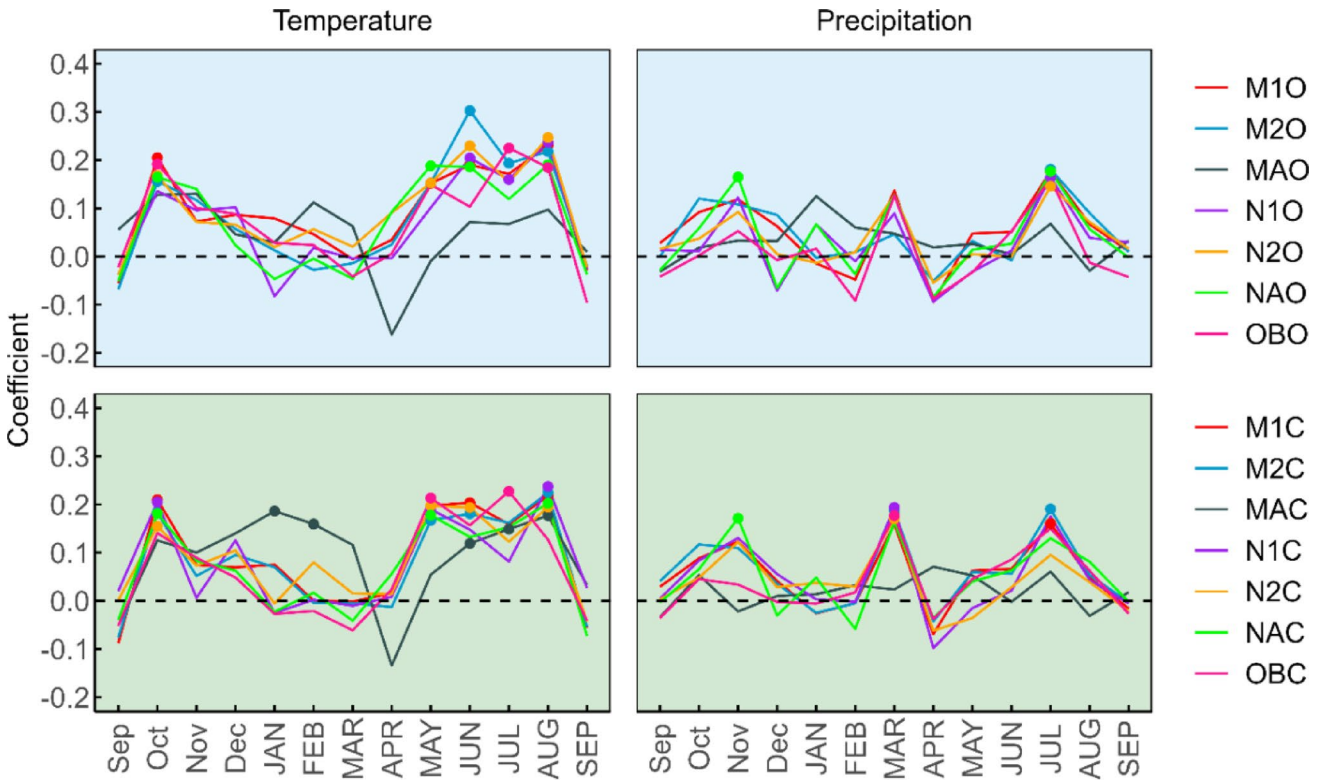


Fig. 4 Static monthly response function analysis of annual basal area increment (BAI) series for open (upper panels) and closed (lower panels) stands, showing correlations with monthly mean temperature (left panels) and monthly precipitation sum (right panels) for 1920–2022. Upper-case month abbreviations indicate current year climate variables, while lower-case abbreviations indicate previous year variables. Month abbreviations: Sep/SEP, September, Oct, October, Nov, November, Dec, December, JAN, January, FEB, February, MAR, March, APR, April, MAY, May, JUN, June, JUL, July, AUG, August. Filled circles denote significant relationships at $\alpha = 0.05$

