



Temperature-induced germination pulses above the alpine tree line

Audrey Palosse^a, Alma Piermattei^{b,c}, Jan Esper^{d,e}, Frederick Reinig^d, Anne Verstege^f, Max Torbenson^d, Mirek Trnka^{e,g}, Tito Arosio^a, and Ulf Büntgen^{a,e,h}

^aDepartment of Geography, University of Cambridge, Cambridge, UK; ^bDepartment of Agricultural Forest and Food Sciences, University of Torino, Torino, Italy; ^cForest Biometrics Laboratory, Faculty of Forestry, Stefan Cel Mare University of Suceava, Suceava, Romania; ^dDepartment of Geography, Johannes Gutenberg University, Mainz, Germany; ^eGlobal Change Research Institute of the Czech Academy of Sciences, Brno, Czech Republic; ^fSwiss Federal Research Institute (WSL), Birmensdorf, Switzerland; ^gInstitute of Agroecosystems and Bioclimatology, Faculty of Agronomy, Mendel University, Brno, Czech Republic; ^hDepartment of Geography, Faculty of Science, Masaryk University, Brno, Czech Republic

ABSTRACT

Subject to a long research tradition, the tree line is considered an important biogeographic indicator of climate changes and associated range shifts. Realized tree line positions and the potential tree line isotherm are, however, rarely in equilibrium because trees are unable to track rapid temperature variations. Often ignored in tree line research, this dilemma constrains the suitability of tree line trees for understanding alpine vegetation responses to anthropogenic warming. Here, we present combined dendrochronological and wood anatomical assessments of 1,351 seedlings and saplings from three subalpine forest species—larch (*Larix decidua* Mill.), pine (*Pinus cembra* L.), and spruce (*Picea abies*)—collected between ~2,200 and 2,600 m.a.s.l. in the Swiss Alps. We found evidence for temperature-induced, pulse-like seedling germination, rather than a continuous, long-term upward movement. Though the species spread across overlapping elevational ranges, larch was found at the highest elevations, followed by spruce and pine. Surprisingly, we found a varying age structure, with no sign of decreasing age toward higher elevations. Spring and summer temperatures promoted germination pulses, but postgermination survival was likely facilitated by species-specific plant traits. Our study demonstrates the importance of seedling and sapling data from above the tree line to understand prevailing vegetation dynamics at cold temperature extremes and also suggests future tree line advancement in the Swiss Alps.

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Introduction

Tree line ecotones are distinct biogeographic phenomena at high elevations and latitudes around the world (Troll et al. 1973; Zhao et al. 2015; Körner 2021). Global tree line positions follow a common isotherm (von Humboldt and Bonpland 1807; Körner 1998, 2021), which approximates the temperature threshold for upright tree growth (Körner 1998, 2007, 2021). One theory to explain this cold range limit is the carbon sink limitation hypothesis (McNown and Sullivan 2013), which states that reduced cambial cell division caused by low temperatures prevents the investment of carbon in growth (Hoch and Körner 2011; Lenz et al. 2013; Cabon et al. 2020). Conversely, the source limitation hypothesis implies that tree growth above the tree line is restricted by limited carbon fixation (Sveinbjörnsson 2000; Sullivan and Sveinbjörnsson

2011), which may result from reduced stomatal gas exchange (Goldstein, Brubaker, and Hinckley 1985) due to low soil temperatures and constrained nutrient availability (Li et al. 2008; Richardson and Friedland 2009; McNown and Sullivan 2013). The loss or partial damage of cell tissue due to freezing stress may also play a role at the tree line (Hadley and Smith 1986), and recent studies further suggested that the lignification of secondary cell walls in woody plants can be limited by cold temperatures (Crivellaro and Büntgen 2020; Crivellaro et al. 2022).

As global temperatures have increased by ~1°C during the twentieth century (Intergovernmental Panel on Climate Change 2021), the tree line isotherm—that is, the thermal limit for upright tree growth—is shifting upward and poleward (Büntgen et al. 2022). The position of the isotherm under rapid

CONTACT Audrey Palosse  alp84@cam.ac.uk; Ulf Büntgen  ub223@cam.ac.uk  Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK.

