

# Evaluating dynamic tree-species-shifting and height development caused by ungulate browsing in forest regeneration using a process-based modeling approach

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## ABSTRACT

Ungulate browsing can prevent the successful regeneration and development of forest-owner-intended and climate-resilient admixed tree species, compromising the future provision of multiple ecosystem services. A reduction of the height increment of palatable tree species caused by ungulate browsing results in a competition shift in favor of less palatable species. While this key process of losing admixed tree species is well understood, forest growth models have not yet captured its full complexity. Therefore, our objectives were to simulate (i) the loss of susceptible tree species from different browsing regimes and its impact on stand development, (ii) changes in the height increment of saplings and trees, and (iii) the shifts in social status during stand development without pre-defined limits a sapling can resist browsing. To address these objectives, we used the process-based model iLand to simulate the exposure of Norway spruce, Silver fir, and European beech stands to varying browsing densities. We successfully reproduced expected dynamic shifts in species composition and height development 24 years after establishment, depending on ungulate pressure and species-specific competitive strength. Stand composition and growth differences already occur with slight changes in ungulate density. When saplings remained in stand structure, independent of the number being browsed, our results led to more individuals with substantially smaller dimensions. We found that dynamic tree species shifting can be simulated realistically by a process-based modeling approach, which can be used to show the strong impact of ungulates on stand development.

## 1. Introduction

Climate change increases the uncertainty under which complex and multivariate forest ecosystem management decisions must be made (Friedrich et al., 2021). Varying management patterns, dynamic disturbance regimes, and the introduction of invasive tree species have already altered stand and regeneration dynamics (Dey et al., 2018). Stabilizing mixed species stands is often relevant, especially considering an ecological perspective and the provision of ecosystem services they support (Knoke et al., 2008; Pretzsch, 2022). Adapting our forests to increasing disturbances under climate change requires establishing economically and ecologically resilient site-adapted tree species (Knoke et al., 2023). Their growth rates and the physical damage they incur, e.g., from ungulate browsing in the early stages of regeneration, play

crucial roles in forest conservation processes (Löf et al., 2018; Millar et al., 2007).

While the ecological dynamics of mature stands are mainly driven by disturbances such as drought, wind, fire, and insect outbreaks, regeneration dynamics are primarily shaped by recruitment and growing conditions (McDowell et al., 2020). These circumstances are determined predominantly by competition for light, nutrients, and water (Rannik et al., 2012). Suppose a plant remains in a low-growth class for longer than others; this represents a disadvantage in the competition for resources, especially light, which can be reinforced by high herbivore densities specific to the species (Bödeker et al., 2021; Connell, 1990; Côté et al., 2004).

Various studies describe the influence of ungulates on forest dynamics by affecting regeneration (Bödeker et al., 2023; Csilléry et al.,

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2022; Gaudry et al., 2022; Unkule et al., 2022). Ungulate damage in Central European forest ecosystems is mainly caused by Roe deer (*Capreolus capreolus* L.) and Red deer (*Cervus elaphus* L.) (Ammer et al., 2010; Linnell et al., 2020). These mammals directly affect trees, especially saplings, by trampling and browsing fresh shoots and buds. Red deer cause significant damage by peeling the bark from stems by scraping their antlers against trees (Gill, 1992).

Ungulate browsing primarily results in a diminished growth rate and, consequently, sapling height (Bödeker et al., 2023; Eiberle and Nigg, 1987; Kupferschmid et al., 2014; Putman, 1996). In a field study, Bergquist et al. (2003) observed that neither browsing nor clipping directly increases mortality rates but strongly reduces height development, especially when saplings are affected continuously for several years. According to Harmer (2001), saplings of some species (e.g., European beech) can tolerate several instances of severe browsing without dying. This suggests that changing the social status within increasing density-dependent competition can lead to what we term “shifted biotic competition”, meaning that delayed height growth within the stand structure chronically discriminates browsed saplings (Clasen et al., 2015; Connell, 1990). Kupferschmid et al. (2014) showed that the height growth and the recreation of Silver fir saplings depend on light availability before and after browsing. Additionally, the dominance within the sapling structure is essential as fast-growing fir saplings can over-compensate browsing-related height loss (Kupferschmid and Bugmann, 2013). Furthermore, suitable soil conditions can promote recovery after browsing events (Csilléry et al., 2022).

Ungulates selectively prefer some species over others (Ammer, 1996; Angst and Kupferschmid, 2023; Borowski et al., 2021; Boulanger et al., 2009), yet their behavior in relation to food availability is notoriously difficult to investigate. Extensive research has evaluated the role of ungulate diets, which, for selective browsers like roe deer, strongly depends on the availability of tree species and supplementary food sources as well as their quality (Hansen and Clark, 1977; Moser et al., 2006). Additionally, species-specific chemical contents, such as nitrogen concentration, influence the palatability of saplings of different species (Burney and Jacobs, 2011; Månsson et al., 2009). Past research reports a wide variety of results regarding the browsing preferences of Roe and Red deer in Europe (Bödeker et al., 2021; Borowski et al., 2021; Boulanger et al., 2009; Szwagrzyk et al., 2020), which can vary spatially and temporally. Furthermore, young trees are strongly influenced by the intensity and frequency of browsing events and, therefore, the over-abundance of ungulates can impede regeneration (Bergquist et al., 2003; Borowski et al., 2021; Côté et al., 2004; Tremblay et al., 2007; Valente et al., 2020).

Considering these challenges, ecosystem modeling, including the interaction between herbivores and modern forest management practices, can show how ungulate browsing interacts with sapling physiology and stand development to better support management planning processes (Champagne et al., 2021). Various ecosystem models can be used to simulate mixed forest development (Fabrika et al., 2018). However, to evaluate the effects of browsing on forest structure, it is necessary to simulate (i) browsing behavior, (ii) sapling development, and (iii) stand development. The modeling of individual saplings is computationally not feasible, particularly for landscape-scale forest models. Therefore, models adopt simplified approaches with lower resolution (e.g., cohorts) and fewer dynamic parameters (König et al., 2022). In addition to ungulate browsing preference, another critical consideration is how well saplings of a given species tolerate browsing. Typically, a growth reduction and a fixed sapling-stress threshold are used to describe the disadvantage a sapling faces from browsing. The fixed sapling-stress threshold indicates the number of consecutive years a sapling can survive browsing.

Several forest growth models have begun incorporating ungulate browsing disturbances (Seidl et al. 2011), and different modeling approaches have been tested in the past decades. For example, mathematical models can emulate the seedling reductions under different

ungulate densities (Lesser et al., 2019; Noonan et al., 2021). Another example is Kautz et al. (2018), who evaluated multiple disturbances, e.g., sapling browsing, by connecting a dynamic global vegetation model, LPJ-GUESS, with a stochastic browsing component. Peringer et al. (2013) used WoodPaM, a spatially explicit model for pasture-woodland, to investigate browsing by domestic ungulates and determined its effects on landscape structures. De Jager et al. (2017) used a biomass extension in LANDIS-II and found that white-tailed deer browsing reduced the above-ground biomass in forest ecosystems. Using the process-based model RReShar, Barrere et al. (2024) found that the regeneration growth of Sessile oak (*Quercus petraea* (Mill.) Liebl.) with admixed European hornbeam (*Carpinus betulus* L.), another palatable and fast-growing species, is more negatively affected by increased resource competition than it benefits from hornbeam as a diverted food source. In this study, we apply the individual-tree process-based model, iLand (Seidl et al., 2012), which is based on a light-use efficiency approach, to explore the dynamic development of sapling and stand growth under multiple browsing scenarios, wherein we vary the ungulate density and species preference.

Considering that ungulate browsing can lead to species-specific regeneration failure (Ammer, 1996; Gill, 1992), we decided to explore the potential for a process-based model to capture dynamic shifts in tree species composition. Specifically, we asked:

Question 1: Are process-based models able to simulate significant losses of tree species caused by browsing in the regeneration layer, and if so, what are the effects on stand composition?

