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RESEARCH PAPER

Elevation affects both the occurrence of ungulate browsing and its effect on tree seedling growth for four major tree species in European mountain forests

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Abstract

Key message In European mountain forests, the growth of silver fir (*Abies alba* Mill.), sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) seedlings is more strongly affected by ungulate browsing than by elevation. But, the constraint exerted by ungulates, in particular the probability for seedlings to be browsed, increases with elevation for most species.

Context While concerns about mountain forest regeneration rise due to their high vulnerability to climate change, the increase in wild ungulate populations and the expansion of their range in the last decades exert an additional constraint on the survival and growth of young trees. Understanding how this constraint can vary with elevation is thus a key to assess the consequences of this population increase for the regeneration of mountain forests.

Aims In this study, we investigate the effect of elevation on (i) the occurrence of browsing for seedlings and on (ii) the reduction in seedling growth induced by ungulate browsing.

Methods We monitored height growth and browsing occurrence on silver fir, sycamore maple, European beech and Norway spruce seedlings across seven elevation gradients (from 400 to 2013 m) located from France to northern Sweden.

Results Seedlings of the two most palatable species—fir and maple—were more likely to be browsed at high elevation while the opposite effect was observed for spruce. Browsing strongly reduced seedling growth for all species but Norway spruce, while elevation had no direct effect on seedling growth. This browsing-induced growth reduction was stronger at high elevation for fir seedlings.

Conclusions Browsing is overall a stronger constraint on seedling growth than elevation for four dominant species of European mountain forests. Elevation can, however, affect both browsing probability and the effect of browsing

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on seedling growth. Our results highlight the importance of taking into account ungulate pressure and its interactive effect with elevation when forecasting the regeneration of mountain forests under a changing climate.

Keywords Ungulate browsing, Climate change, Elevational gradient, Plant–herbivore interactions, Mountain forests, Attractant-decoy hypothesis

1 Introduction

Mountain forests are keystone ecosystems known to provide a wide range of services to human society, e.g. protection against natural hazards, carbon storage or timber production (Schirpke et al. 2019; Stritih et al. 2021). In addition to being particularly vulnerable to climate change (Thuiller et al. 2005), mountain forests are increasingly threatened by the current dynamics of ungulate populations. Indeed, the past decades have witnessed an important increase in wild ungulate populations in the Northern Hemisphere, in terms of both abundance and geographical range (Fuller and Gill 2001; Milner et al. 2006; Beguin et al. 2016). As a consequence, ungulate damage is a growing concern for agricultural production, forest ecosystems sustainability and conservation areas (Reimoser and Putman 2011). Ungulates are key drivers of forest regeneration leading to reduced seedling growth and survival and to changes in plant assemblages benefiting species that are less palatable or more tolerant to browsing (Boulanger et al. 2015; Laurent et al. 2017). In mountain forests, elevation can also be a driver of trees' demographic performance, mainly through a sharp decrease in temperature with increasing elevation which reduces growth (Marcora et al. 2013; Jiang et al. 2022; Muñoz Mazón et al. 2022), but also through changes in e.g. direct solar radiations or snow pack thickness in winter (Körner 2007, 2012). Many of the environmental conditions that change along elevation gradients can also affect the browsing pressure exerted on seedlings, e.g. snow cover (Hallinger et al. 2010) and tree species composition (Champagne et al. 2016), or seedlings' response to browsing, e.g. climate (Barton and Shiels 2020; Champagne et al. 2021). The resultant effect of elevation on the constraint exerted by deer on forest regeneration remains, however, largely unknown. As high-elevation regions are expected to experience amplified warming (Pepin et al. 2015), understanding how elevation and deer browsing interactively affect natural forest regeneration is crucial to anticipate the consequences of global changes for mountain forests.

The effect of elevation on browsing was a matter of conflicting results (Speed et al. 2013; Ameztegui and Coll 2015; Herrero et al. 2016). First, because several species of ungulates only use woody species as alternate forage during winter when their main food resources (e.g. herbs and shrubs) become scarce (Heggberget et al. 2002), browsing rates on tree seedlings could increase at higher elevation, where the winter season is harsher. This would be consistent with the attractant-decoy hypothesis, which predicts that plants avoid herbivory when surrounded by more palatable neighbours that divert browsing (Ruttan and Lortie 2013). The opposite effect could, however, also be expected: theories predicting food selection at broad spatial scales suggest that ungulates are rather expected to primarily browse vegetation in feeding patches with abundant and highly palatable forage (Bee et al. 2009; Kuijper et al. 2009), which should mostly be located at low elevation, where productivity is higher. A typical illustration is the observation that several ungulate species such as red deer (*Cervus elaphus* Linnaeus) (Kropil et al. 2015) or roe deer (*Capreolus capreolus* L.) (Cagnacci et al. 2011) can migrate downslope in winter, where conditions are milder. In addition, more frequent browsing occurrences on seedlings could also be expected at low elevations due to a thinner snow pack, since snow cover has a protective effect against browsing, particularly on small seedlings (Hallinger et al. 2010). Overall, it remains thus largely disputed how elevation might affect the browsing pressure exerted by ungulates on tree seedlings.

Environmental variations along elevation gradients also exert strong effects on seedling performance, with potentially complex interactions with browsing. For instance, theoretical studies showed that herbivory should have a stronger impact on plant performance in conditions of low resource availability (Wise and Abrahamson 2005). In mountain ecosystems, resource availability can be strongly conditioned by elevation (i.e. higher temperatures leading to reduced water availability at low elevation, higher cloud cover reducing light availability at high elevation) (Körner 2007, 2012). In practice, however, studies that investigated the interactions between climate and browsing on seedling growth produced contrasted results. At the tree line, herbivory by large mammals can either decrease (Brodie et al. 2012; Vuorinen et al. 2020) or increase climate effect on seedling growth (Speed et al. 2011; Sanders-DeMott et al. 2018). Similarly, in controlled conditions, reduced water availability can have a positive (Hawkes and Sullivan 2001) or neutral (Kullberg and Welander 2003; Barton and Shiels 2020) effect on seedling tolerance to browsing.

While it is crucial to keep in mind that environmental changes along elevation gradients are not perfectly

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analogous to those expected to occur in time with climate change, elevation-driven temperature gradients remain a powerful research tool to infer the ecological response of organisms to climate change (Körner 2007; Sundqvist et al. 2013). Investigating the relative effect of elevation and browsing on seedling growth could provide insights into the relative importance of changes in temperature and ungulate populations for forest regeneration. Several studies have indeed suggested that browsing might have stronger impact than climate in controlling tree regeneration (Cairns and Moen 2004; Speed et al. 2010; Herrero et al. 2012, 2016), which could have strong repercussions for future changes in tree species distribution. For instance, Fisichelli et al. (2012) showed that across North America, high browsing pressure could annihilate the positive effect of temperature on the growth of temperate tree species, thus pushing the temperate–boreal transition zone further south.

In this study, we analysed the joint response of tree seedling performance to elevation and browsing in tree species of mountainous forests throughout Europe. We focused on silver fir (*Abies alba* Mill.), sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.), which are four of the most dominant and economically important tree species in European mountains. We analysed seedling growth and browsing damage along seven elevational gradients, spread across a European latitudinal gradient reaching from France to northern Sweden, through Germany and Poland. Based on these data, we explored the following questions:

1. How does elevation affect the occurrence of browsing for the seedlings of these four species?
2. Are there interactive effects of elevation and browsing on tree seedling growth?
3. Is seedling growth more affected by elevation or by browsing?