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warming represents the “potential” tree line, which trees may eventually reach after adjustment of the realized tree line to warmer conditions (Körner 2021). However, trees are sessile and thus unable to track changes in the elevational and latitudinal position of the tree line isotherm. The realized and potential tree lines are therefore rarely, if ever, in equilibrium (Büntgen et al. 2022), and a difference of around 300 m between the lower realized and higher potential tree line positions has been reported under anthropogenic global warming (Büntgen et al. 2022). Yet, many studies overlook this apparent lag and consider climatic response of the realized tree line to predict future movements (Holtmeier and Broll 2005; Kullman and Kjällgren 2008; Harsch and Bader 2011; Schickhoff et al. 2015; Vitali et al. 2018; Chhetri and Thai 2019; Mienna et al. 2020; Hansson, Dargusch, and Shulmeister 2021; Chen et al. 2022; Dandan, Deshuai, and Jianqin 2022).

To overcome this, it could be argued that research efforts should focus on monitoring vegetation above the tree line, where the impacts of warming on young trees, which ultimately will constitute the future tree line, may be better understood. For instance, the distribution of seedlings and saplings of alpine and boreal forest trees at their elevational and latitudinal margins has been investigated (Germino, Smith, and Resor 2002; Mamet and Kershaw 2013; Piermattei, Garbarino, and Urbinati 2014; Bognounou et al. 2018; Frei et al. 2018). Additionally, recruitment patterns of arctic and alpine tree line species have been linked to increasing temperatures (Esper and Schweingruber 2004; Hofgaard, Dalen, and Hytteborn 2009; Piermattei, Renzaglia, and Urbinati 2012; Büntgen et al. 2015, 2018; Lu et al. 2016; Vitali et al. 2019; Malfasi and Cannone 2020; Dolezal et al. 2021). However, many of these studies are limited by their small sample size and a lack of wood anatomical and dendrochronological measurements. The latter caveat prevents the accurate assessment of variables such as root length, bark thickness, xylem diameter, and even plant age. Such data, however, are likely to hold valuable information for untangling the impact of climate on alpine vegetation.

Here, we combine dendrochronological and wood anatomical techniques and present a unique data set of 1,341 excavated seedlings and saplings above the realized upper tree line in the Swiss Alps. We aim to utilize dendrochronological and wood anatomical measurements to assess the recruitment patterns and growth of three species and discuss our findings with respect to species-specific germination strategies, potential survival strategies, and future tree line dynamics.

Materials and methods

Sampling took place in the Lötschental Valley in the Swiss canton Valais (Büntgen 2006; Moser et al. 2010). This inner-alpine valley is surrounded by several summits exceeding 3,500 m.a.s.l., and the upper tree line is located at approximately 2,100 to 2,300 m.a.s.l. Mean annual temperature is 2.5°C at the tree line and 5°C at the valley bottom, and mean annual precipitation exceeds 800 mm (Cabon et al. 2020). Our study sites were located above the villages of Kippel and Wiler on a north-facing slope between 2,200 and 2,600 m.a.s.l. (46.371–46.386° E and 7.772–7.795° N). This slope aspect was chosen as south-facing slopes in the region are extensively used for alpine pasturing and we aimed to avoid disturbance caused by grazing. We sampled in late September toward the end of the growing seasons of 2017 and 2018. The lower elevation limit of our sampling gradient was constrained by the local timberline (i.e., the upper limit of continuous, closed forests), whereas the upper limit was defined by the highest seedling. All larch, pine, and spruce seedlings (<10 cm aboveground height) and saplings (10–40 cm aboveground height) along the transect were excavated, Global Positioning System coordinates recorded, and the complete above- and belowground plant fractions labeled and archived in plastic bags. A total of 1,351 samples were collected during all field campaigns.