In addition to influencing species composition, ungulates also substantially impact regeneration height growth and stand height development (Bernard et al., 2017; Bödeker et al., 2023; Eiberle and Nigg, 1987; Kupferschmid et al., 2014). Here, we evaluated the question:

Question 2: How do different ungulate densities influence sapling height growth and trees top heights?

Amongst directly causing species-specific recruitment failures from physical damage (Question 1), selective browsing might also indirectly influence stand species composition if preferentially browsed species exhibit growth reduction (Question 2). This would undermine their ability to compete for essential resources such as light, water, and nutrients. This mechanism describes disadvantages caused by losing competitive strength and changing social status within density-dependent competition structures during stand development (Clasen et al., 2015; Connell, 1990). For this reason, we also evaluated differences between the development of stands featuring fixed sapling-stress thresholds, a limit of consecutive years that a sapling can tolerate browsing, compared to stands without these assumptions. Consequently, the stand development is only influenced by interspecific resource competition, excluding explicit mortality from browsing events.

Question 3: Are there notable differences between simulation results with and without pre-defined sapling-stress thresholds?

## 2. Methods

### 2.1. Stand structure

To evaluate sapling and stand development under different browsing regimes, we simulated regeneration planting assuming a  $100 \times 100\text{m}^2$  parcel with our model. In this study, we designed a mixed stand consisting of three common species in Central Europe (Brus et al., 2012): Norway spruce (*Picea abies* L. H.Karst.), Silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.). To establish this composition, we randomly allocated virtual 2-year-old saplings with a height of 0.3 m and similar stem numbers each (Fig. 1, stand development). The site conditions were similar to those of a plantation, with no seeds available in the soil. Additional natural regeneration, older trees, and surrounding

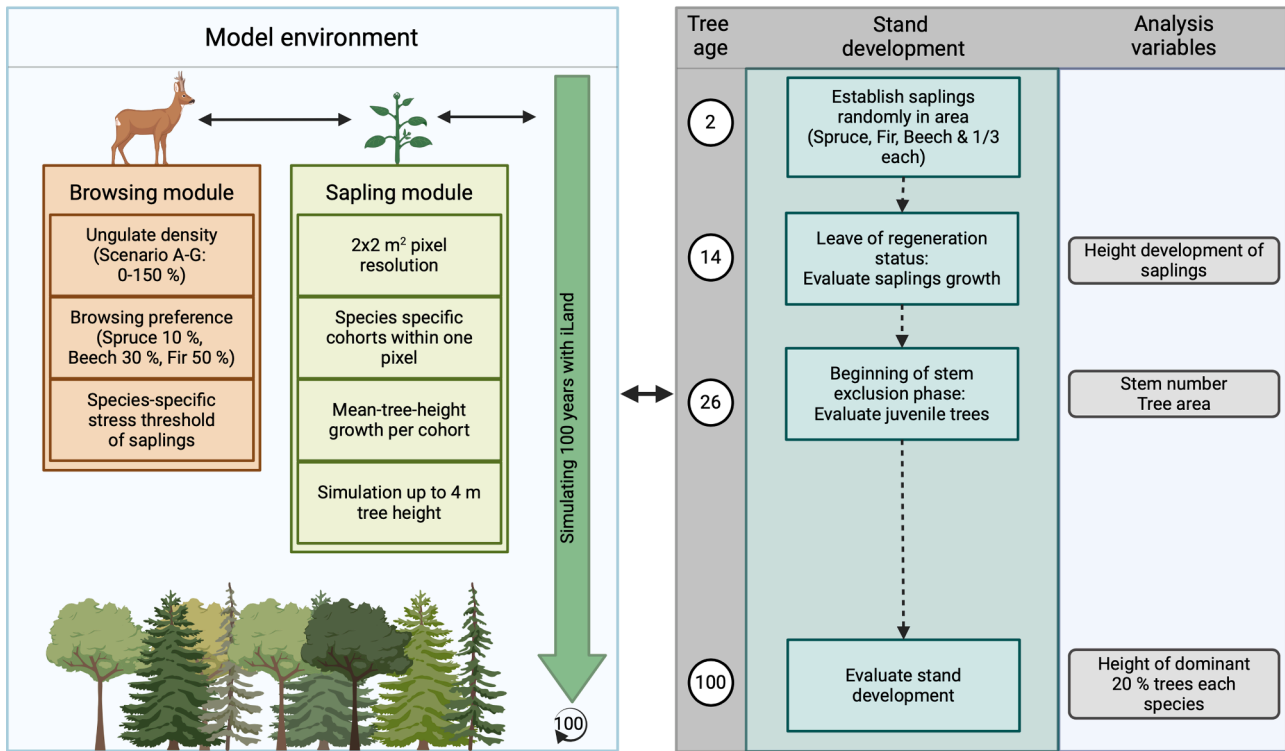


Fig. 1. Overview of model structure (left) and stand development with analysis variables (right).

stands were not considered and did not impact the growth of young trees in our model to minimize other influences. Furthermore, no silvicultural interventions were conducted, such as tending and thinning operations. Soil conditions were adapted to common values for Central Bavaria (Germany), where forests with spruce, beech, and fir occur. We applied historical climate data from 1981 to 2005 (Mean annual precipitation: 895 mm, mean annual temperature 8.58 °C), and a sensitivity analysis for the climate conditions was conducted (see Section 3.4 and Supplementary material).

### 2.2. Browsing assumptions

Since browsing assumptions can vary spatially and temporally, in this study, we assume that three factors mainly determine ungulate browsing, i.e., for simulating the effects of roe deer (Fig. 1 and Table 1, browsing assumptions). First, a species-specific browsing preference is necessary to describe the tendency of ungulates to browse certain tree species. Our assumption for reference browsing preferences was drawn from the available literature (Angst and Kupferschmid, 2023; Borowski et al., 2021; Boulanger et al., 2009). The reference browsing preferences, representing average ungulate density in our study area, was 10 % for Norway spruce, 30 % for European beech, and 50 % for Silver fir. These preferences are discussed in Section 4.2, and a sensitivity analysis was conducted (see Section 3.4 and Supplementary material).

Additionally, to address the impact of ungulate density on browsing effects, which has already been demonstrated (Champagne et al., 2021; Tremblay et al., 2007), we changed the assumed ungulate density in different scenarios (Table 1). The product of both constants, browsing preference, and ungulate density, represents the probability that a sapling cohort will be browsed in a given year, which we term browsing probability (Eq. (1)).

Eq. (1): Browsing probability for one sapling cohort per year.

$$\text{browsing probability} = \text{browsing preference} * \text{ungulate density} \quad (1)$$

As a reference scenario (A), we used 0 % ungulate density, so browsing is

Table 1  
Overview of the simulated scenarios.

SCENARIO	UNGULATE DENSITY (UD)	BROWSING PREFERENCE	STRESS THRESHOLD
A	0 %		Enabled (EST):
B	25 %		Norway spruce 3 years,
C	50 %	Norway spruce 10 %,	European beech 3 years,
D	75 %	European beech 30 %,	Silver fir 5 years
E	100 %		
F	125 %	Silver fir 50 %	
G	150 %		
DST	150 %		Disabled (DST)

absent. For the following scenarios, we increased the ungulate density by an additional 25 %-points for each subsequent scenario (Table 1). Considering an expected 100 % ungulate density, we assume that Norway spruce has an anticipated browsing probability of 10 % p.a., European beech of 30 % p.a., and Silver fir of 50 % p.a., exerted on all cohorts in the area.

The third browsing parameter is a species-specific stress threshold for saplings, explained above. This threshold defines a limit of consecutive years that a sapling can survive without height increment (Table 1), i.e., when any height increment is prevented by browsing. To address the hypothesis of changing social tree position within enlarging density-dependent competition (shifted biotic competition, question 3), we tested one scenario without this threshold (DST). In this scenario, saplings remain in the stand and do not die due to browsing impacts (i.e., they can tolerate unlimited browsing damages that result in loss of height growth indefinitely).

The impact of a single browsing event is heavily discussed in the literature. Our study assumes that browsed saplings show no height growth when affected, but they remain at the same height for the entire year. In our model, only saplings ≤ 2 m are subject to browsing; beyond this height, we assume the leading shoot is no longer affected by browsing but rather by competition with other trees.