2 Materials and methods

2.1 Study sites, species and sampling

Seven elevational gradients (sites) were sampled, in four European countries (France, Germany, Poland and Sweden) covering a large latitudinal (from 44° to 67°) and elevational (from 446 to 2013 m above sea level) range (Fig. 1 and Table 1). Sampled sites were all located in mountain forests and were overall representative of the local forest structure (i.e. even or uneven-aged low intensity management in all sites except in the Bavarian Forest National Park (FNP) which is a protected area with no management). Free-ranging populations of ungulates occurred in each site (see species list in Table 1). All sites were covered by a 30-cm-deep snow cover or more during winter (Appendix 1). The dominant tree species, the ungulate
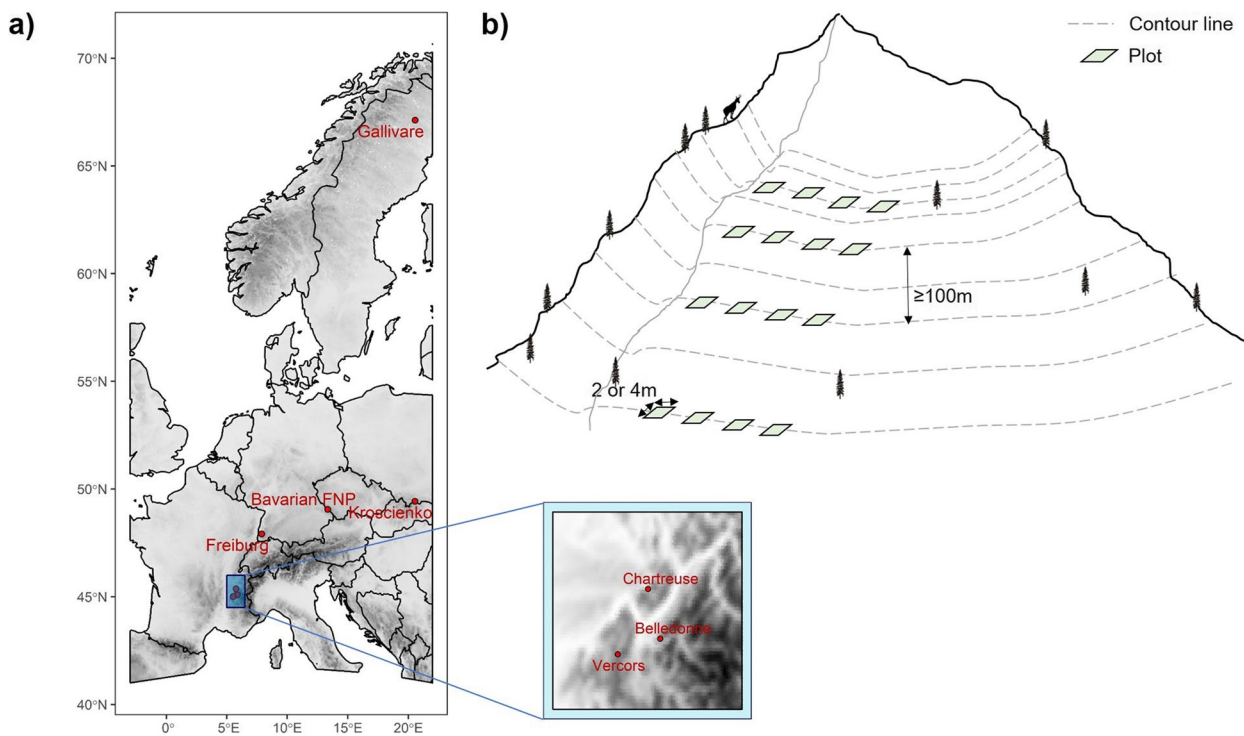

Fig. 1 Map of the European latitudinal gradient of study sites (**a**), each site including an elevation gradient (**b**)

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Table 1 Description of the seven field sites showed in Fig. 1

Site elevational gradient	Mean latitude	Mean longitude	Elevational range	Temperature range (°C)	Precipitation (mm)	No. of transects	No. of plots	Woody species present[a]	Ungulate species present[b]
Vercors	44° 59′ N	05° 30′ E	1200–1400	1.8–2.7	1110–1152	2	6	*ABAL*, *ACPS*, BEPU, *FASY*, *PIAB*, PIUN, SOAR, SOAU	CC, CE, CI, OGm
Belledonne	45° 05′ N	05° 50′ E	547–2013	− 1.1 to 5.7	916–1440	7	26	*ABAL*, ACPL, *ACPS*, CABE, CASA, *FASY*, FREX, QUPE, *PIAB*, PICE, PIUN, PRAV, POTR, SOAU, TIPL	CC, CE, CI, OGm
Chartreuse	45° 22′ N	05° 45′ E	524–1520	1.1–5.8	960–1282	3	17	*ABAL*, ACPL, *ACPS*, CABE, COAV, *FASY*, FREX, *PIAB*, PIUN, SOAR, SOAU, TICO	CC, CE, CI, OGm
Freiburg	47° 55′ N	07° 53′ E	560–1260	1.2–5	1002–1513	6	24	*ABAL*, *ACPS*, *FASY*, FREX, LADE, *PIAB*, SOAU	CC, CE
Bavarian FNP	49° 03′ N	13° 20′ E	765–1355	2–7.2	894–1295	4	30	*ABAL*, ALGL, ALIN, ACPL, *ACPS*, BEPU, *FASY*, FREX, *PIAB*, POTR, PRAV, SOAU, TABA, TIPL	CC, CE
Krościenko	49° 26′ N	20° 33′ E	500–1100	− 0.1 to 1.6	751–987	4	16	*ABAL*, ACPL, *ACPS*, BEPE, COAV, *FASY*, FREX, *PIAB*, PRAV, POTR, SOAU, TICO	CC, CE
Gällivare	67° 07′ N	20° 33′ E	400–608	− 8.3 to − 9.2	486–512	4	16	ALIN, BEPU, *PIAB*, PISY, SAsp	AA, CC

Climate variables—annual mean temperature range and annual mean cumulative precipitation range—were obtained from WorldClim model (Hijmans et al. 2005). Species selected for this study are shown in italicized characters

[a] Tree species: *ABAL Abies alba* Mill., *ALGL Alnus glutinosa* (L.) Gaertn., *ALIN Alnus incana* (L.) Moench, *ACPL Acer platanoides* L., *ACPS Acer pseudoplatanus* L., *BEPE Betula pendula* Roth, *BEPU Betula pubescens* Ehrh., *CABE Carpinus betulus* L., *COAV Corylus avellana* L., *CASA Castanea sativa* Mill., *FASY Fagus sylvatica* L., *FREX Fraxinus excelsior* L., *LADE Larix decidua* Mill., *QUPE Quercus petraea* (Matt.) Liebl., *PIAB Picea abies* (L.) H. Karst., *PICE Pinus cembra* L., *PISY Pinus sylvestris* L., *PIUN Pinus uncinata* Ramond ex DC., *PRAV Prunus avium* L., *POTR Populus tremula* L., *SAsp Salix* sp., *SOAR Sorbus aria* (L.) Crantz, *SOAU Sorbus aucuparia* L., *TABA Taxus baccata* L., *TICO Tilia cordata* Mill., *TIPL Tilia platyphyllos* Scop

[b] Ungulate species: *AA Alces alces* Linnaeus, *CC Capreolus capreolus* (L.), *CI Capra ibex* Linnaeus, *CE Cervus elaphus* Linnaeus, *OGm Ovis gmelini musimon* (Pallas)

species present, local climate and site characteristics are listed in Table 1 and in Rabasa et al. (2013). Extraction of climatic data for each site is provided in Appendix 2.