The total above- and belowground stem and root lengths were recorded using a measuring tape, and root collar diameters were measured with digital calipers at 0.1-mm precision. Samples were split at the root collar using a benchtop bandsaw and stem sections were soaked in warm water for softening. A WSL-lab microtome was used to slice thin sections of 20 to 40 µm (three to four for each sample), which were placed on microscope slides with a drop of glycerin and a glass cover (Gärtner et al. 2015). Bark thickness and xylem diameter of each cross section were measured at 0.1-mm precision under a light microscope with 10× magnification. Annual growth rings were microscopically counted to determine the cambial age and germination year of each sample. Species-specific variations in morphological and anatomical plant traits (i.e., stem and root length, root collar diameter, bark thickness, and xylem diameter), as well as age/germination patterns, were evaluated using descriptive statistics. Simple linear regression models were fitted in RStudio v1.2.5033 (2019) to investigate relationships between each measured plant trait and elevation for

individual and combined species. Assumptions of each model were checked using scatterplots (linearity), residuals versus fit plots (independence of errors and equal variances), and histograms of both standardized and regular residuals (normality of errors).

Homogenized, high-resolution, $0.25^\circ \times 0.25^\circ$, monthly minimum, mean, and maximum temperatures from 1971 to 2017 were extracted from the E-OBS v23.1e data set (Cornes et al. 2018). Spring (March–May; MAM), summer (June–August; JJA), growing season (AMJJAS), autumn (September–November; SON), and winter (December–February; DJF) averages were calculated from the monthly data to account for inter-seasonal temperature effects on plant germination (Renard, McIntire, and Fajardo 2015; Bader et al. 2017). April to September (AMJJAS) temperature averages were considered to explore the impacts of warming over the tentative growing season.

Germination frequency and seasonal temperature data were tested for normality using Shapiro-Wilk tests. If both of the variables to be correlated with each other were normally distributed ($p < .05$), a Pearson's correlation test was used. If one or both variables were not normally distributed, a Spearman's correlation test was used instead. Correlations between germination frequency and temperature were calculated over the entire temporal extent of the combined data set (1971–2017), as well as over shorter species-specific windows. Years where no germination occurred were excluded automatically. The same climate response analysis was repeated for precipitation totals (E-OBS v23.1e; Cornes et al. 2018).

Results

Species Composition and Age Distribution

The dominant species in our study was pine (649 samples), followed by larch (500 samples) and spruce (202 samples). The three species spread across overlapping elevational ranges but were concentrated at different elevations (Figure 1, Figure 2). Larch showed the largest elevational distribution from 2,263 to 2,599 m.a.s.l., followed by spruce from 2,356 to 2,560 m.a.s.l. and pine from 2,216 to 2,520 m.a.s.l. Plant ages differed systematically among species and with elevation (Figure 2). Most samples were between three and eighteen years (i.e., germination years from 2000 to 2015), with the oldest sample being a forty-eight-year-old larch sapling. Spruce samples were on average older (fourteen years) than larch (eleven years) and pine (eight years). We found a positive relationship between age and elevation (Figure 2). Though this relationship did not explain much variance ($R^2 = 0.0\text{--}0.15$), it was significant for larch, pine, and the combined samples ($p < .05$).

Germination Frequency and Climate Variability

Germination frequency followed a bell shape, reaching its highest point in 2011 when a total of 240 samples germinated in one summer (Figure 3A). In this year, the largest number of pine samples germinated ($n = 174$). The germination peaks of larch and spruce were found in 2010 ($n = 59$) and 2008 ($n = 21$), respectively. Germination–climate correlations were significant for