### 2.3. Modelling

We used the individual-based forest ecosystem model iLand (Version 1.1.2 MSCV, Build Aug 9 2022) (Rammer and Seidl, 2022) to simulate stand development. iLand is process-based and simulates trees individually and dynamically, depending on resource availability. Resource allocation is modeled using a light-use efficiency approach that includes climatic and edaphic influences. This model defines saplings as trees up to 4 m tall and simulates them as cohorts on  $2 \times 2\text{m}^2$  cells. While a species is limited to a single cohort on a cell, cohorts of multiple species can coexist and compete. Within these cohorts, every species was simulated with a mean-tree height growth, mainly determined by light availability. Light availability in a cell depends on the canopy shading of trees taller than 4 m and does not include shading within the sapling layer. As soon as one sapling reaches 4 m in height, one individual tree of that species is recruited, and all remaining saplings within that cell die, regardless of the tree species (Seidl et al., 2012).

We adapted the parameters of iLand's browsing module according to our browsing assumptions for species-specific browsing probabilities and ungulate densities and kept model default values for the species-specific stress thresholds (EST) of saplings (Rammer, 2021).

To retain model integrity, we did not modify any fundamental simulation processes in iLand. iLand was successfully used in multiple studies previously, and evaluation experiments showed that the model simulated meaningful ecological responses and growth patterns, particularly in Central Europe (Rammer and Seidl, 2015; Seidl et al., 2017; Sommerfeld et al., 2021; Thom et al., 2022).

We used iLand's integrated forest management (Rammer and Seidl, 2015) to simulate the sapling planting. Each cell consisted of cohorts of all three species. Besides this, no management was conducted. The simulation was repeated 100 times for each scenario (Fig. 1).

### 2.4. Analysis

We focused on two stand characteristics to evaluate tree species loss caused by ungulates, specifically stem number and occupied area. Balanced stem numbers are crucial for mixed species stand development and were counted at age 26, at the start of the stem exclusion phase, where fir and beech have the highest stem numbers ( $> 4\text{ m}$  tree height) during the simulated period. At this peak, most trees overcame the sapling status and were simulated individually. After this point, stem numbers decreased again due to self-thinning from the intensification of tree-level competition. Furthermore, stand dynamics are influenced by the area a single tree uses, which provides a more balanced comparison of broadleaf trees and conifers. Here, we used sums of the predicted tree area (TA) (Dahm, 2006) covered by a tree to compare the area needs of all species (Eq. (2)).

Eq. (2): Calculation of tree area (TA) in  $\text{m}^2$ ,  $i$ =individual tree,  $n_s$ =number of trees per species,  $s$ =tree species,  $\alpha$  and  $\beta$ =species-specific constants, BA=basal area.

$$TA_s = \sum_{i=1}^{n_s} \alpha_s + \beta_s * BA_i \quad (2)$$

Absolute and relative tree area values were obtained at the beginning of the stem exclusion phase (tree age 26) and at the end of the simulation (tree age 100).

We also evaluated the height development of saplings and adult trees (height  $> 4\text{ m}$ ). The statistical analysis for the regeneration was executed only for saplings in the height stage of 1.3 to 4 m and at age 14, which is the last year all species and scenarios were still represented in the models sapling stage. Additionally, we analyzed the dominant height, using the dominant 20 % of trees (20 % highest diameters at 1.3 m tree height) for each species. Since we wanted to know the influence of browsing on long-term stand development, we used tree age 100 for analysis.

To evaluate the theory of shifted biotic competition as a changing social position triggered by density-dependent competition within stand development introduced by browsing (Question 3), we used scenarios G and DST to check for differences at age 100 caused by the stress threshold. Here, browsing has the strongest influence on stand development due to a high ungulate density (150 % ungulate density).

The data management and analysis were conducted in R (Version 4.2.1). To evaluate differences between scenarios, we used Cohen's  $d$  effect size (Eq. (3)) (Cohen, 1992).

Eq. (3): Cohen's  $d$  effect size (Cohen, 1992).  $d$ =effect size,  $\mu$ =mean of the group,  $\sigma$ =standard deviation. Used effect size interpretation:  $|d| < 0.2$ : negligible,  $0.2 < |d| < 0.5$ : small,  $0.5 < |d| < 0.8$ : moderate,  $|d| > 0.8$ : large.

$$d = \frac{\mu_x - \mu_y}{\sigma} \quad (3)$$

## 3. Results

### 3.1. Shifts of tree species proportions (Question 1)

#### 3.1.1. Stem numbers

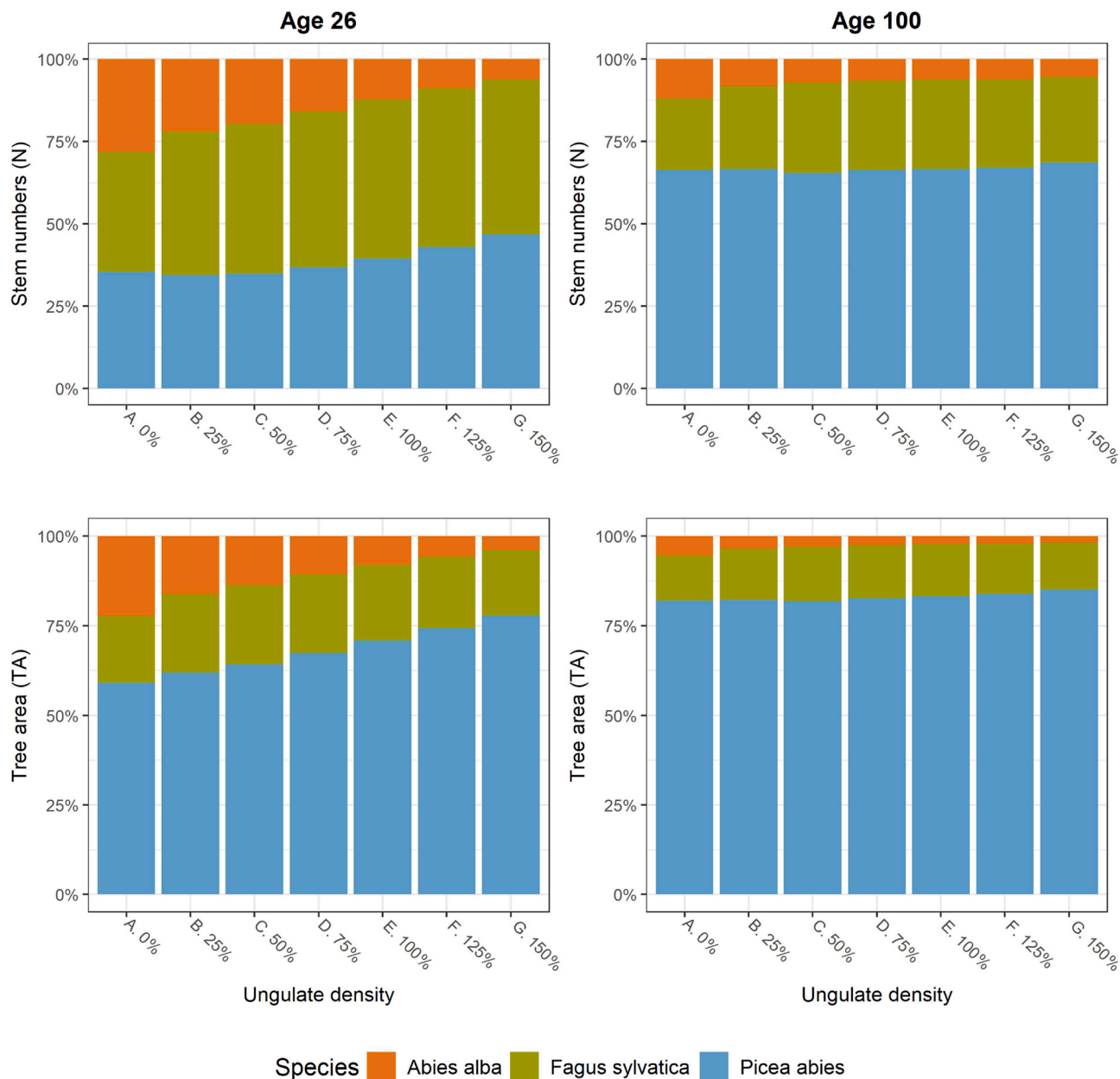
Fig. 2 (top left) illustrates with relative stem numbers at tree age 26 how Norway spruce and European beech dominated the stand in scenarios with browsing (B - G). At the same time, Silver fir generally had lower relative numbers. The data indicate that at this age, the proportion of spruce slightly declined from scenario A to C but increased as game browsing intensified. Conversely, stem numbers of Silver fir consistently decreased with rising ungulate density, ranging from 28 % without browsing (Scenario A) to 6 % with strong browsing pressure in scenario G. Beech initially experienced an increase in stem proportions from 36 % in scenario A to 48 % in scenario E, followed by a slight decline. By tree age 100 (Fig. 2, top right), fir almost vanished, beech also showed smaller proportions, and spruce dominated.