We focused on silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* (L.) H. Karst.), European beech (*Fagus sylvatica* L.) and sycamore maple (*Acer pseudoplatanus* L.) (Table 1) that were the four most abundant tree species across all sites and in each of the plots selected within sites. They display different ecological strategies: sycamore maple and Norway spruce are considered post-pioneer species, while silver fir and

European beech are late-successional species (Rameau et al. 1993).

On each site, we sampled seedlings at different elevation levels, which were separated by at least 100 m in elevation, except for Swedish transects (i.e. 50 m), where the temperature decreases more rapidly with increasing elevation (Stone and Carlson 1979). The total number of elevation levels sampled varied from 2 to 7 depending on the length of the elevation gradient. In all sites but Bavarian Forest National Park, we established between four to six circular plots per elevation level (plots were

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20 m in radius; see details in Rabasa et al. (2013)). In the Bavarian FNP, the plots were located every 100 m along four transects, for a total of 30 plots. To minimize the effect of forest management, we selected within each site plots with no evidence trees having been harvested over the past 4 years (defined as no observation of recent stumps in the vicinity of the plot).

In each plot, seedlings (defined in this study as young trees with a height < 70 cm) were sampled in square-shaped subplots located in the centre of each plot. The density of small seedlings can be extremely variable at small spatial scale (depending on the distance to a seeding tree and local light availability). Therefore, we used a sampling protocol that allowed adjusting to this natural variability. More specifically, the size of subplots varied among species depending on the local seedling density: 4 m^2 when seedling density was sufficient to sample 5 individuals per species, 16 m^2 in plots of overall low seedling abundance. We sampled a minimum of 5 seedlings and up to 20 seedlings per species per plot. When more than 20 seedlings per species were present in a plot, we randomly sampled seedlings with different heights. We verified a posteriori that height distribution was consistent whether there was a random selection of seedlings (i.e. in plots with more than 20 seedlings) or not (see Appendix 3). In rare cases, it was not possible to find 5 seedlings of each species in the plots so we randomly sampled up to 5 seedlings (< 70 cm) of each dominant species at each elevation searching up to 100 m away from the plot (while avoiding the 100-m search radius of nearby plots). The height of each seedling was measured, and browsing marks were recorded (1 when the terminal shoot was browsed during the current year, 0 when not). The annual height growth of each seedling was measured as the length of the last shoot. Seedlings were sampled at the end of the growing season in each site and elevation to ensure that fully expanded shoots were measured. Measuring the last shoot length is a common proxy for seedling growth (e.g. see Canham et al. (1994) and Palmer and Truscott (2003)). Using such a metric does not capture overcompensation by new shoots replacing the apical one, but we assumed this pattern to be negligible as polycyclic growth is rare in mountain forests, especially for small seedlings. Seedlings were sampled in 2010, except in 2017 for the Bavarian Forest National Park site. In total, 2981 seedlings were measured (Bernard et al 2023).

2.2 Statistical analysis

2.2.1 Effect of climate on browsing occurrence
We tested the effect of elevation on browsing occurrence (binary variable (Br)) separately for each tree species. In addition to the effect of elevation (Z), we chose to take into account seedling height (Ht) because taller seedlings

may be more apparent than smaller ones (Diaci 2002; Nichols et al. 2015). We included an interaction between elevation and seedling height because taller seedlings might be less protected by the snow pack (Visscher et al. 2006). We used a generalized mixed linear model for browsing probability (p_{Br}) (model 1) with a binomial error term and a logit link function

$$\text{logit}(p_{Br}) = \alpha_0 + \alpha_1 Ht + \alpha_2 Z + \alpha_3 Z \times Ht + \theta_{S/ZL} + \varepsilon \quad (1)$$

Elevation and seedling height (Ht) were centred and scaled. Elevation, seedling height and their interaction were treated as fixed effects. Elevation level (ZL) and sites (S) were treated as random effects, with elevation level nested in the site ($\theta_{S/ZL}$). We chose to treat the site as a random effect to avoid biases related to between-sites variations in unobserved environmental conditions (e.g. in ungulate density and thus ungulate pressure). Elevation level was also treated as a random effect to account for the fact that plots located at the same elevation level are spatially clustered. α is the estimated parameter, and ε is the error term.

2.2.2 Effect of climate and browsing on seedling growth
Second, to test the relative effects of elevation and browsing (Br) on seedling growth, i.e. as measured by the last shoot length (LSL), we used a linear mixed model (2) with here again seedling height (Ht) as a covariate to account for the fact that taller seedlings tend to grow faster.

$$\log(\text{LSL}) = \beta_0 + \beta_1 Ht + \beta_2 Z + \beta_3 Br + \beta_4 Z \times Br + \theta_{S/ZL} + \varepsilon \quad (2)$$

The response LSL was log-transformed to match the normality assumption. Elevation (Z), browsing (Br) and seedling height (Ht) were centred and scaled. We included an interaction between elevation and browsing to test if elevation had an influence on seedling growth response to browsing. We added the same random effects as described before ($\theta_{S/ZL}$), i.e. elevation level nested in the site, and ε is the residual normal error.

2.2.3 Model validation
For each model, we graphically checked that the structure of the residuals matched the assumptions of normality and homoscedasticity. Because Norway spruce was the only tree species present in the coldest site (Gällivare) which also had a very different climate from the other sites (mean annual temperature = − 8.7 °C vs. mean annual temperatures comprised between + 0.3 and + 3.2 °C in the other sites), we first ran the models without this site. For Norway spruce, we repeated each model after adding data from Gällivare to check whether the trends were driven only by this particular site. Results related to these analyses are reported in Appendix 4

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(Table 5 and Fig. 6) for model 1 and Appendix 5 (Table 6 and Fig. 7) for model 2.

Mixed models were fitted using *glmer* and *lmer* functions from *lme4* package, in R version 3.4.1 (R Core Team 2019), and model statistics were obtained using *lmerTest* package (Bates et al. 2014; Kuznetsova et al. 2017).

3 Results

The residuals of the models are analysed in Appendix 6 and show that hypotheses of the model are respected.

3.1 Effects of elevation on browsing probability

Browsing probability (p_{Br}) increased significantly with seedling height for all species, whereas elevation had