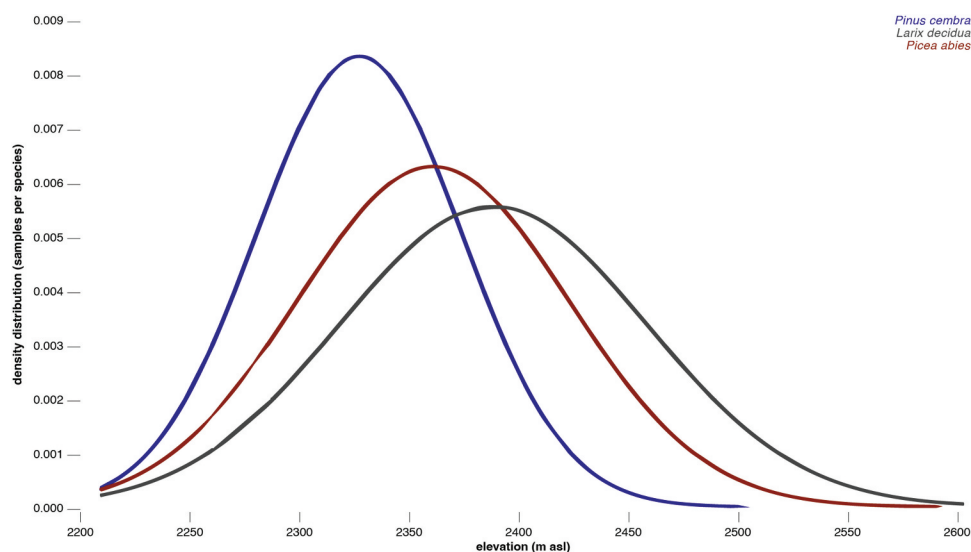


Figure 1. Distribution curves displaying species-specific elevational ranges, with colors representing the different species: pine (blue), larch (gray), and spruce (red).

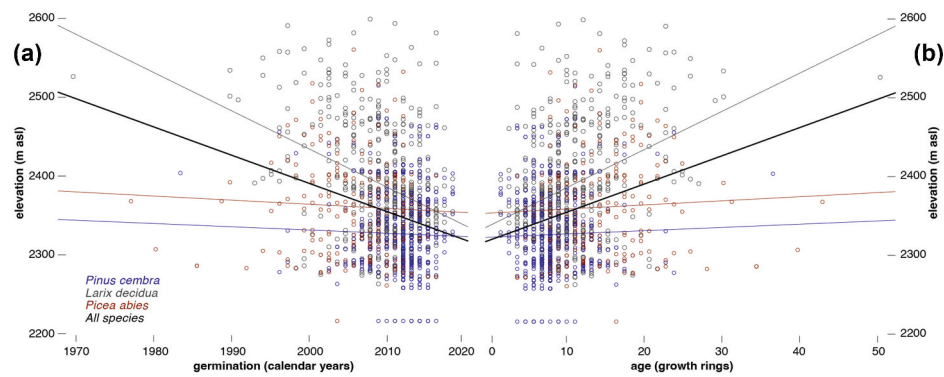


Figure 2. Regression analyses between elevation and germination/age. Color coding is representative of the three different species, and black displays the trend for all species combined. (a) Species-specific and overall sample linear relationships between elevation and sample germination. (b) Species-specific and overall sample linear relationships between elevation and sample age.

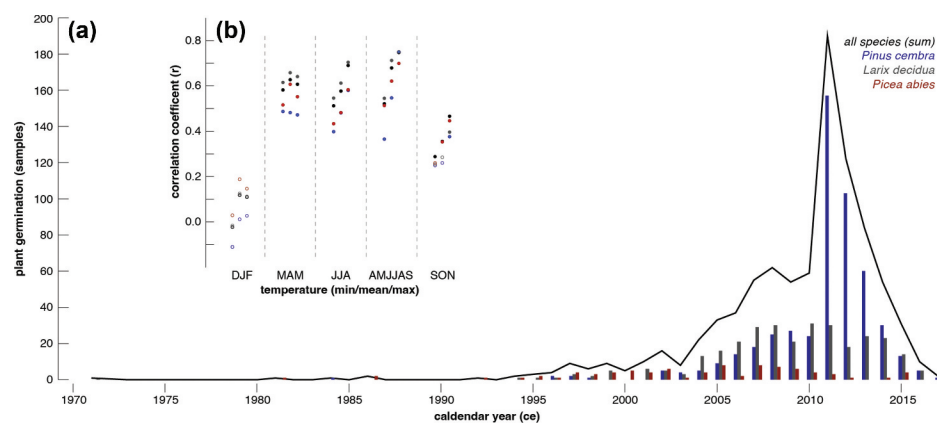


Figure 3. Species-specific differences in germination timings and the relationship between germination and average seasonal land surface temperature, with colors representing the different species and black representing germination frequency for the three species combined. (a) Graph depicting germination timings between 1970 and 2017 and peaks for the three studied species as well as general germination trends for all species combined. (b) Plot displaying correlation results for germination–temperature correlations. The x-axis displays seasonal averages from winter (SON), spring (MAM), summer (JJA), growing season (AMJJAS), and autumn (SON) for the year of germination. Points are displayed for each seasonal average from left to right for maximum, mean, and minimum seasonal temperature in this respective order.

all species with spring, summer, and growing season minimum, mean, and maximum temperatures ($p < .05$; Figure 3B). Strongest correlations were recorded for larch ($r = 0.55$ – 0.75), followed by spruce ($r = 0.43$ – 0.70) and pine ($r = 0.40$ – 0.56). Pine correlated strongest with growing season minimum temperatures, though ($r = 0.75$). Correlations with autumn temperatures were weaker overall ($r = 0.25$ – 0.45) and significant across all species only for minimum temperatures ($p < .05$).