Comparing the absolute stem numbers of spruce at tree age 26 showed negligible ( $|d| < 0.2$ ) to small ( $0.2 < |d| < 0.5$ ) effect sizes (Appendix 1). However, the result indicated large ( $|d| > 0.8$ ) effect sizes across all combinations for fir (Appendix 2). This is because the absolute stem numbers of fir decreased as ungulate pressure strengthened. Most scenario combinations of beech exhibited large effect sizes, which expressed higher stem numbers with increasing browsing pressure than scenario A (0 % ungulate density), except for high browsing pressure in scenario G (150 % ungulate density) (Table 2 and Appendix 3).

#### 3.1.2. Shifts in tree area proportions

At age 26, the tree area proportions of spruce increased with higher ungulate pressure, dominating the stand with 59 % of the total shares in scenario A to 78 % in scenario G (Fig. 2, bottom left). At the same time, the area covered by fir decreased from 22 % of the total area in scenario A to 4 % in scenario G. Beech initially showed an increase from scenario A to C, but then declined again from scenario D to G. By the age of 100 (Fig. 2, bottom right), spruce became more dominant, covering more than 82 % of the total area across all scenarios. Fir had minimal proportions, with just 5 % in scenario A and even less in other scenarios. Beech followed a similar trend as at age 26, with increasing proportions from scenario A to C and decreasing shares with higher browsing pressure, but with smaller proportions.

Regarding the absolute tree area at age 26, spruce covered a larger area with increasing browsing pressure up to scenario D. After that, the area shrank compared to scenario A (without browsing) (Table 3). Large effect sizes were observed for spruce at this age, although some comparisons showed smaller effects. Fir exhibited a sharp decline in tree area of  $-87\%$  from scenario A to G, and large effect sizes for all combinations were found. This emphasizes the substantial decline of fir's tree area due to browsing. Beech covered larger areas in scenarios with moderate browsing pressure (B-D) when compared to scenario A. In



**Fig. 2.** Species proportions based on stem numbers (N) and on tree area (TA) in m<sup>2</sup> for every experimental tree species at different scenario modeling years (A: 0 % ungulate density, B: 25 % ungulate density, C: 50 % ungulate density, D: 75 % ungulate density, E: 100 % ungulate density, F: 125 % ungulate density, G: 150 % ungulate density).

**Table 2**

Mean stem numbers (N) and standard deviation (sd) of simulated scenarios for all tree species at age 26 for all iterations, including relative value compared to scenario A in % (RV). Scenarios: A-G: 0 % - 150 % ungulate density.

Age	Scenario	Picea abies			Abies alba			Fagus sylvatica		
		N	sd	RV	N	sd	RV	N	sd	RV
26	A. 0 %	805	28	100.0 %	645	24	100.0 %	829	40	100.0 %
	B. 25 %	805	29	100.1 %	515	25	79.8 %	1019	41	123.0 %
	C. 50 %	799	26	99.3 %	450	24	69.7 %	1042	42	125.7 %
	D. 75 %	802	26	99.7 %	346	23	53.7 %	1028	48	124.0 %
	E. 100 %	799	27	99.3 %	247	22	38.3 %	978	45	117.9 %
	F. 125 %	799	29	99.2 %	165	15	25.6 %	899	44	108.4 %
	G. 150 %	797	27	99.0 %	107	14	16.6 %	798	35	96.3 %

**Table 3**

Mean tree area (TA) in m<sup>2</sup> and standard deviation (sd) of simulated scenarios for all tree species at ages 26 and 100 of all iterations. Relative value compared to scenario A in % (RV). Scenarios: A-G: 0 % - 150 % ungulate density.

Age	Scenario	Picea abies			Abies alba			Fagus sylvatica		
		TA	sd	RV	TA	sd	RV	TA	sd	RV
26	A. 0 %	7520	177	100.0 %	2838	108	100.0 %	2366	118	100.0 %
	B. 25 %	7692	185	102.3 %	2005	102	70.7 %	2721	113	115.0 %
	C. 50 %	7635	167	101.5 %	1627	88	57.3 %	2624	109	110.9 %
	D. 75 %	7581	173	100.8 %	1209	82	42.6 %	2443	118	103.3 %
	E. 100 %	7438	177	98.9 %	846	75	29.8 %	2219	104	93.8 %
	F. 125 %	7333	182	97.5 %	560	52	19.7 %	1967	99	83.1 %
	G. 150 %	7232	163	96.2 %	360	48	12.7 %	1696	79	71.7 %
100	A. 0 %	11,242	339	100.0 %	728	128	100.0 %	1744	288	100.0 %
	B. 25 %	11,322	326	100.7 %	479	108	65.9 %	1962	315	112.5 %
	C. 50 %	11,263	357	100.2 %	396	88	54.4 %	2094	328	120.1 %
	D. 75 %	11,278	330	100.3 %	347	85	47.7 %	2012	305	115.4 %
	E. 100 %	11,321	353	100.7 %	305	85	42.0 %	1956	367	112.1 %
	F. 125 %	11,358	367	101.0 %	284	88	39.0 %	1898	339	108.8 %
	G. 150 %	11,457	311	101.9 %	238	69	32.7 %	1757	297	100.8 %

contrast, scenarios with higher browsing pressure (E-G) resulted in a covered area decrease of about 28 % when compared to scenario A. Comparisons of beech's tree area revealed large effect sizes between all scenarios, except A-D with moderate ( $0.5 < |d| < 0.8$ ) effect size.

At age 100, the +2 % increase of spruce's absolute tree area corresponded to negligible to small effect sizes for most comparisons and moderate effects for some comparisons. Conversely, the strong decline of the covered area of fir at age 100 exposed large effect sizes between most scenarios. Some exceptions indicate small to moderate effects. Regarding browsing influence (B-G), beech had higher proportions than scenario A, up to +20 % (Scenario C). Some larger effect sizes were observed, but most comparisons did not yield remarkable differences for this species at this age.

### 3.2. Height development (Question 2)

#### 3.2.1. Sapling height

As browsing pressure increased, the average height growth of saplings decreased across all species, although the intensity of this decline varied (Fig. 3, bottom part). The extent of the decrease compared to scenario A at age 14 is summarized in Table 4. Here, fir suffered the most and lost 63 % of its height development within 12 years. The model indicated large effect sizes for all comparisons and tree species.

#### 3.2.2. Dominant tree height ( $H_{T20}$ ) development

We also analyzed the height of the dominant 20 % of trees for each species at age 100. Spruce exhibited the tallest trees during the simulation, followed by beech, then fir (Fig. 3 and Table 5). It should also be noted that the dominant stand was mainly composed of spruce. Beech had smaller stem numbers, and fir had less than 10 trees left in this section.

We found that each subsequent increase in ungulate density resulted in small to moderate effect sizes regarding top heights for spruce. Other comparisons revealed large effect sizes, and dominant spruces gained 3 % more height with strong browsing affection compared to scenario A. Comparisons between scenario A and browsing scenarios (B-G) showed large effects for fir, which had a mean tree number count of between 5 and 9 individuals per iteration. Comparisons with the next highest ungulate density resulted in negligible to small effect sizes; other comparisons revealed moderate to large effects. Between scenarios A and G, fir faced a 5 % loss in mean dominant tree height. Especially during the juvenile age (age 30), the differences between browsing scenarios occur more clearly. For beech, negligible to small effect sizes were observed for most comparisons of dominant tree height at age 100. Overall, the height of this species decreased by about 1 % with rising ungulate pressure.