more contrasted effects (Fig. 2 and Table 2). Maple seedlings were more likely to be browsed at high elevation. In contrast, elevation had a negative effect on the browsing probability in Norway spruce (Fig. 2 and Table 2), and this effect was also observed when including the Swedish site Gällivare (Fig. 8 in Appendix 6). For fir seedlings, there was a significant interaction between height and elevation (Table 2), so that for the tallest seedlings only, browsing probability was higher at high elevation. The probability for beech seedlings to be browsed was unaffected by elevation. When significant, the effect of elevation on browsing probability was overall of similar magnitude than the effect of height (Fig. 2b).
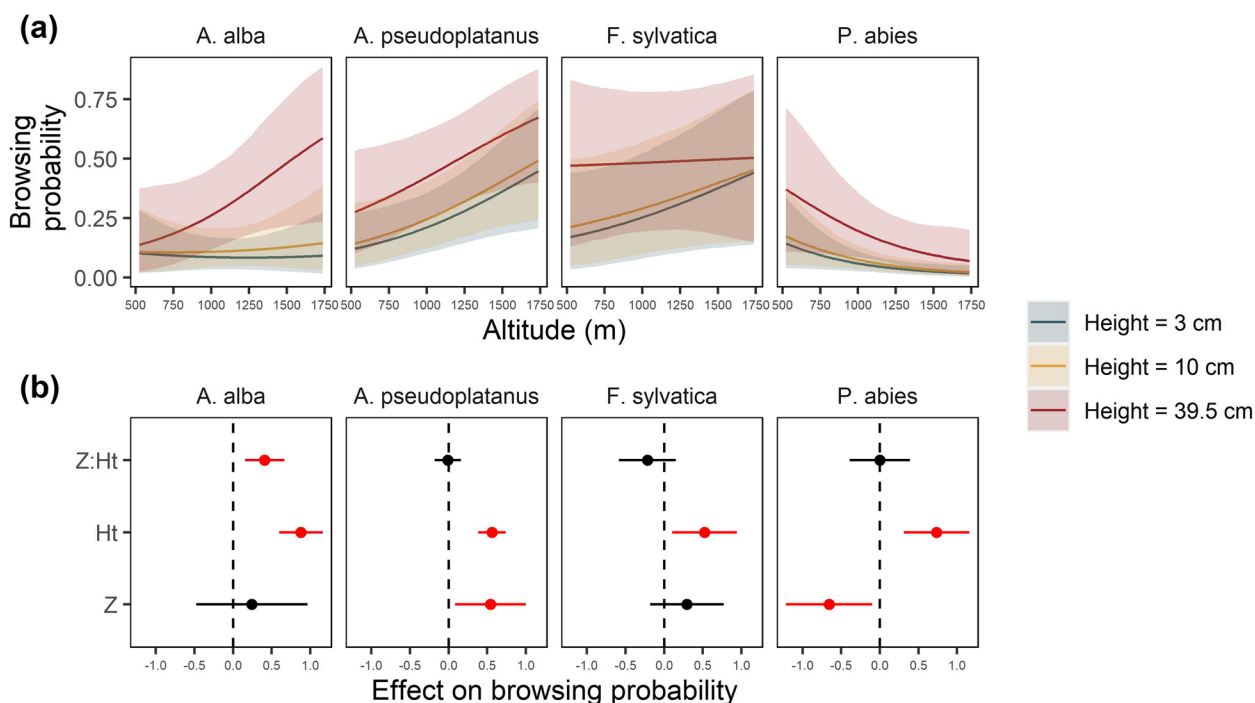

Fig. 2 **a** Effect of elevation (*Z*) on browsing probability predicted by the model (with 95% confidence interval). Height values correspond to the 10%, 50% and 90% quantiles of seedling height across all species. **b** Estimate and 95% confidence interval of the parameters estimated by the model for each species. Parameters shown in red are significant at *α* = 0.05

Table 2 Statistics (estimates (est) and standard deviation (sd)) of the parameters and intercept (Int.)

	A. pseudoplatanus		*F. sylvatica*		*P. abies*		*A. alba*	
	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a
Int	− 0.78 (0.39)	0.044	− 0.66 (0.62)	0.290	− 2.56 (0.34)	< 0.001	− 1.87 (0.42)	< 0.001
Z	0.54 (0.23)	0.020	0.29 (0.24)	0.226	− 0.66 (0.28)	0.021	0.24 (0.37)	0.506
Ht	0.56 (0.09)	< 0.001	0.52 (0.21)	0.014	0.74 (0.22)	< 0.001	0.88 (0.14)	< 0.001
Z:Ht	− 0.01 (0.09)	0.918	− 0.22 (0.19)	0.246	0 (0.2)	0.996	0.41 (0.13)	0.002

[a] *p* value of the models predicting the effect of seedling height (Ht) and elevation (Z) on browsing probability for each species when the Swedish site Gällivare is not included. Results written in italics indicate significance at 5%

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3.2 Relative effects of climate and browsing on seedling growth

Browsing reduced seedling growth (as measured by the last shoot length) for all species but Norway spruce, with a particularly strong effect in fir and beech (Fig. 3 and Table 3). Unbrowsed seedlings had an average growth rate of 2 cm year^{-1} and 3 cm year^{-1} (for fir and maple, respectively), while browsed seedlings grew by only 0.5 cm year^{-1} (Fig. 3).

Elevation had an overall very weak effect on seedling growth. For silver fir, there was a significant interaction between elevation and browsing (Table 3) so that browsing only reduced seedling growth at high elevation (Fig. 3a). The interaction between elevation and browsing was also significant for beech and Norway spruce (Table 3), but its magnitude was too weak to affect the hierarchy between browsed and unbrowsed seedlings. Besides, the interaction was no longer significant for Norway spruce when the Swedish site Gällivare was included (Appendix 5). Lastly, height growth increased with seedling height for all species, although the trend was not significant for silver fir (Fig. 3c), which was the species with the smallest range of seedling height (75% of the seedlings were less than 8.0 cm tall).
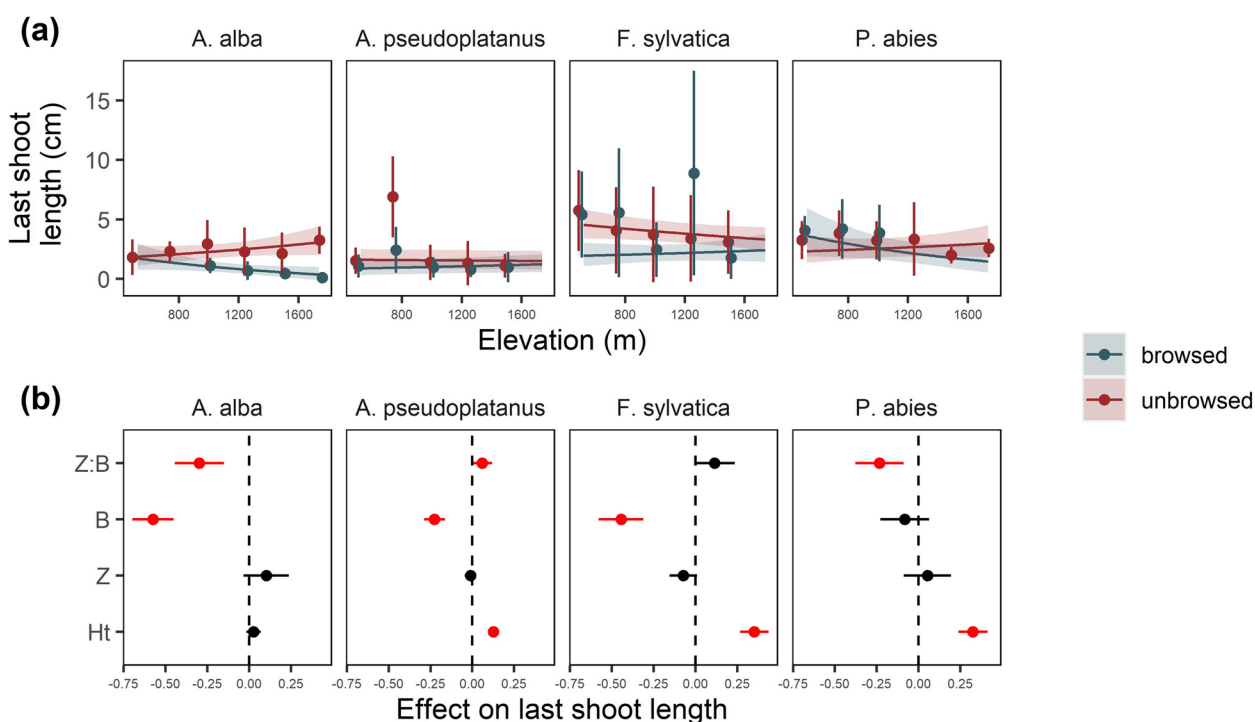

Fig. 3 a Effect of elevation (*Z*) and browsing (*B*) on seedling last shoot length. Data were averaged by elevation class (±standard deviation), each point covering an elevation class of 250 m and being placed on the *x*-axis at the centre of this elevation class. Regression lines show the prediction with 95% confidence interval by the model. Height was set to its mean value across the dataset (i.e. 10 cm). Seedlings with extreme height values (i.e. below 10% quantile and above 90% quantile) were not included in elevation classes. **b** Estimate and 95% confidence interval of the parameters estimated by the model for each species. Parameters shown in red are significant at *α* = 0.05

Table 3 Statistics (estimates (est) and standard deviation (sd)) of the parameters and intercept (Int.)