Plant Trait Characteristics

The longest sample was an 88-cm larch sapling (total plant length). Larch represented the longest samples on average ($X = 25.4$ cm), followed by pine (23.1 cm) and spruce (22.1 cm). Interestingly, the belowground lengths, ranging from 11.3 to 13.3 cm among species,

exceeded the aboveground values, which range from 9.9 to 12.3 cm (Figure 4A). Overall, larch samples were wider (Figure 4B), with root collar diameter values averaging 7.0 mm (5.2 mm for spruce and 4.0 mm for pine). Moreover, larch samples had thicker bark ($X = 1.5$ mm, compared to 0.95 mm for spruce and 0.92 mm for pine) and wider xylems ($X = 5.7$ mm) than spruce ($X = 4.31$ mm) and pine ($X = 3.39$ mm). We found a negative relationship between aboveground length and elevation (Figure 5A), significant for spruce ($p < .001$), pine ($p < .001$), and all species combined ($p < .05$). An inverse relationship was observed between elevation and belowground length (Figure 5B), strongest for all species, followed by larch, pine, and spruce (all $ps < .001$). In addition, xylem diameter increased with elevation (Figure 5C), with the same pattern of decreasing strength according to species as for belowground

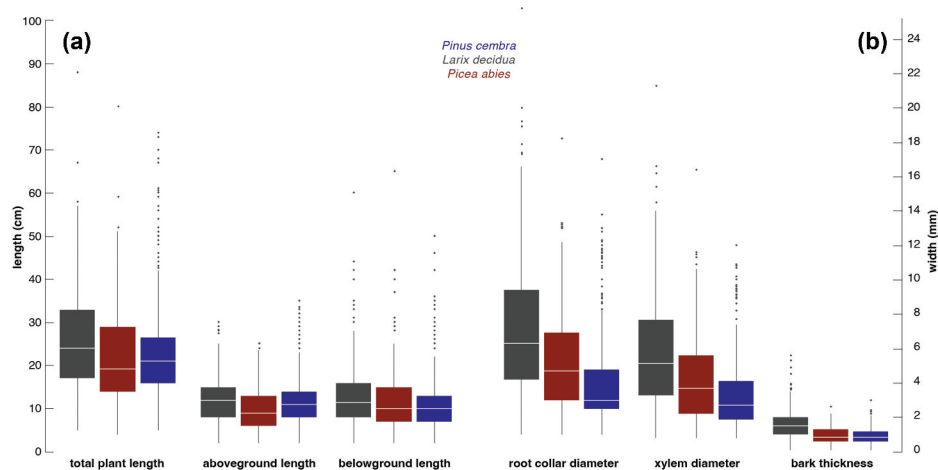


Figure 4. Box plots displaying species-specific measurements of anatomical and morphological traits, with colors representing the different species. (a) Variations in measurements for total, aboveground, and belowground plant length. (b) Variations measurements for root collar diameter, xylem diameter, and bark thickness width. See Figure 5 for linear trends and relationships between plant traits and elevation.