### 3.3. Shifted biotic competition (Question 3)

When comparing the effects of a species-specific stress threshold during sapling status at age 100, large effect sizes can be noted between scenarios with disabled (DST) and enabled (EST, scenario G) sapling stress thresholds (Appendix 4). For fir, large effect sizes were observed for stem numbers, tree area, DBH (diameter at 1.3 m tree height), and general tree height. This species showed higher values for stem number and tree area as with the enabled limit; and with the disabled limit, average DBH and general tree height were smaller (Fig. 4). For spruce and beech, small effect sizes can be noted for the represented tree area, and other comparisons did not reveal notable distinctions.

### 3.4. Sensitivity runs

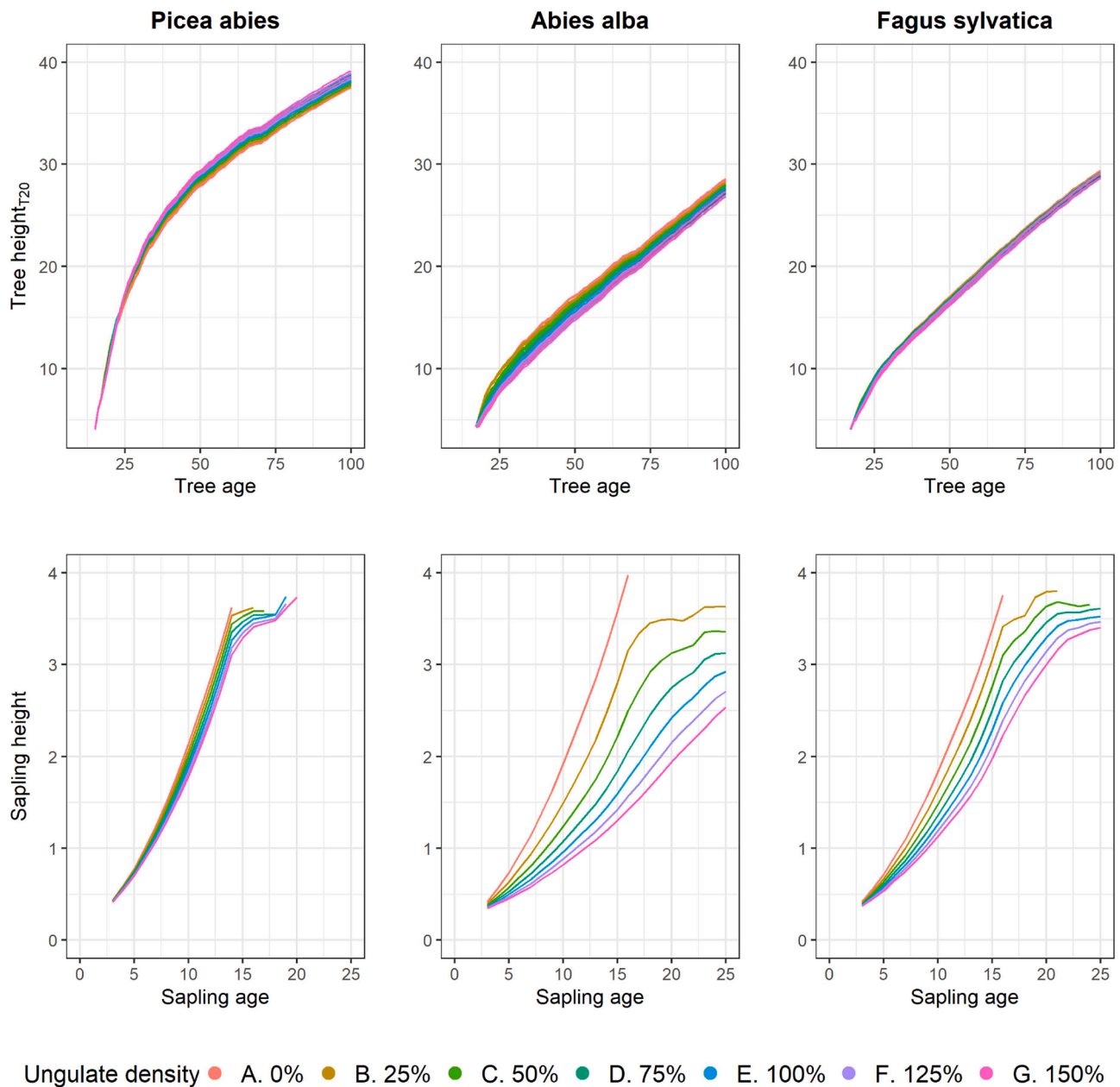
To assess how the selected browsing parameters affected stand development, we conducted five sensitivity runs with 10 repetitions each (Supplementary material). Results showed that sapling height development, regardless of species strongly depended on the chosen browsing preferences and decreases with higher browsing affection. This influence cascaded into subsequent stand development with changing stem proportions, tree areas, and height development.

When analyzing the impacts of climate scenarios without disturbance influences, only minor changes were observed. There were slight differences within height development, but the proportions of each species in terms of stem numbers and covered areas (TA) remained stable.

## 4. Discussion

### 4.1. Results

Our study evaluated whether browsing experiments using process-based models can help to simulate species-shifting effects caused by ungulates. According to stem numbers and tree area proportions at age 26, heavy browsing scenarios support Norway spruce, whereas Silver fir is chronically and strongly suppressed. This result corresponds with several well-known observations of field studies like those conducted by Ammer (1996) and Gill (1992). Contrary to the results of Rammig et al. (2007), who predicted a decline in spruce stem numbers with higher browsing probability, our simulation captured, but possibly overestimated, the past competitive advantage of spruce over fir and beech. This is consistent with field studies that indicated high browsing pressure supports spruce (Bernard et al., 2017; Unkule et al., 2022). For beech, we noticed a trend of increasing stem numbers and area proportions as ungulate density increased, even though beech exhibited a higher browsing preference than spruce. This can be associated with



**Fig. 3.** Mean dominant tree height (Tree height<sub>T20</sub>) & sapling height development (in m) over age (in years) of simulated scenarios. Models sapling status restricts sapling height up to 4 m. Scenarios: A-G: 0 % - 150 % ungulate density.

**Table 4**

Mean sapling height ( $H_{\text{Sapling}}$ ) in m, standard deviation (sd), and relative values (RV) compared to scenario A of sapling age 14. Scenarios: A-G: 0 % - 150 % ungulate density.

Scenario	Picea abies			Abies alba			Fagus sylvatica		
	$H_{\text{Sapling}}$	sd	RV	$H_{\text{Sapling}}$	sd	RV	$H_{\text{Sapling}}$	sd	RV
A. 0 %	3.63	0.00	100.0 %	3.20	0.00	100.0 %	3.02	0.00	100.0 %
B. 25 %	3.53	0.01	97.5 %	2.47	0.02	77.3 %	2.71	0.01	89.6 %
C. 50 %	3.44	0.01	95.0 %	1.97	0.02	61.5 %	2.43	0.02	80.6 %
D. 75 %	3.35	0.01	92.5 %	1.65	0.02	51.6 %	2.20	0.02	73.0 %
E. 100 %	3.27	0.01	90.1 %	1.44	0.02	45.1 %	2.02	0.02	66.8 %
F. 125 %	3.18	0.02	87.8 %	1.30	0.02	40.6 %	1.87	0.02	62.0 %
G. 150 %	3.11	0.02	85.7 %	1.19	0.01	37.2 %	1.75	0.02	58.0 %

retrospective field studies of Nagel et al. (2015) or results published by Angst & Kupferschmid (2023). A logical explanation for this development is not only a stochastic, predictable evolution of browsing affection, but also the additional competitive development from the

availability of resources (e.g., light) resulting from the loss of fir saplings.