	A. pseudoplatanus		*F. sylvatica*		*P. abies*		*A. alba*	
	est (sd)	*p*[a]	est (sd)	*p*[a]	est (sd)	*p*[a]	est (sd)	*p*[a]
Int	0.92 (0.16)		1.56 (0.09)		1.26 (0.12)		1.22 (0.09)	
Ht	*0.13 (0.01)*	*< 0.001*	*0.35 (0.04)*	*< 0.001*	*0.32 (0.04)*	*< 0.001*	0.03 (0.02)	0.232
Z	−0.01 (0.02)	0.692	−0.07 (0.04)	0.374	0.05 (0.07)	0.748	0.1 (0.07)	0.408
B	*− 0.23 (0.03)*	*< 0.001*	*− 0.46 (0.07)*	*< 0.001*	−0.1 (0.08)	0.247	*− 0.59 (0.06)*	*< 0.001*
Z:B	*0.06 (0.03)*	*0.044*	0.11 (0.06)	0.066	*− 0.24 (0.08)*	*0.002*	*− 0.3 (0.07)*	*< 0.001*

[a] *p* value of the models predicting the effect of elevation (*Z*), seedling height (*Ht*) and browsing (*B*) on seedling last shoot length for each species when the Swedish site Gällivare is not included. Results written in italics indicate significance at 5%

4 Discussion

Based on seven elevation gradients from Central to Northern Europe, we show that elevation can affect both the probability of being browsed and the browsing-induced growth reduction of seedlings for four emblematic tree species of European mountain forests. We also show that seedling height growth is more strongly affected by ungulate browsing than by environmental changes along elevation gradients for the four studied species. Given the tight correlation between elevation and temperature (Körner 2007), this suggests that for these four species, changes in ungulate populations could exert a constraint on the regeneration that is comparable in magnitude to the expected increase in temperature under future climatic scenarios (without considering other components of climate change such as drought or other disturbances).

4.1 Palatable seedling species are more frequently browsed at high elevation

We found that for the two most palatable species (i.e. silver fir and maple), seedlings located at higher elevation were more likely to be browsed by ungulates. Our finding is consistent with the idea that higher availability of alternative forage (i.e. forbs and herbaceous species) at low elevation, where productivity is higher and winter conditions are milder, leads to a lower browsing intensity on woody species (Gordon and Prins 2008). Indeed, browsing on woody species often occurs because of a lack of more palatable resource during low food-availability periods (Redjadj et al. 2014), except for roe deer (Storms et al. 2008; Barančeková et al. 2010) and moose (Felton et al. 2021) that feed mostly on woody plants. As forbs and herbaceous species are more abundant and less protected by snow as elevation decreases, our result would be consistent with a shift of food choice towards plants with a higher and more easily accessible nutritional content (Ruttan and Lortie 2013). The adverse effect could also have been expected, with ungulates exerting a higher browsing pressure in feeding patches where forage availability is higher (Bee et al. 2009; Kuijper et al. 2009), especially since species such as red deer (Kropil et al. 2015) or roe deer (Cagnacci et al. 2011) have been reported to migrate downslope in winter, where conditions are more favourable. In that regard, the results from our correlative study tend to support the idea that food selection at local scale is more important in driving the browsing probability on a given species than food selection at broad spatial scale (Champagne et al. 2016). To draw more solid conclusions on this question, the development of methodological approaches to quantify ungulate density that are both easy to implement at continental scale and comparable between and within sites would be an important step.

For the four species, taller seedlings displayed a higher probability of being browsed, which is in agreement with

the observation that ungulates barely eat close to the ground (Renaud et al. 2003) and rather browse taller seedlings that are more detectable and less energetically costly to search (Bergquist and Örlander 1998; Bergström and Bergqvist 1999; Kullberg and Bergström 2001; Diaci 2002). In general, this size preference was consistent across the full climatic gradient. For silver fir, however, we observed that height only increased the browsing probability at high elevation, which is likely related to the protective effect of snow (Visscher et al. 2006). Indeed, in most of our study sites, minimum snow cover at high elevation during winter was 20 cm (Appendix 1), so that seedlings below 20 cm are always protected by the snow pack while the protection of higher seedlings depends on snow depth. Our results thus support the idea that the presence of a thick snow cover at high elevation should further amplify the already existing effect of seedling height on the probability to be browsed. The presence of a snow cover in winter could also explain our observation that Norway spruce seedlings are preferentially browsed at low elevation, unlike the other species. Indeed, unlike maple or fir that can also be browsed in spring and summer, Norway spruce is exclusively browsed in winter (Storms et al. 2008). As we focused our sampling on seedlings below 70 cm (most being smaller than 40 cm), spruce seedlings of this size were likely only accessible to ungulates at low elevation in winter. Taken together, our results show that the browsing pressure exerted on young seedlings in mountain forest is highly driven by elevation. This correlation could arise from both changes in the availability of alternative forage and protection by the snow pack.

4.2 Stronger effects of browsing than elevation on seedling growth

For all species, we found that browsing strongly impacted seedlings' growth, except for Norway spruce that is the least palatable species. This is consistent with the findings of Motta (2003) on rowan (*Sorbus aucuparia* L.) and Norway spruce: in highly browsed sites, there was no more rowan growing beyond a browsing height (100–160 cm), whereas Norway spruce was barely affected by browsing. The same pattern was found in fenced designs for silver fir and Norway spruce, with very few silver fir seedlings exceeding 20 cm in height in unfenced plots while Norway spruce growth only slightly differed between fenced and unfenced plots (Bernard et al. 2017). In lowlands, the palatability of European beech is equivalently low (Boulanger et al. 2009) or even lower (Mann 2009) than that of spruce, but browsing on beech may occur in mountainous areas when there is less alternate food resource (Heinrichs et al. 2012; Diaci et al. 2012).

In contrast, elevation had no effect on seedling growth for the four studied species, while faster growth rates could have been expected at low elevation where

conditions are warmer, implying longer growing season that should promote seedling growth (Fisichelli et al. 2014). Using an elevation gradient, Callaway (1998) showed that higher productivity at low elevation could be offset by stronger competitive interactions, which would be consistent with our results. Yet, the most striking result is that the effect of elevation on height growth was negligible compared to the effect of browsing for all the studied species. This stronger browsing effect is consistent with studies reporting the ability of ungulate herbivory to affect the climatic limit of the tree line (Cairns and Moen 2004; Speed et al. 2010; Herrero et al. 2012, 2016) or hinder growth responses to changes in temperature (Post and Pedersen 2008; Fisichelli et al. 2012). While it remains important to keep in mind that the changes in environmental conditions along elevational gradients are not perfectly analogous to those expected in the context of climate change, they remain strongly temperature-driven and can thus be informative on the ecological response of organisms to climate change (Körner 2007; Sundqvist et al. 2013). Considering the important magnitude of the temperature gradient within our study sites (i.e. 3.3 °C in average; see Appendix 2), our results suggest that for the four tree species we studied, the general trend of increasing wild ungulate populations could represent a comparable threat to their natural regeneration than temperature increase expected under global warming. It is thus crucial that future studies analyse jointly the effect of all components of climate change (e.g. CO_2 concentration and disturbance regimes) and ungulate browsing on forest regeneration to draw clear conclusion.