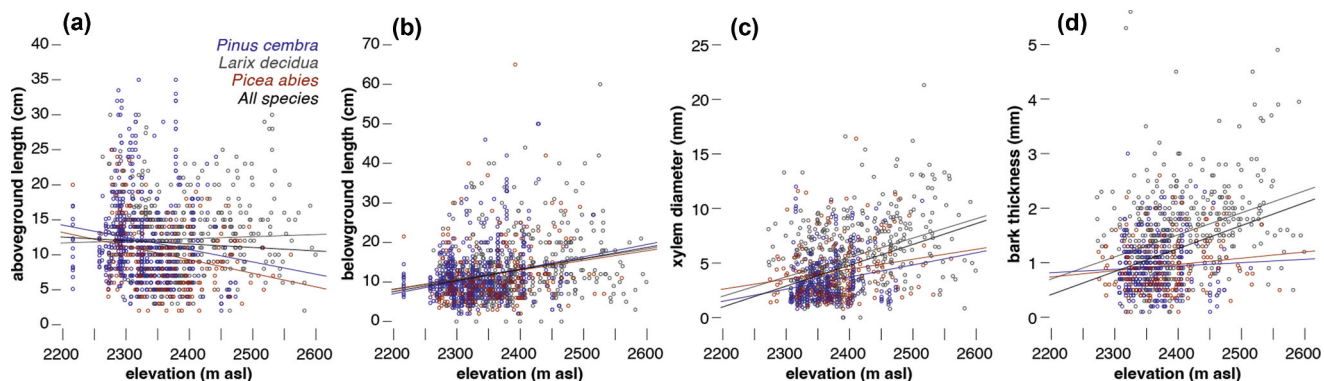


Figure 5. Regression analyses between elevations and various of the measured anatomical and morphological traits. Color coding is representative of the three different species, and black displays the trend for all species combined. (a) Species-specific and overall sample linear relationships between elevation and sample total plant length. (b) Species-specific and overall sample linear relationships between elevation and aboveground length. (c) Species-specific and overall sample linear relationships between elevation and xylem diameter. (d) Species-specific and overall sample linear relationships between elevation and bark thickness.

length. The relationship between bark thickness and elevation was positive (Figure 5D) but only significant for larch and all species combined ($p < .001$). Positive relationships were also observed between elevation and root collar diameter, as well as total stem length (not shown).

Discussion and conclusions

Our results indicated that there is a varying species composition along the elevational transect (Figure 1). Though regression analyses showed that age increases with elevation (Figure 2), except for spruce, where the relationship is nonsignificant ($p = .190$), the low R^2 values observed are also a testament to the variability

present in the age data. The latter contradicts the expected gradual decrease in tree age above the tree line associated with seedling recruitment reported in previous research (Leonelli et al. 2010; Shrestha, Hofgaard, and Vandvik 2014; Gatti et al. 2019) and implies that recruitment is active across the entire ecotone above the tree line (Piermattei, Renzaglia, and Urbinati 2012). In the following we propose potential explanations for the observed age distribution and its link to species composition by outlining factors influencing different stages of seedling recruitment including dispersal, germination, survival, and growth.

Firstly, spruce and larch seed dispersal is exclusively carried out by wind (Mosca et al. 2018), whereas dispersal of pine seeds is connected to *Nucifraga*

caryocatactes, commonly known as the European nutcracker bird (Neuschulz et al. 2017). At high elevations, low vegetation and protection from tall trees reduce habitat viability, so pine seeds may be consumed and dispersed within the bird's habitat range near the tree line edge. In comparison, wind dispersal may reach higher elevations given the high wind velocities associated with lack of forest cover above the tree line (Kašpar, Hošek, and Trembl 2017; André, Lavergne, and Carcaillet 2023). This could explain the concentration of pine seedlings, both old and young, on the lower band of the ecotone and the wider and overlapping elevational ranges of spruce and larch samples higher on the transect.

Our results on germination–climate correlations indicate that warm temperatures support germination “pulses” of seeds that successfully disperse and survive pregermination (e.g., predation and freeze damage). We found a germination peak in 2011, which was a particularly warm year and observe positive correlations between germination frequency and temperature during spring, summer, and growing seasons (Figure 3). This interpretation is further supported by a lack of significant correlations between germination frequency and winter temperatures and in line with previous work (Körner and Paulsen 2004; Mamet and Kershaw 2013; Lett and Dorrepaal 2018), which suggests that warm soil temperatures catalyze the enzymatic reactions necessary for embryo growth, thereby enabling germination to occur (Ali and Elozeiri 2017).