Spruce exhibited overwhelming dominance according to stem numbers and covered area at age 100, while the growth of both fir and

**Table 5**

Height of dominant 20 % of trees ( $H_{T20}$ ), standard deviation (sd), relative value compared to scenario A (RV), dominant stem number ( $N_{T20}$ ) at tree age 100. Scenarios: A-G: 0 % - 150 % ungulate density.

Scenario	Picea abies				Abies alba				Fagus sylvatica			
	$H_{T20}$	sd	RV	$N_{T20}$	$H_{T20}$	sd	RV	$N_{T20}$	$H_{T20}$	sd	RV	$N_{T20}$
A. 0 %	37.8	1.4	100.0 %	49	28.5	0.6	100.0 %	9	29.3	0.7	100.0 %	16
B. 25 %	37.9	1.4	100.4 %	49	28.0	0.8	98.6 %	6	29.1	0.8	99.5 %	19
C. 50 %	38.1	1.4	100.8 %	48	27.8	0.9	97.7 %	6	29.0	0.9	99.2 %	20
D. 75 %	38.3	1.4	101.4 %	47	27.6	1.0	96.9 %	5	29.0	0.9	99.2 %	20
E. 100 %	38.5	1.4	101.8 %	47	27.4	1.2	96.3 %	5	28.9	1.0	98.9 %	19
F. 125 %	38.6	1.4	102.3 %	47	27.1	1.3	95.1 %	5	29.0	1.0	98.9 %	19
G. 150 %	38.9	1.4	102.9 %	47	27.1	1.2	95.3 %	4	28.9	1.1	98.6 %	18

beech were substantially suppressed. This was the case regardless of browsing conditions and increasing ungulate pressure on spruce. Following the initial phases of stand establishment, this pattern underscores that fir in particular, requires silvicultural intervention during tending and thinning operations. This observation reinforces the critical need for earlier under-canopy-establishment of fir to promote balanced stand development and maintain species diversity (Albanesi et al., 2008). A reduction of browsing pressure would thus provide a precondition for enhanced fir proportions but is not enough to sustain said proportions. We selected favorable forest growth conditions and excluded any disturbances that favored spruce. Because of this we caution not to overinterpret the results for stand age 100. However, we regard the tree species and dendro-ecological shifts simulated in response to increasing browsing pressure until age 26 as robust. These shifts are probably also valid under worse climate scenarios, as many disturbance risks are age-dependent. In contrast to many field studies (Ammer, 1996; Candaele et al., 2023; Nopp-Mayr et al., 2020), which only differentiate between fenced and non-fenced areas, our results showed notable shifts in stem numbers and tree area proportions after 24 years of simulation caused by browsing affection, even with 25 %-point changes in ungulate density.

The height development of trees is a crucial factor for tree competition. Our results show that slower sapling height increment is caused by increasing browsing pressure for all species. Especially for fir, a palatable species, an increment loss of 54 % after 12 years between scenario E (100 % ungulate density) and A (fenced) already implies the failure of many saplings. Even with the strong shade tolerance of fir in the juvenile stage (Brzeziecki and Kienast, 1994), this development results in permanent repression and a strong competitive disadvantage. This occurs because substantial height loss increases mortality, especially under high browsing pressure (Eiberle and Nigg, 1987; Motta, 2003). As we were simulating on a  $100 \times 100\text{m}^2$  square without an older tree canopy above, fir cannot play out its shade tolerance during the juvenile stage against other species. The permanent canopy pressure of spruce instead causes a permanent suppression effect, resulting in a diminished growth rate of fir. To interpret the top-height development of fir and beech, it is essential to consider the lower stem numbers that result from increased mortality during the sapling stage. Saplings of all three species initially suffer under high ungulate pressure, but the height growth of spruce later accelerates and suppresses the admixed species. Over time, spruce profits from high ungulate densities due to less competition (Brzeziecki and Kienast, 1994).

The well-performing development of spruce in our simulations with historical climate, either height growth or stem numbers, is unlikely today, even in unmanaged forests, because of the effects of climate change and its associated disturbances (McDowell et al., 2020). Since our study aimed to analyze the effects of browsing, additional disturbances or management decisions were not implemented. However, the survival probability of spruce until age 100 would rather range between 0.4 and 0.5 (Brandl et al., 2020), thus the exclusion of disturbances is a strong assumption that favors spruce. According to stem numbers and the area proportions of the tree species, beech benefits from moderate

browsing scenarios. Conversely, sapling height development suffers under high browsing pressure. Considering these two results, the well-performing beech development underlines the theory of improved resource availability (especially light) caused by fir mortality and could be even higher with realistic levels of spruce disturbances (Seidl and Rammer, 2017; Unkule et al., 2022) or regular forest management options, which ensure the forest-owner intended mixed species composition. Considering this, it should be noted that process-based models, like iLand, can simulate interspecific competition structures caused by ungulate browsing, which affects tree height development individually.

According to Harmer (2001), saplings of certain species can resist several years of browsing impact and a loss of height increment without dying, which leads to the theory of shifted biotic competition as an indirect mortality effect of browsing pressure (Clasen et al., 2015; Connell, 1990). Excluding the standard fixed sapling-stress threshold helped to identify the effect caused by such a fixed sapling-stress threshold. Here, the stem numbers of all species increased without considering this threshold (Scenario DST). Consequently, our simulated stand consisted of more palatable species (fir and beech), but with substantially reduced sizes (dominant and general tree heights, DBH). The loss of overall size in the presence of admixed species with high ungulate preference illustrates how these trees are significantly suppressed and struggle to establish themselves adequately given the high tree densities in this scenario. This impedes the intended successful stabilization of mixed species stands and the associated ecosystem services they provide. We only analyzed differences for strong browsing affection (150 % ungulate density); the effects with less ungulate pressure are expected to be weaker.

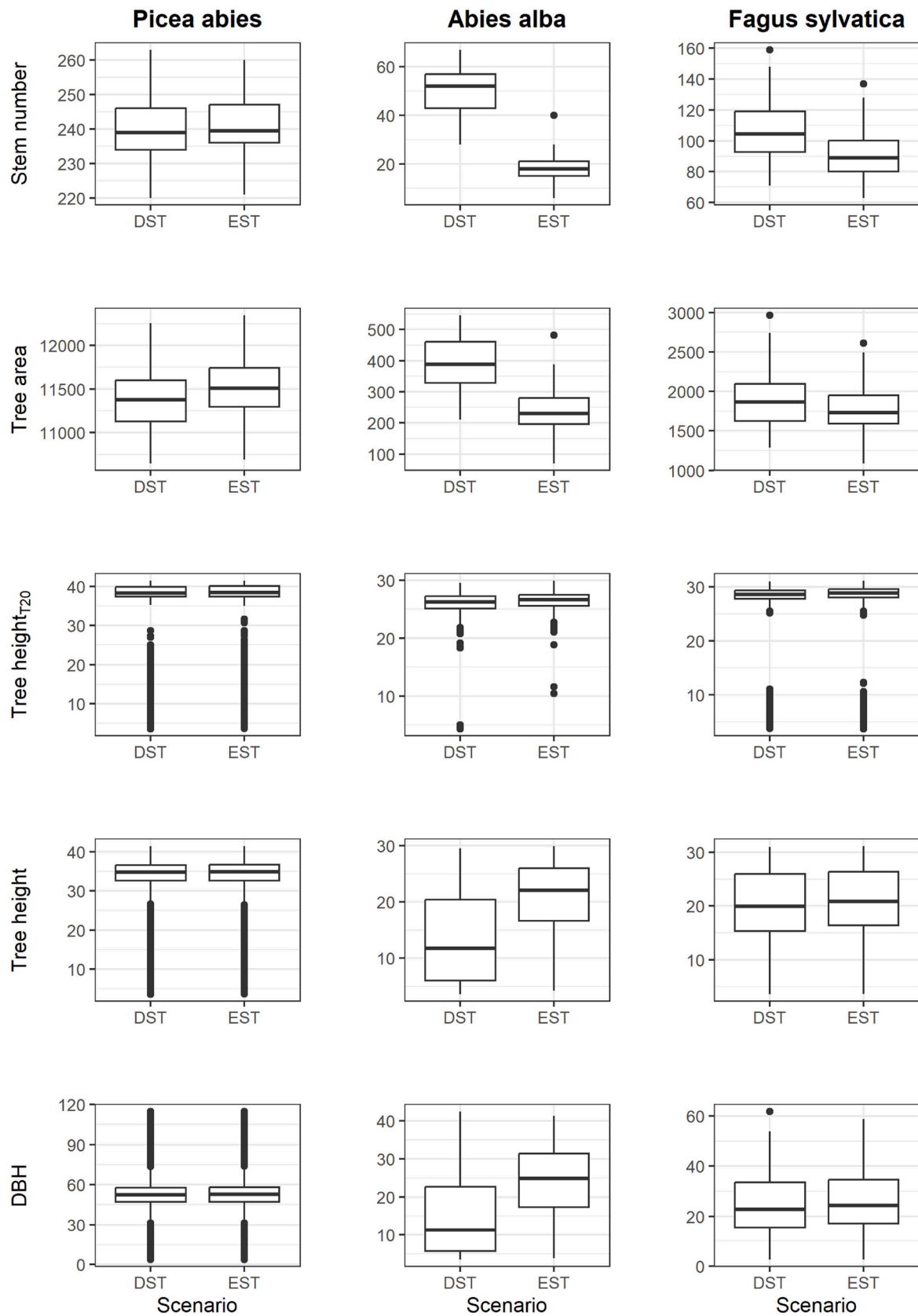
We used historical climate (1981–2005) for growth simulation, and it should be added that sapling growth and tree height development are shifting due to climate change (Millar et al., 2007; Pretzsch et al., 2014). Sensitivity runs were conducted for different climate scenarios (RCP 2.6, RCP 4.5, and RCP 8.5), where only minor differences regarding height development can be noted (see Section 3.4 and Supplementary material).