4.3 Elevation affects the growth reduction induced by browsing

We found weak and often significant interactive effects of elevation and browsing on seedling growth. In particular, we found a quite strong interaction for silver fir seedlings, whose height growth was more strongly reduced by browsing at high elevation. This most likely relates to the colder conditions, shorter growing season and reduced direct irradiance in the PAR at high elevation (Körner 2012), which leaves less time and resources for seedlings to compensate for the loss of photosynthetic tissue due to browsing (Wise and Abrahamson 2005). Previous studies had shown that lower availability of resources such as light (Baraza et al. 2010) or water (Hawkes and Sullivan 2001) can modulate the browsing-induced growth reduction. But, our study is, to our knowledge, the first to demonstrate that changing environmental conditions along elevation gradients can affect seedlings' response to browsing. When put in perspectives with our result on browsing probability, it implies that silver fir seedlings are both more frequently browsed and more severely impacted by browsing at high elevation. As such, our results shed light on the mechanisms explaining how ungulate browsing can affect the limit of the tree line for some tree species (Cairns and Moen 2004; Speed et al. 2010; Herrero et al. 2012, 2016) and advocates for more studies on the interactive effects of climate and herbivory on forest regeneration (Champagne et al. 2021; Segar et al. 2022).

5 Conclusion

Our results reveal that for four major tree species in European mountain forests, the first stage of tree regeneration is overall more strongly impacted by browsing pressure than by environmental changes observed along elevation gradients. This suggests that the general trend of increasing native ungulate populations will likely exert a major constraint on the regeneration of European mountain forests. It would thus be important to analyse how these effects on the first regeneration stage, which is a key bottleneck in tree population dynamics (Clark et al. 1999), translate into impacts at ecosystem level. Furthermore, we show that for several species, elevation influences both the intensity of the browsing pressure and the impact of browsing on seedling growth. Therefore, forecasting future dynamics of European mountain forests should be based on models, considering the critical impacts of increasing density of ungulates, and their interactions with elevation.

Appendix 1
Snow cover per site

Table 4 Characteristics (presence, thickness, period for the estimation) of the snow cover in all sites

Country	Site	Winter snow cover		
		Presence	Average (min, max) thickness (cm)	Period
Sweden	Gällivare	Yes	69 (53–87)	DJF 2009–2010
Germany	BFNP	Yes	35 (1–80)	DJF 2016–2017
Germany	Freiburg	Yes	54 (28–82)	DJF 2017–2018
Poland	Krościenko	Yes	30 (20–50)	DJF 1991–2013
France	Chartreuse	Yes	60 (20–100)	Overall estimate
France	Belledonne	Yes	60 (20–100)	Overall estimate
France	Vercors	Yes	60 (20–100)	Overall estimate

Data obtained from Peter Kjellander, Marco Heurich, Christoph Dreiser and Georges Kunstler, personal communications, and Szwed et al. (2017)

DJF December, January and February

Appendix 2
Climate in each site
General approach

To derive the fine scale spatio-temporal variation experienced by seedlings along each elevation gradient, we first downscaled the long-term mean monthly temperature (over the period 1960–1990) of WorldClim database, version 1 (Hijmans et al. 2005), at the transect level using the local elevation based on a moving-window regression method (Kunstler et al. 2011; Zimmermann et al. 2007). Then, to account for inter-annual variability, we used data from CHELSA portal (T_{mean}), version 1.2 online (Karger et al. 2017, 2018), to derive annual anomalies and correct the long-term monthly mean temperature of WorldClim. Lastly, we also extracted at each plot location the mean annual precipitation (P_{mean}) from CHELSA portal, version 1.2 online (Karger et al. 2017, 2018).

Correction of anomalies and calculation of mean winter temperature

All sites but Bavarian Forest National Park   All sites but Bavarian Forest National Park (BFNP) were sampled in 2010 so we considered mean December 2009 and January and February 2010 temperature data. At each plot of all sites but BFNP, mean winter temperature (T_{wint}) was calculated for each month as

$$T_m = T_{m\_meanWCdownscaled} + \Delta T_{m\_CHELSA}$$

where $\Delta T_{m-meanCHELSA}$ is the anomaly of the monthly CHELSA temperature for a given year (computed as the difference between the monthly temperature of that year and the long term).

Then, for the winter before sampling: $T_{wint} = (T_{Dec09} + T_{Jan10} + T_{Feb10})$ / 3

BFNP   BFNP was sampled in 2017, so we considered mean December 2016, January 2017 and February 2017 temperature data. However, CHELSA version 1.2 online contains data up to 2013. Since we had data measured from weather stations at this site, we decided to correct downscaled mean monthly temperature data by the anomalies of the weather stations. Therefore, at each plot of BFNP, mean winter temperature was calculated for each month as

$$T_m = T_{meanWCdownscaled} + \Delta T_{m\_Station}$$

Then, for the winter before sampling: $T_{wint} = (T_{Dec16} + T_{Jan17} + T_{Feb17})$ / 3
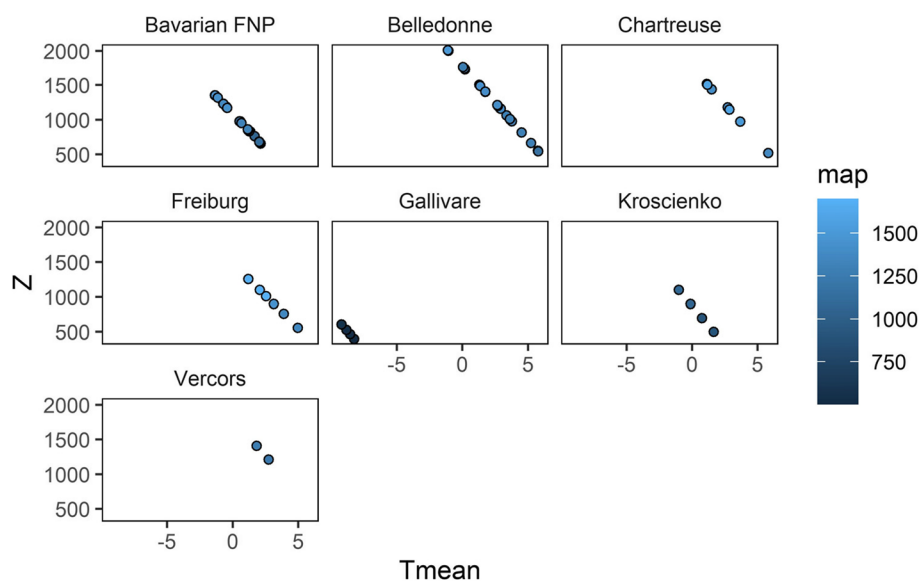
Climate along each elevation gradient

Fig. 4 Mean annual temperature (T_{mean}, °C), annual precipitation (map, mm year^{-1}) and elevation (Z, m) of the elevation levels in each site

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Appendix 3

Height distribution of seedlings

In plots where we found more than 20 seedlings of a given species, we randomly selected 20 of the available seedlings.