Over the entire period from 1925 to 2022, BAI in open stands generally exceeded that in closed stands. Exceptions occurred in 1958 and between 1985 and 2002, when BAI in closed stands was higher than in open stands for several years (Fig. 3b). During this period, the MAC stand experienced an extraordinary growth spurt, with BAI peaking at approx. 80 cm^2 compared to approx. 30 cm^2 at the MAO stand. This extreme increase was followed by abrupt declines in 2004 and again in 2018 (Fig. 3a). Trees in the closed stands M2C and N1C also exhibited higher BAI than their corresponding open stands (M2O and N1O), although differences were less pronounced than at the MA stands (Fig. 3a). Excluding the MA stands reduced the overall difference in BAI between open and closed stands (Fig. 3c). Statistical tests comparing BAI between open and closed stands from 2000 to 2022 revealed regional variation between the South Tyrolean MA sites and the North Tyrolean sites. Considering all sites, no significant differences were detected, apart from 2022, when BAI differed at $\alpha = 0.1$ ($p = 0.088$). When the MA stands were excluded, significant differences emerged at $\alpha = 0.05$ for multiple years. From 2004 to 2022, the difference in BAI between open and closed stands approached statistical significance ($p = 0.052$, Fig. S3).

Response functions

Significant growth responses ($p < 0.05$) were observed in both open and closed stands for the following climate variables: previous year's October temperature, current year's summer temperature (May–August average), current year's March precipitation, and current year's July precipitation. In both stand types, radial growth was more strongly correlated with temperature than with precipitation, with maximum correlation coefficients of 0.30 for temperature and 0.19 for precipitation (Fig. 4). The moving response function analysis revealed an increasing positive influence of both summer temperature and precipitation over time. The effect of summer temperature became significantly positive from the 1950s onward, while March and July precipitation showed a trend toward positive coefficients (Fig. 5).

Drivers of tree growth

The final generalized linear mixed model included 12 predictor variables and three significant interactions and explained 70.3% of the variance in BAI (Table 4). Comparison of conditional and marginal models indicated that the

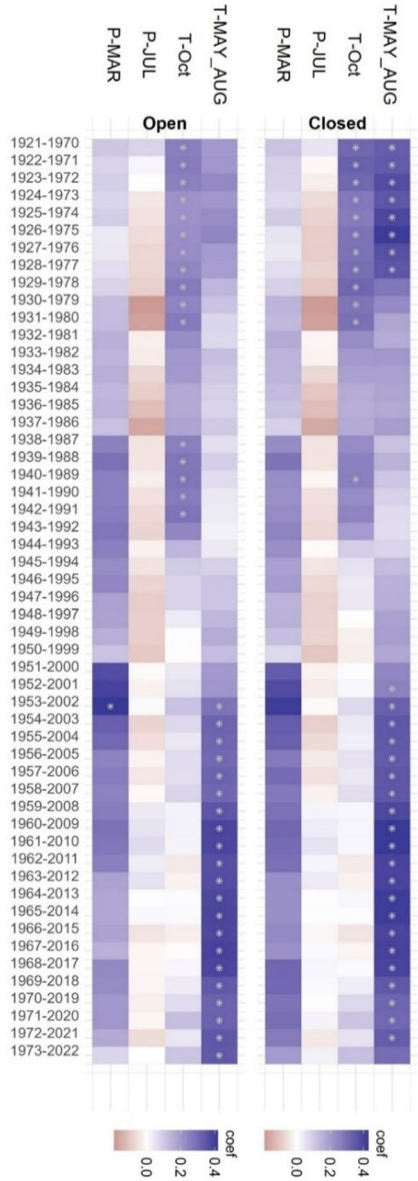


Fig. 5 Moving response function analysis (50-year window) of annual basal area increment (BAI) series for open (bottom) and closed (top) stands, showing correlations with the climatic variables that exhibited the strongest relationships in the static analysis for 1920–2022. T, temperature; P, precipitation. Upper-case month abbreviations indicate current year climate variables, while lower-case abbreviations indicate previous year variables. Month abbreviations: Sep/SEP, September; Oct, October; Nov, November; Dec, December; JAN, January; FEB, February; MAR, March; APR, April; MAY, May; JUN, June; JUL, July; AUG, August. Colors represent correlation coefficients, and significant correlations ($p < 0.05$) are marked with an asterisk

random effect of individual trees was significant (LRT) but accounted for only a small proportion of the total variance (ICC = 0.005). All predictors were significant ($p < 0.05$), except for mowing/grazing and afforestation. Previous year's BAI (β = 0.46) and current year's summer temperature (β = 0.11) exhibited the strongest positive effects on current BAI, followed by July precipitation (β = 0.06). Slope (β = 0.01), southerness (β = 0.03), and elevation (β = 0.06) also positively influenced radial growth. Among the remaining climate variables, previous year's October temperature (β = 0.06) and current year's March precipitation (β = 0.04) showed positive effects. In contrast, stand basal area (β = −0.04), mowing/grazing (β = −0.01), and larch budmoth (β = −0.04) negatively affected growth. After stepwise elimination of statistically non-significant interactions, three significant interaction effects were retained ($p_{\text{Bonferroni}} \leq 0.05$). The interaction between summer temperature and July precipitation positively affected BAI (β = 0.06), whereas the interactions between mowing/grazing and larch budmoth (β = −0.09), and between larch budmoth and afforestation (β = −0.11), negatively affected growth.