## 4.2. Methods and limitations

### 4.2.1. Browsing variables

The effect of browsing on regeneration has already been tested by different study approaches (Ammer, 1996; Augustine and McNaughton, 1998; Bödeker et al., 2023; Csilléry et al., 2022). To implement and evaluate the impact of ungulate browsing on a simulated ecosystem, we used constant species-specific browsing preferences, ungulate density, and fixed stress thresholds during sapling status. The browsing preference of deer is crucial for evaluating browsing effects, but is difficult to determine and can vary spatially and temporally. Studies in forest ecosystems are strongly driven by ungulate density and available food, so most studies are based on species selectivity indices like Ievlev's selectivity index (Boulanger et al., 2009; Szwagrzyk et al., 2020) or Simpson's index (Borowski et al., 2021). Studies we encountered used areas with several tree species, often with even more palatable species, e.g.,





**Fig. 4.** Comparison between enabled (EST) and disabled (DST) stress threshold at age 100 with 150 % ungulate density, tree area in m<sup>2</sup>, Tree height<sub>T20</sub>=height of 20 % dominant trees in m, tree height in m, DBH=diameter at 1.3 m tree height in cm.

sycamore maple (*Acer pseudoplatanus* L.) or rowan (*Sorbus aucuparia* L.) (Bödeker et al., 2023; Borowski et al., 2021; Boulanger et al., 2009), whereas our simulated ecosystem only consisted of spruce, fir, and beech. Borowski et al. (2021) modeled proportions of browsed saplings with a high ungulate density in 2017 between 0.30 and 0.55 for fir and 0.20 to 0.35 for beech. In a recent study in Switzerland, Angst & Kupferschmid (2023) stated that regarding palatability, ungulates prefer fir saplings, followed by beech and, lastly, spruce. Thus, we used fixed browsing preferences (Table 1) and kept these for the whole period of our simulated forest development, regardless of seasonal changes in browsing habits. For example, seeing 100 % ungulate density as an expected density results in browsing probabilities of 10 % p.a. for spruce, 30 % p.a. for beech, and 50 % p.a. for fir affecting all saplings within our area, independently of the abundance and species. These browsing probabilities principally reflect preferences, as mentioned by Angst & Kupferschmid (2023), who additionally concluded that rare species are browsed more often, which can only be implemented to a limited extent with the chosen preferences. Furthermore, the conducted sensitivity runs symbolize the variability for sapling and stand development, which the chosen browsing preferences can generate (see Section 3.4 and Supplementary material).

Ungulate movement and habitat preferences characterize ungulate density and behavior within habitats (Lamont et al., 2019; Putman and Moore, 1998; Valente et al., 2020). Determining the exact number of ungulates is challenging, so we used constant relative densities to simulate different scenarios (Table 1), resulting in a browsing probability per year. Habitat preference, changes in ungulate density, and seasonal differences in browsing behavior were not considered in our approach. Furthermore, the browsing height was restricted by a two-meter sapling threshold, which has also been used by other studies (Rammig et al., 2007). The loss of height and the recreation of saplings after browsing are species-specific and have been intensely discussed. For example, Angst & Kupferschmid (2023) show that beech saplings can act dynamically, and it is well known that some species produce a second terminal shoot during the growing season. In another study, Kupferschmid & Bugmann (2013) revealed that the recreation of saplings depends on the dominance level of the saplings. To keep the model parsimonious, we assumed a loss of the annual height growth in the affected year but no other damage to the sapling, regardless of the tree species. We do not expect that these simplifications compromised the basic validity of our results.

#### 4.2.2. Stand establishment and model setup

For this study, we simulated a newly established stand with three common Central European tree species (Brus et al., 2012) in an open area of  $100 \times 100\text{m}^2$ , which can result from damage caused by bark beetles or wind (McDowell et al., 2020; Seidl and Rammer, 2017). Therefore, all species were established simultaneously in our model, resulting in the same resource situation for all saplings. However, forest managers in Central Europe use an advance establishment of fir and beech in the under canopy to advance these admixed species and enhance the stands resilience (Knoke et al., 2023). This would have been suitable silvicultural management, especially for the two species fir and beech, which are known to be highly shade tolerant during the establishment phase (Brzeziecki and Kienast, 1994). Tree recruitment of fir is slower with increasing gap size (Albanesi et al., 2008), whereas spruce profits from the light availability of our simulated scenarios. When open areas occur, additional silvicultural management can support sapling growth for moderately browsed areas (Ficko et al., 2018) and adapt species composition, primarily through tending and thinning, according to forest owners' intention. Moreover, the model had no disturbance effects that would influence the proportions (McDowell et al., 2020; Rammig et al., 2007; Thom et al., 2017). In natural systems, saplings compete not only with other saplings for resources such as light and space, but with other ground flora (Langmaier and Lapin, 2020; Pröll et al., 2014). Harmer (2001) stated that this only has minor effects on

sapling development, and therefore, blurring effects caused by competition with grasses and shrubs were not included in our simulation.

Most modeling approaches are based on single-species stands, which do not directly consider interspecific competition structures for species composition and height development (Champagne et al., 2021; Clasen et al., 2015). In addition, the effects of (over-)abundance of ungulates are complex to diminish (Côté et al., 2004; Scheffer et al., 2001). Our application of iLand allowed us to investigate mixed stand development considering these often overlooked elements. Light availability is a crucial driver for saplings (Csilléry et al., 2022; Kupferschmid et al., 2014), so the light-use efficiency approach, as iLand uses for simulating sapling and individual tree development with density-dependent competition (Seidl et al., 2012), is a logical and suitable methodology.

## 5. Conclusion

Our study corroborates the suitability of process-based models to simulate dynamic shifts of tree species proportions caused by ungulate browsing. Species-specific tree height development with different browsing intensities was also demonstrated. Shifts in tree-species proportions and height development of forest ecosystems are strongly driven by ungulate browsing and competition, which can force insufficient stand development according to management interests. Even with minor changes in ungulate density, most effects responded significantly, and therefore, ungulate management can help to maximize the provision of several ecosystem services. Following the theory of shifted biotic competition, this resulted in increased numbers of individuals of palatable species, characterized by substantially smaller dimensions. Our study was conducted on a small-scale forest ecosystem with simulated site conditions of Central Europe. Further investigations should focus on large-ecosystem evaluation and also integrate ungulate habitat selection and browsing behavior with seasonal preferences, possibly using an agent-based ungulate approach.