To verify the randomness of our selection, we compared the height distribution of seedlings when the number of seedlings of this species is lower than 20 (i.e. no random selection) or not (i.e. random selection).
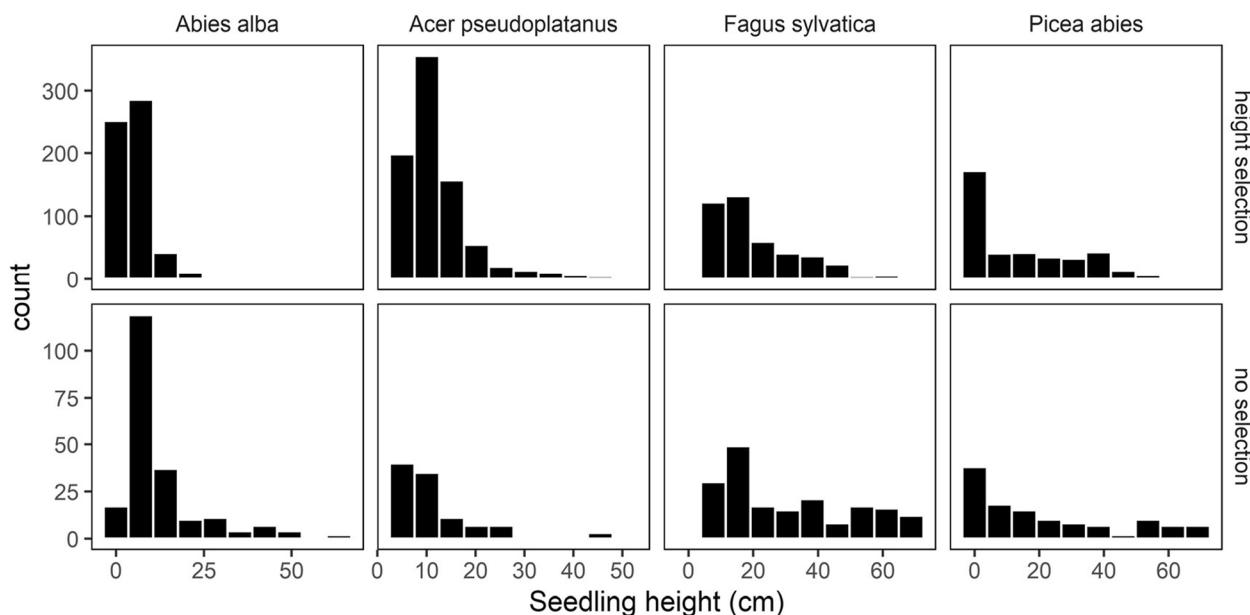

Fig. 5 Height distribution of the seedlings of each studied species depending on whether they were present in a plot with more (no height selection) or less (height selection) than 20 seedlings present

Overall, the height distribution of each species is consistent regardless of whether seedlings were randomly selected or not.

Appendix 4

Effect of elevation on browsing probability when the Swedish site Gällivare is included

Table 5 Statistics (estimates (est) and standard deviation (sd)) of the parameters and intercept (Int.)

	A. pseudoplatanus		*F. sylvatica*		*P. abies*		*A. alba*	
	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a
Int	− 0.78 (0.39)	0.044	−0.66 (0.62)	0.290	− 2.22 (0.29)	< 0.001	− 1.87 (0.42)	< 0.001
Z	0.54 (0.23)	0.020	0.29 (0.24)	0.226	− 0.93 (0.28)	0.001	0.24 (0.37)	0.506
Ht	0.56 (0.09)	< 0.001	0.52 (0.21)	0.014	0.71 (0.2)	< 0.001	0.88 (0.14)	< 0.001
Z:Ht	−0.01 (0.09)	0.918	−0.22 (0.19)	0.246	0.01 (0.19)	0.970	0.41 (0.13)	0.002

[a] *p* value of the models predicting the effect of elevation (Z) and height (Ht) on browsing probability when the Swedish site Gällivare is included. Results written in italics indicate significance at 5%
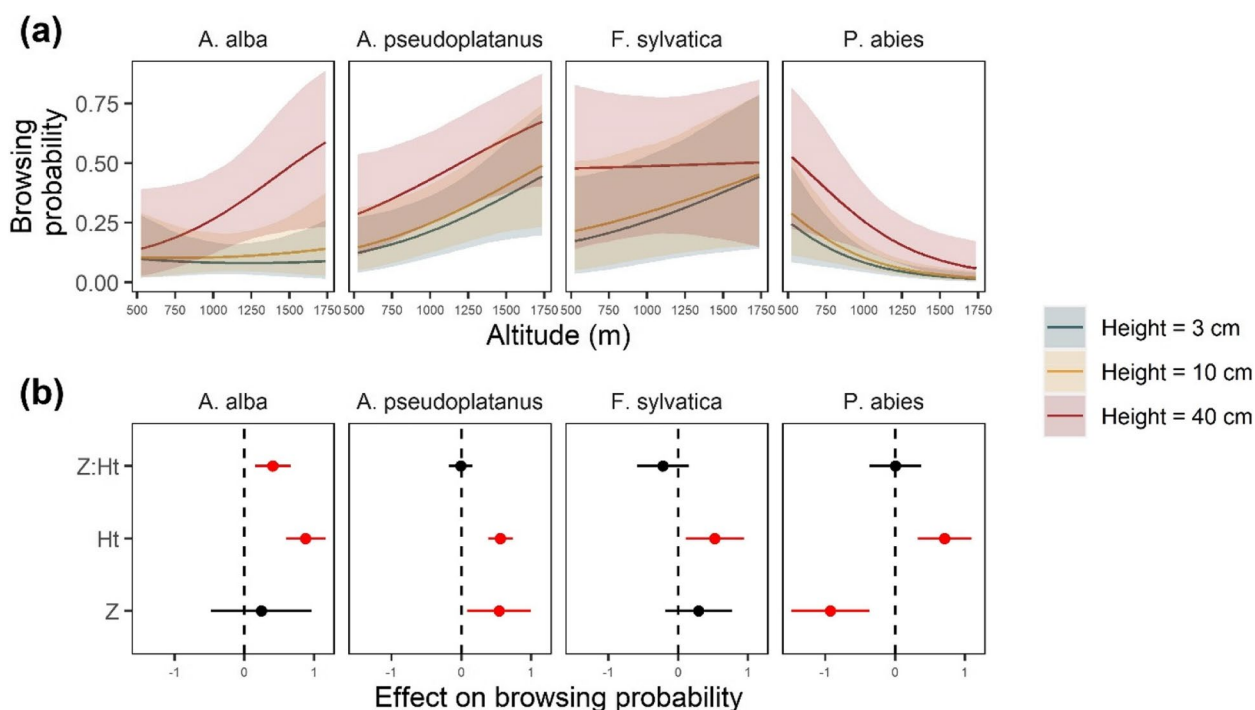
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Fig. 6 a Effect of elevation on browsing probability predicted by the model (with 95% confidence interval) when the Swedish site Gällivare is included. Height values correspond to the three 10%, 50% and 90% quantiles of seedling height across all species. **b** Estimate and 95% confidence interval of the parameters estimated by the model for each species. Parameters shown in red are significant at $a = 0.05$. Z, elevation effect; Ht, height effect; Z:Ht, interaction between elevation and seedling height

Appendix 5

Effect of browsing and elevation on seedling growth when the Swedish site Gällivare is included

Table 6 Statistics (estimates (est) and standard deviation (sd)) of the parameters and intercept (Int.)