The positive relationship between temperature and germination frequency could also be due to microsite interactions between warmth and water availability. Water is necessary for germination, because it nourishes the seed embryo by carrying soil nutrients and softens the seed shell to allow this embryo to burst (Han and Yang 2015). Increasing temperatures trigger snowmelt, providing higher levels of soil moisture through infiltration (Germino, Smith, and Resor 2002), and prevent ground frost from accumulating and preventing water movement through frozen soil (Luo et al. 2019). Though snow data were not included in our analysis, Buchmann et al. (2023) discussed the possibility of homogenizing existing Swiss snow depth data, which could possibly be incorporated in future research aiming to understand the interactions between snow cover and germination.

In cases where temperature negatively impacts soil moisture—for instance, through increased evaporation—excessively high temperatures can be detrimental to germination (Guo, Shen, and Shi 2020; Ramírez et al. 2022). This is because once optimum soil temperature is reached, enzymatic activity will decrease, and seeds may

die under excessive thermal stress (Wieser, Oberhuber, and Gruber 2019; Bailey, Elliott, and Schliep 2021). This could explain why spring, rather than summer, correlated strongest with germination.

There is some indication of species-specific germination responses to climate. For instance, pine samples were found at lower elevations and thus may be less impacted by temperature, because the effects of climate on vegetation species are most pronounced near climatic thresholds, at higher elevations (Yu et al. 2011). This theory may clarify why pine climate–germination correlations are weaker than those for larch and spruce. We also see that germination of all species, individual and combined, is correlated to autumn minimum temperatures, but only spruce is impacted by mean and maximum temperatures (Figure 3). This could indicate a lower temperature threshold for germination onset in this species, but no evidence exists to support this theory, and our results may rather reflect data set limitations. To confirm species-specific germination responses, finer scale local climate data should be used in the future. Nevertheless, our findings imply that increasing global temperatures leading these germination pulses above the tree line will promote tree line advancement, given that specimens survive postgermination, as described in the following.

The survival of specimens in extremely cold climates, as prevalent above the Lötschental tree line, depends on species-specific morphological and anatomical traits allowing samples to thrive at different elevations. Larch reached the highest elevations and was the only species present above 2,560 m.a.s.l. (Figure 1). A potential explanation could be the thicker bark of larch ($X = 1.5$ mm) compared to spruce and pine (Figure 4), providing increased thermal protection of the cambium cell layer to prevent frost damage and disruption of cellulose and lignin (Pausas 2014). This theory is supported by the fact that larch is the only species in which bark thickness significantly increased with elevation ($p < .001$). Another hypothesis is that the longer roots of larch samples could facilitate root water uptake at higher elevations. Gharun et al. (2020) demonstrated that soil water content decreases with elevation in the Swiss Alps, because the ground is frozen for long periods due to the cold climate. Soil ice formation prevents root water uptake, combined with strong winds, which contribute to evaporation, resulting in “frost drought” (Pellet and Hauck 2017). Thus, facilitating moisture access through long root systems would increase this species' chance of survival (Badalotti, Anfodillo, and Grace 2000). Enhanced root water uptake in larch compared to other species may also result from its wider xylem as well because the strongest relationship between xylem diameter and

elevation (Figure 5). Larger xylem cells (which are associated with larger xylem size) allow for more hydrophobic surface area and more structural strength to facilitate water transport enhancing water uptake from low-moisture soils (Pereyra et al. 2012). Moreover, during frost drought, the risk of xylem embolism is high and thus having a larger xylem reduces the risk of all xylem cells losing their conductivity (Hacke et al. 2006).

Interestingly, aboveground length was the only variable which decreased with elevation (Figure 5). The observed increase in root collar diameter and length with elevation, among other variables, demonstrates that cold temperatures are not limiting growth at higher elevations but that instead the plant is not investing in growing upright. The survival of shorter plants at high elevations may be facilitated by their proximity to the ground, protecting them from aerodynamics which impose extremely cold air temperatures on tall trees (Scherrer and Körner 2010; Körner 2021). This phenomenon would indicate no carbon limitation at high elevations but support the carbon sink hypothesis and in fact suggests that by engineering a warmer microclimate, seedlings and saplings will continue to grow at such elevations. Because plant height is commonly associated with age, it would be trivial to assume that short saplings at high elevations are younger, supporting the common theory that age progressively decreases with elevation. Our findings therefore highlight the importance of collecting comprehensive data sets encompassing a wide array of variables. We encourage similar research including as many anatomical and morphological plant traits as possible.