Discussion

We investigated changes in climate sensitivity and long-term growth trends of dominant larch trees in open and closed stands, focusing on how increasing competition following land-use changes, particularly stand abandonment, influenced growth. Sampling biases, however, are a well-known concern in dendrochronological studies (Cherubini et al. 1998). For instance, focusing exclusively on large-diameter trees – as in our study – may produce a spurious long-term positive growth trend if smaller individuals are excluded, a phenomenon referred to as the "big-tree selection bias" (Brienen et al. 2012). Moreover, faster-growing trees tend to be shorter-lived and are therefore often underrepresented in samples, resulting in a "slow-grower survivorship bias," which can likewise inflate apparent growth trends.

In our study, these potential biases are likely of limited concern. Mean DBH ranged consistently between 58 and 75 cm across stands, while tree ages varied substantially within both open and closed stands (Table 2), indicating that the sampled cohorts comprised both fast- and slow-growing individuals. In addition, the inclusion of a one-year time lag of BAI as an independent variable accounted for individual growth trajectories and was highly significant in the model. Taken together, the observed differences in long-term growth trends between open and closed stands are therefore more plausibly interpreted as a response to changes in competition following land-use change rather than as a direct climatic signal. If climate – particularly growing-season temperature – were the primary growth-limiting factor and competitive interactions were negligible, basal area increment would be expected to increase more uniformly across stands, irrespective of stand density, assuming constant climate sensitivity (see below).

Table 4 Results of the final generalized linear mixed model (GLMM) with basal area increment (BAI) of individual trees over the period 1920–2022 ($n = 11{,}651$) as the response variable

Predictor variable	Parameter estimates (Fixed coefficients)				Marginal effects	
	β	SE	Exp(B)	*p*	AME	*p*
Intercept	2.98223	0.01891	19.732	< 0.001		
Elevation	0.05925	0.00452	1.061	< 0.001	1.371	< 0.001
Slope	0.00751	0.00382	1.008	0.049	0.174	0.048
Southerness	0.02989	0.00384	1.03	< 0.001	0.691	< 0.001
Stand basal area	−0.04303	0.00464	0.958	< 0.001	−0.996	< 0.001
Summer temperature (curr)	0.11095	0.00439	1.117	< 0.001	2.507	< 0.001
October temperature (prev)	0.05602	0.00389	1.058	< 0.001	1.296	< 0.001
March precipitation (curr)	0.03861	0.00363	1.039	< 0.001	0.893	< 0.001
July precipitation (curr)	0.0635	0.00382	1.066	< 0.001	1.704	< 0.001
Time lag	0.45848	0.00439	1.582	< 0.001	10.607	< 0.001
Mowing/grazing	−0.00599	0.0127	0.994	0.637	−0.8	0.002
Larch budmoth	−0.04429	0.01621	0.957	0.006	0.132	0.54
Afforestation	0.02735	0.01883	1.028	0.146	1.459	< 0.001
Summer temperature (curr) × July precipitation	0.05976	0.00442	1.062	< 0.001		
Mowing/grazing × Larch budmoth	−0.08995	0.0212	1.094	< 0.001		
Larch budmoth × Afforestation	−0.10738	0.03514	0.898	0.002		

Model fit	R^2	*df*	*p*
Conditional	0.703	16.000	< 0.001
Marginal	0.702	15	< 0.001
LogLikelihood	−38648.478	ICC	0.00511
AIC	77332.957	LRT (*p*)	133 (< 0.001)
Deviance	77296.957	maxvif	2.070
Residual *DF*	11,633	meanvif	1.402
Chi-squared/*DF*	0.131		

Shown are the fixed effects and marginal effects, along with key model fit parameters. Predictors included climate, site, stand, land-use, and growth disturbance variables. curr, current year; prev, previous year; *p*, significance level; β, standardized coefficient; SE, standard error of β; Exp(B), odds ratio; AME, average marginal effects; AIC, akaike information criterion; ICC, intraclass correlation coefficient for a random effect; LRT, likelihood ratio test; maxvif, maximum variance inflation factor among predictors; meanvif, mean variance inflation factor among predictors