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## CRediT authorship contribution statement

**Dominik Holzer:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kai Bödeker:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Werner Rammer:** Writing – review & editing, Software. **Thomas Knoke:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dominik Holzer reports financial support was provided by German Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors comply with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110741](https://doi.org/10.1016/j.ecolmodel.2024.110741).

Appendix

Appendix 1: Cohen's d effect size of tested variables for Norway spruce (*Picea abies*). UD=ungulate density, N = stem number, TA = tree area, sapling height, dominant tree height. Effect size interpretation:  $|d| < 0.2$ : negligible,  $0.2 < |d| < 0.5$ : small,  $0.5 < |d| < 0.8$ : moderate,  $|d| > 0.8$ : large

Picea abies													
N - Age 26							N - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	-0.021	0.203	0.093	0.193	0.217	0.297	0%	0.215	0.584	0.900	1.067	1.162	1.333
25%		0.220	0.112	0.209	0.233	0.311	25%		0.381	0.701	0.878	0.974	1.149
50%			-0.112	-0.004	0.028	0.103	50%			0.307	0.494	0.587	0.754
75%				0.104	0.132	0.211	75%				0.200	0.294	0.460
100%					0.031	0.104	100%					0.090	0.248
125%						0.068	125%						0.158

Picea abies													
TA - Age 26							TA - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	-0.950	-0.674	-0.349	0.460	1.043	1.695	0%	-0.242	-0.060	-0.107	-0.229	-0.330	-0.660
25%		0.319	0.619	1.398	1.957	2.639	25%		0.174	0.136	0.003	-0.105	-0.422
50%			0.322	1.146	1.737	2.452	50%			-0.043	-0.164	-0.265	-0.579
75%				0.814	1.400	2.081	75%				-0.127	-0.232	-0.558
100%					0.588	1.214	100%					-0.104	-0.407
125%						0.585	125%						-0.289

Sapling height - Age 14							Dominant tree height - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	18.016	22.675	30.242	35.391	37.181	46.750	0%	-0.413	-0.880	-1.554	-1.937	-2.494	-3.094
25%		9.473	17.388	23.539	27.088	35.031	25%		-0.437	-1.073	-1.453	-1.971	-2.566
50%			7.425	13.706	18.166	24.718	50%			-0.646	-1.045	-1.566	-2.187
75%				6.495	11.502	17.485	75%				-0.422	-0.937	-1.587
100%					5.335	10.761	100%					-0.492	-1.142
125%						4.831	125%						-0.681

Appendix 2: Cohen's d effect size of tested variables for Silver fir (*Abies alba*). UD = ungulate density, N = stem number, TA = tree area, sapling height, dominant tree height. Effect size interpretation:  $|d| < 0.2$ : negligible,  $0.2 < |d| < 0.5$ : small,  $0.5 < |d| < 0.8$ : moderate,  $|d| > 0.8$ : large

Abies alba													
N - Age 26							N - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	5.346	8.142	12.676	17.405	23.890	27.239	0%	2.024	2.600	3.031	3.247	3.220	3.917
25%		2.649	6.983	11.429	16.876	20.003	25%		0.661	1.129	1.394	1.424	2.133
50%			4.360	8.812	14.060	17.225	50%			0.454	0.727	0.786	1.443
75%				4.410	9.192	12.367	75%				0.284	0.365	1.002
100%					4.331	7.569	100%					0.093	0.698
125%						3.918	125%						0.566

Abies alba													
TA - Age 26							TA - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	7.926	12.233	16.956	21.326	26.798	29.504	0%	2.097	3.012	3.505	3.880	4.043	4.757
25%		3.972	8.638	12.969	17.935	20.692	25%		0.842	1.363	1.786	1.985	2.662
50%			4.907	9.506	14.720	17.772	50%			0.568	1.044	1.273	1.993
75%				4.618	9.482	12.636	75%				0.486	0.728	1.408
100%					4.419	7.668	100%					0.247	0.872
125%						3.986	125%						0.588

Sapling height - Age 14							Dominant tree height - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	60.524	94.004	124.606	145.499	167.236	200.259	0%	0.852	1.351	1.562	1.574	1.801	2.263
25%		28.458	47.588	60.552	71.116	81.988	25%		0.450	0.766	0.919	1.228	1.456
50%			17.517	29.470	38.617	47.056	50%			0.363	0.575	0.924	1.067

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Abies alba									
N - Age 26					N - Age 100				
75%		12.053	21.000	28.819	75%		0.247	0.616	0.663
100%			8.734	16.011	100%			0.363	0.349
125%				7.020	125%				-0.071

Appendix 3: Cohen's d effect size of tested variables for European beech (*Fagus sylvatica*). UD = ungulate density, N = stem number, TA = tree area, sapling height, dominant tree height. Effect size interpretation:  $|d| < 0.2$ : negligible,  $0.2 < |d| < 0.5$ : small,  $0.5 < |d| < 0.8$ : moderate,  $|d| > 0.8$ : large

Fagus sylvatica													
N - Age 26							N - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	-4.716	-5.187	-4.491	-3.497	-1.665	0.817	0%	-0.894	-1.445	-1.223	-1.035	-1.005	-0.654
25%		-0.553	-0.195	0.973	2.854	5.816	25%		-0.597	-0.360	-0.254	-0.156	0.236
50%			0.313	1.483	3.340	6.286	50%			0.237	0.291	0.424	0.820
75%				1.082	2.808	5.445	75%				0.073	0.193	0.587
100%					1.781	4.453	100%					0.105	0.461
125%						2.535	125%						0.381

TA - Age 26							TA - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	-3.077	-2.275	-0.659	1.318	3.655	6.650	0%	-0.721	-1.135	-0.904	-0.641	-0.490	-0.045
25%		0.874	2.400	4.626	7.097	10.505	25%		-0.413	-0.164	0.017	0.194	0.669
50%			1.588	3.804	6.308	9.737	50%			0.259	0.399	0.588	1.078
75%				2.015	4.362	7.411	75%				0.168	0.354	0.848
100%					2.477	5.644	100%					0.163	0.595
125%						3.009	125%						0.443

Sapling height - Age 14							Dominant tree height - Age 100						
UD	25%	50%	75%	100%	125%	150%	UD	25%	50%	75%	100%	125%	150%
0%	37.124	55.318	64.264	85.839	93.959	97.338	0%	0.452	0.559	0.549	0.765	0.753	0.963
25%		20.210	33.065	47.942	56.290	61.572	25%		0.144	0.162	0.391	0.394	0.620
50%			13.933	26.437	34.730	40.578	50%			0.027	0.245	0.255	0.473
75%				10.803	18.783	24.768	75%				0.204	0.216	0.424
100%					8.551	15.096	100%					0.020	0.230
125%						6.696	125%						0.204

Appendix 4: Cohen's d effect size of tested variables for differences between EST (enabled stress-threshold) and DST (disabled stress-threshold). Cohen's d effect size interpretation:  $|d| < 0.2$ : negligible,  $0.2 < |d| < 0.5$ : small,  $0.5 < |d| < 0.8$ : moderate,  $|d| > 0.8$ : large

Variable	Species	Mean EST	Mean DST	Cohen's d
Stem number	<i>Picea abies</i>	241	240	-0.138
	<i>Abies alba</i>	18	50	4.461
	<i>Fagus sylvatica</i>	90	107	0.997
Tree area	<i>Picea abies</i>	11510	11380	-0.396
	<i>Abies alba</i>	238	392	2.013
	<i>Fagus sylvatica</i>	1763	1903	0.431
Dominant tree height	<i>Picea abies</i>	35.54	35.98	0.049
	<i>Abies alba</i>	26.35	25.99	-0.182
	<i>Fagus sylvatica</i>	27.51	27.56	0.010
Diameter at breast height	<i>Picea abies</i>	52.6	52.5	-0.003
	<i>Abies alba</i>	23.9	14.7	-0.993
	<i>Fagus sylvatica</i>	25.6	24.0	-0.147
Height	<i>Picea abies</i>	33.82	33.85	0.005
	<i>Abies alba</i>	20.82	13.47	-1.054
	<i>Fagus sylvatica</i>	20.91	19.88	-0.160

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