We conclude that recruitment patterns above the Lötschental tree line are driven by (1) warm spring and summer temperatures driving germination pulses and (2) plant-specific anatomical and morphological adaptations supporting survival and growth postgermination. Warming temperatures will facilitate seedling recruitment and lead to an upward tree line shift in the Alps. However, this conclusion is limited by the many interacting factors that influence recruitment above the tree line. An example was previously given regarding the interplay between reduced soil water and nutrients at high elevations, which may be either positively or negatively impacted by temperature. Should the latter be true, the reduction in available resources may enhance interspecies competition, highlighting the importance for adaptive morphological traits such as long roots and wider xylems to increase survival chances (Badalotti, Anfodillo, and Grace 2000; Pereyra et al. 2012). The impact of climate variables, such as temperature and precipitation, with the moisture and nutrient availability in the seedbed may also differ based on

substrata and soil type and thus impact germination timings of various species and at different locations (Johnson and Yeakley 2016). Another example is the impact of topography, which may mask the effects of warming by enhancing wind velocity, promoting cold air, and restricting the amount of solar radiation (Corripio 2003; Holtmeier and Broll 2010). Solar radiation is also determined by slope aspect, with south-facing slopes receiving less incoming radiation, potentially increasing the effects of warming (Zheng et al. 2021). The impact of natural disturbances, such as avalanches, landslides, and fires, may restrict advancement (Holtmeier and Broll 2019; Wang et al. 2019). Moreover, animals may interfere with survival both post- and pregermination by grazing, trampling, or moving specimens (Wielgolaski, Hofgaard, and Holtmeier 2017). Lastly, the influence of human impact on tree line position is nonnegligible. Although we avoided human disturbance as much as possible with our slope selection, if historic tree lines were lowered due to human activity, a lag effect would be expected, making advancement currently invisible. These complex interactions between abiotic and biotic drivers of tree line dynamics come together to create microsite conditions and species-specific climate–growth/germination responses and render the isolation and analysis of a single factor difficult. We suggest future research to continue sample small specimens above the tree line while obtaining as many environmental measurements as possible (e.g., soil nutrients, moisture, solar radiation) to ameliorate our understanding of microsite and microclimate impacts on alpine vegetation.

Although our study used over 1,000 samples, there remain data related and methodological limitations that may have impacted our findings and conclusions. For one, samples were not cross-dated; thus, sample ages and resulting germination dates are minimum estimates. In addition, the temporal scale for germination–climate correlations is quite short, constraining the significance of correlations and perhaps contributing to inconsistencies in autumn temperature correlations. The climate data used for correlations also have their own limitations. Monthly climate values extracted from the E-OBS data set consist of interpolated data from various land stations, and these approximate values cannot represent the climate conditions at small spatial scales. This is especially relevant because the study sites are smaller than a gridded cell (Frei et al. 2018). Moreover, our hypotheses regarding species-specific anatomical and morphological traits are based on species-specific elevational ranges being dictated by climate, but no analysis of the impact of climate on growth was conducted. Performing additional regression tests to explore the

association between plant traits and accurate temperature measurements across our elevational transect could support the hypotheses.

Despite its limitations, this study has demonstrated that seedling and sapling data can successfully be used to study vegetation dynamics above the tree line. The development of this data set, and its utilization, should set the groundwork for wood anatomical and dendroecological research to rethink tree line dynamics and look beyond trees. We propose three research avenues to motivate future projects: (1) investigations of age distribution and species composition in various sites above the tree line, (2) measurements of site- and species-specific factors influencing plant survival and growth in alpine vegetation, and (3) applications of dendrochronological and wood anatomical techniques away from tree species and to herbs and shrubs with annual growth increments.

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Disclosure statement

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Author contributions

U.B. conceived the study and created all figures. A.Pa., J.E., F.R., A.V., and U.B. conducted fieldwork. A.Pa. and A.Pi. prepared samples and performed the statistical analyses. A.Pa. and U.B. wrote the manuscript with input from M.T. and J.E. All authors contributed to discussion and approved submission. A.Pa. and U.B. revised the manuscript.

Data availability

All data used in this study will be freely available upon personal request.

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