Climate-growth relationships

At the end of the 20th century (1977–2000), rapid warming significantly enhanced tree radial growth across many regions of the Northern Hemisphere (Liu et al. 2023). The Alps, in particular, experienced an exceptional temperature increase of approx. + 2 °C over the past century, more than double the average warming rate of the Northern Hemisphere (Schumacher et al. 2024). According to the IPCC (2023), global surface temperatures have risen faster since 1970 than during any other 50-year period in the past 2000 years, coinciding with significant increases in larch radial growth in both open and closed stands during the late 20th century (Fig. 2). Our results confirm that summer temperatures are the strongest driver of larch growth, as they promote cambial activity and wood formation (Büntgen et al. 2007; Rossi et al. 2007). In addition, a positive relationship between favorable conditions in the previous autumn and subsequent radial growth has been observed across the Alps (Obojes et al. 2024; Saulnier et al. 2019), likely due to an extended photosynthetic period that enhances carbohydrate storage for needle, shoot, and root development in the following growing season (Wieser et al. 2009). The higher sensitivity of larch to temperature compared to precipitation is consistent with previous studies on high-elevation trees in the Central Alps (Körner 2012; Büntgen et al. 2007; Oberhuber 2004).

However, the correlation coefficients between temperature and growth were lower than expected, suggesting that temperature exerts a less pronounced influence on larch growth in the subalpine zone (1600–1900 m a.s.l.) compared to the species' lower and upper distribution limits, as reported for the French Alps by Rozenberg et al. (2020). In mid-elevation stands, water availability currently constrains tree growth primarily during extreme years characterized by exceptionally warm and dry growing seasons. This is supported by the finding that July precipitation promotes BAI at some sites (Fig. 4). Our results contradict hypothesis H2: May-August temperature remains the dominant climatic driver of radial growth, although increasing stand density may have intensified competition for limited resources in closed stands (see below). Thus, within the study area, an

increase in stand density does not appear to alter the temperature sensitivity of larch radial growth.

On the other hand, changing moisture conditions are expected to play an increasingly critical role in shaping future larch growth responses. Both static (Fig. 4) and moving response function analyses (Fig. 5) of closed stands suggest that, as stand density increases, March precipitation may become progressively more important over time. In particular, the rising atmospheric moisture demand, i.e., vapor pressure deficit (VPD), under continued warming has been identified as a growing constraint on tree growth (Babst et al. 2019; Breshears et al. 2013). Trotsiuk et al. (2021) reported that European larch is increasingly limited by VPD during longer, warmer, and drier summers at elevations above 1200 m a.s.l. In the inner-alpine, dry Matschertal, extreme drought years have already caused pronounced growth reductions, highlighting the rising impact of drought stress, particularly in dense stands (Obojes et al. 2018).

Topographic effects on growth

At high-elevation treelines, cambial activity in coniferous species is primarily triggered when air temperatures exceed a threshold of approx. 5 °C (Rossi et al. 2007). The positive relationship between elevation and growth observed in our study suggests that rising air temperatures have enhanced radial growth at higher elevations by reducing temperature limitations on cambial activity and extending the growing season (Camarero et al. 2021). The observed positive effect of southerness on larch growth can be attributed to higher solar radiation on south-facing slopes, which increases soil temperatures and promotes earlier onset of cambial activity. Sanmiguel-Vallelado et al. (2021) showed for Mountain pine (*Pinus uncinata*) that higher soil temperatures (≥10 °C) during the early growing season in June stimulate fine root activity and initiate cambial activity, thereby supporting radial growth.

Growth disturbance effects

The synchrony between bud break and the hatching of larch budmoth larvae is optimal at elevations of 1700 to 2000 m a.s.l., resulting in the most pronounced outbreaks in subalpine forests. (Wermelinger et al. 2018), a pattern also observed in the larches studied here. While older literature described the larch budmoth as the most dangerous pest of larch forests (Coaz 1894), recent studies from the Upper Engadine in Switzerland indicate that although defoliation weakens trees, fewer than 1% of larch individuals typically die during an outbreak, and overall growth loss is minimal (Baltensweiler and Rubli 1984). Consistent with these findings, our GLMM results show that the larch budmoth had a small negative effect on individual radial growth ($\beta = -0.0443$, Exp(B)=0.957, $p<0.01$), but the average marginal effect across the population was not significant (AME=0.132, $p=0.54$). This indicates that while individual trees may experience reduced growth during outbreaks, the overall impact on stand-level radial growth is minor.