	A. pseudoplatanus		F. sylvatica		P. abies		A. alba	
	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a	est (sd)	p^a
Int	0.92 (0.16)		1.56 (0.09)		1.29 (0.11)		1.22 (0.09)	
Ht	*0.13 (0.01)*	*< 0.001*	*0.35 (0.04)*	*< 0.001*	*0.32 (0.04)*	*< 0.001*	0.03 (0.02)	0.232
Z	−0.01 (0.02)	0.692	−0.07 (0.04)	0.374	0.07 (0.07)	0.483	0.1 (0.07)	0.408
B	*− 0.23 (0.03)*	*< 0.001*	*− 0.46 (0.07)*	*< 0.001*	−0.03 (0.06)	0.461	*− 0.59 (0.06)*	*< 0.001*
Z:B	*0.06 (0.03)*	*0.044*	0.11 (0.06)	0.066	−0.1 (0.06)	0.105	*− 0.3 (0.07)*	*< 0.001*

[a] p value of the models predicting the effect of elevation (Z), height (Ht) and browsing (B) on annual seedling growth (LSL) when the Swedish site Gällivare is included. Results written in italics indicate significance at 5%
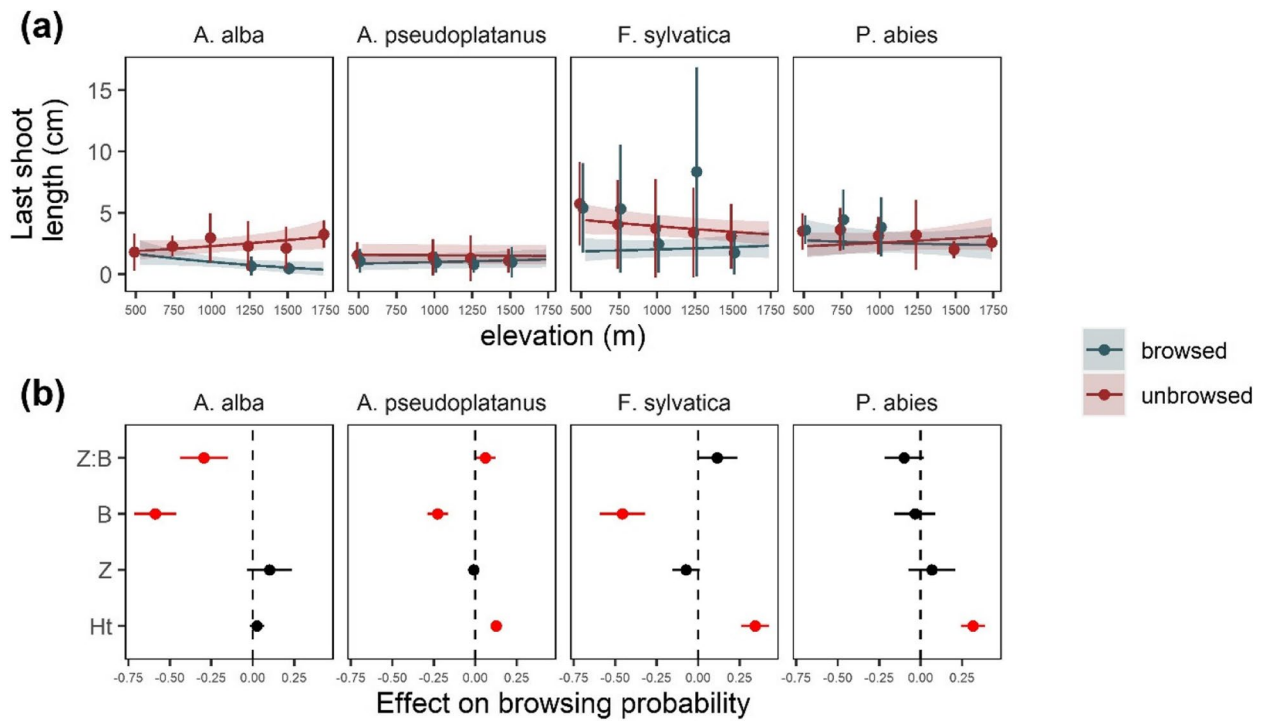
Fig. 7 Effect of elevation (*Z*), browsing (*B*) and seedling height (Ht) and of the interaction between elevation and browsing (*Z:B*) on seedling last shoot length when the Swedish site Gällivare is included. Data were averaged by elevation class (± standard deviation), each point covering an elevation class of 250 m and being placed on the *x*-axis at the centre of this elevation class. Regression lines show the prediction with 95% confidence interval by the model. Height was set to its mean value across the dataset (i.e. 10 cm). Seedlings with extreme height values (i.e. below 10% quantile and above 90% quantile) were not included. **b** Estimate and 95% confidence interval of the parameters estimated by the model for each species. Parameters shown in red are significant at $\alpha = 0.05$

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Appendix 6

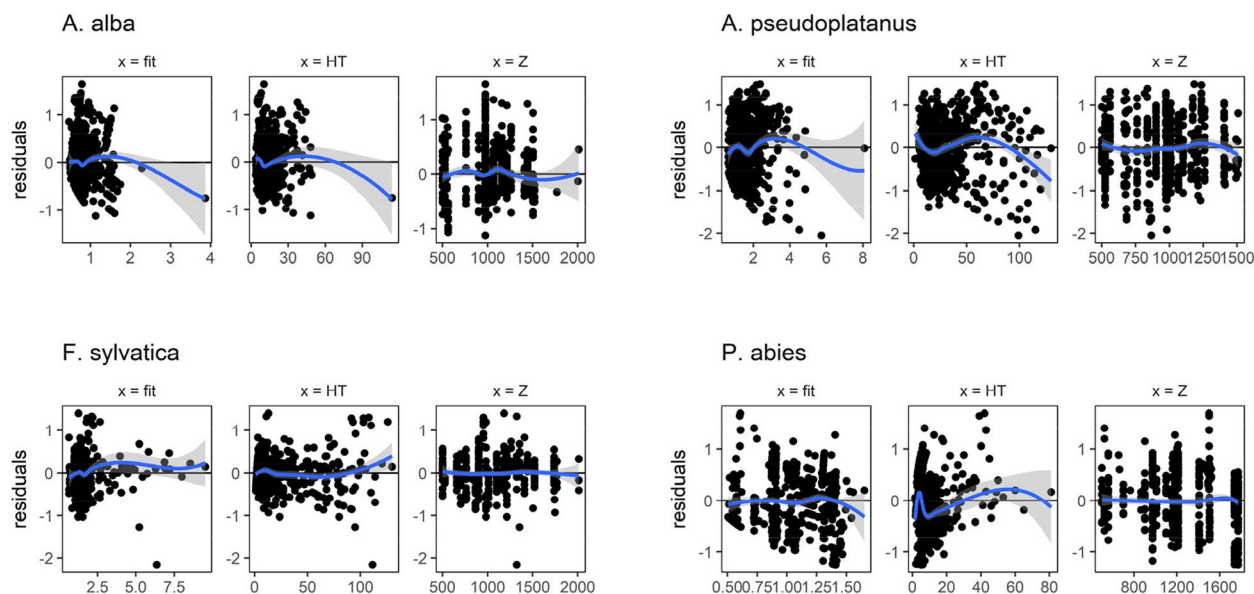## Structure of the residuals of the growth model

Fig. 8 Relation between the residuals of the growth model when the Swedish site is not included and the fitted values, height (Ht) and elevation (Z) for each species

Code availability
The R script to reproduce the analyses is freely available on GitHub at https://github.com/jbarrere3/BaccaraPaper/tree/main.

Authors' contributions
MB, JB, XM, SS, VB, HJ, EG, SGR, FV and GK conceived the ideas and designed methodology. EG, RB, SGR, GK and MH collected the data. MB, JB and GK analysed the data. MB, JB, XM and GK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Availability of data and materials
Data are archived in the following Zenodo repository: https://zenodo.org/records/10370097.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors gave their informed consent to this publication and its content.

Competing interests
The authors declare that they have no conflict of interest.

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