Land-use effects on growth

For centuries, larch grasslands have been maintained through traditional land-use practices such as hay mowing and livestock grazing (Fontana et al. 2014; Schulze et al. 2007). Grazing returns approx. 50–70% of ingested biomass to the soil via nutrient-rich excreta (Gilmullina et al. 2020), whereas mowing typically leaves only about 20% of the harvested biomass as green litter due to collection losses (Sanaullah et al. 2010). Consequently, biomass removal through mowing and grazing leads to continuous nutrient export, gradually reducing soil fertility and ultimately constraining tree growth (Ciais et al. 2008; Prietzel et al. 2015).

In addition to hay production and grazing, larch grasslands have historically been used for timber harvesting (Fontana et al. 2014; Schulze et al. 2007). Thinning, defined as the selective removal of trees, plays a key role in maintaining the open structure of these landscapes by reducing stand density, preserving a sparse overstory, and promoting the development of forage-rich ground vegetation (Garbarino et al. 2011). Previous studies have shown that thinning can substantially enhance tree growth and vitality by alleviating competition and increasing the availability of light, nutrients, and water (Pothier 2002; Simard et al. 2004). Accordingly, the negative effect of stand basal area ($p<0.001$) on BAI indicates that open stands benefit from improved resource availability, supporting our hypothesis (H1). The role of increasing stand density as a driver of growth decline aligns with the findings of Ara et al. (2023), who reported decreasing tree growth with increasing time since thinning, particularly beyond 25 years. The particularly strong growth response observed at the driest site in the Matschertal suggests greater soil water availability in managed open stands, consistent with findings from a dry inner-alpine valley in Switzerland (Giuggiola et al. 2016). When accounting for mowing/grazing and afforestation, the observed decrease in BAI after 2000 can be explained: in thinned, continuously managed stands, mowing or grazing reduces BAI over the long term by removing nutrients, whereas afforestation initially increases BAI, likely because the cessation of land use retains nutrients until competition intensifies and BAI subsequently declines more sharply. When combined with larch budmoth occurrence, these variables have amplified effects on BAI, which is to be expected.

As an alternative or complementary explanation, the diminishing growth-enhancing effect of rising temperatures in both stand types after 2000 may indicate that optimal temperatures for radial growth have been reached or surpassed (cf. D'Arrigo et al. 2004). This interpretation is supported by the significant positive interaction between summer temperature and July precipitation in the GLMM ($\beta = 0.0598$, $p < 0.001$), indicating that the positive effect of warm summers on growth depended on sufficient moisture availability. Accordingly, growth was reduced in particularly hot and dry years, suggesting that drought stress moderated or even offset the warming-induced growth response. In line with these findings, Obojes et al. (2018) reported a comparable decline in BAI in larch stands within an inner-Alpine dry valley up to 1700 m a.s.l., whereas a continuously increasing BAI – reflecting a positive temperature response – was observed only at 2200 m a.s.l. In their study, larch growth remained precipitation-limited up to elevations exceeding 1700 m a.s.l., which corroborates our results, given that the mean elevation of our study stands was 1723 ± 64 m a.s.l.

Conclusions

The divergence problem (DP) describes a decline in climate sensitivity or an increasing mismatch between trends in climate warming and stem growth (D'Arrigo et al. 2008). In examining whether competition, expressed as stand density, modulates the climate sensitivity of larch growth, we found that growing-season temperature has remained the dominant climatic driver of larch stem growth in recent decades, irrespective of temporal changes in stand density resulting from land-use change (managed vs. abandoned larch grasslands). However, in recent decades, BAI has decoupled from the temperature trend in both managed and abandoned stands, indicating broader environmental control on tree growth, most likely due to increasing water limitation. The stronger BAI decline in closed, densifying stands compared to open stands supports this interpretation and highlights the amplifying role of competition under increasingly water-limited conditions. Continued warming is expected to raise atmospheric water demand, further constraining tree growth (cf. Babst et al. 2019; Trotsiuk et al. 2021), implying additional growth limitations for larch in the study area. Our results demonstrate that adaptive management practices, such as thinning, can mitigate the negative effects of stand densification on larch growth. Future research should therefore focus on how stand structure interacts with microclimatic and environmental conditions, both above and below ground, to improve our understanding of management options for sustaining tree growth under ongoing climate change.

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Data availability Data are available on reasonable request to the corresponding author.

Code availability Not applicable.

Declarations

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

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