The prospects of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst) in mixed mountain forests under various management strategies, climate change and high browsing pressure

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Abstract

In European mountain forests, the future of silver fir and Norway spruce appears to be uncertain, especially given the threat of climate change to both species and browsing pressure to fir. Stand development of mixed Dinaric mountain forest in Slovenia was simulated using the ForClim model for the period 2010-2110 to explore the prospects of both target species under five management scenarios (business-as-usual, no management, single tree selection, fir conservation, exclusion of browsing) and three climate scenarios (current climate and two climate change scenarios).

Simulations under the current climate revealed a decrease in fir proportion from 53% in 2010 to 14-37% in 2110, while the proportion of spruce remained relatively constant (13% in 2010 and 9-13% in 2110). Climate change may intensify the decline of both species along an elevation gradient. An upward shift was projected for fir in the observed period; in low-elevation stands (600-800 m a.s.l.) fir could almost disappear, while at high elevations (1050-1400 m a.s.l.) our simulations projected an increase in the proportion of both fir and spruce. No single management strategy proved to be significantly beneficial for either species.

The most promising were the fir conservation-oriented scenario and the exclusion of browsing; large ungulates strongly impacted the development of fir, but not that of spruce. Forest management affords different options for maintaining both species, but its capacity to prevent fir decline under climate change and high browsing pressure is limited. Concurrent measures of wildlife management and silviculture should be applied to maintain conifers in the studied forests.

Keywords: Stand dynamics; tree species composition; decline; Dinaric Mountains; ForClim

Introduction

Within a particular range of variability, changes in the structure and composition of forests are a fundamental part of their dynamics (Oliver and Larson 1996). However, forests are heavily influenced by humans, and this has resulted in dramatic changes in forest cover, forest productivity, and provisioning of ecosystem services globally (FAO 2010). Relative to the global scale, changes in forest stands at a regional and local spatial scale can be of different intensity and orientation and can be driven by various factors, of both natural and anthropogenic origin, which often act together and are interrelated. In recent times, human induced factors, especially forest management, climate change and wildlife management, have gained greater importance compared to natural factors (e.g. Millington et al. 2013), foremost among them being forest management.

In Europe, forest management has induced changes in the composition and structure of forests, as well as in their spatial distribution. The promotion of conifers and especially the anthropogenic expansion of Norway spruce (*Picea abies*) markedly changed the structure and composition of a large part of European forests (Spiecker 2000). However, the impact on the composition and structure of forest stands depends greatly on the silvicultural system applied in the region (e.g. Sendak et al. 2003). Uneven-aged forest management practiced in some areas across Europe (e.g. France, Germany, Slovenia, Switzerland) was based on natural regeneration and therefore promoted near-to-natural stand structure and composition. However, even in these cases, conifers, especially silver fir (*Abies alba*), were often directly or indirectly (e.g. by the plenter silvicultural system) favored (Schütz 2001).

Climate change has been recognized as an important driver of forest change across Europe (Lindner et al. 2010) and globally (FAO 2010). Changes in climate conditions may potentially trigger alerations in the phenology of tree species, shifts in their distribution range through altered 'climate envelopes' or community shifts (Walther et al. 2002). In addition, climate change may cause changes in the establishment potential (e.g. Mok et al. 2011) and growth rates of tree species (e.g. Jolly et al. 2001; van der Maaten-Theunissen et al. 2013), or increased mortality of tree species (e.g. Allen et al. 2015), all of which may result in the decline of particular tree species (e.g. Camarero et al. 2011) or shifts in species' distribution range (e.g. Cailleret and Davi 2011; Didion et al. 2011). In addition, climate change may severely alter the disturbance regime, characterized by an increased frequency of extreme events such as wind throws, drought or insect outbreaks (e.g. IPCC 2013), which may greatly impact the dynamics of forest stands (e.g. Temperli et al. 2013).

Browsing by large ungulates and pasture may additionally considerably influence the dynamics of forest stands. The differing palatability of tree species significantly affects their dynamics. In the mixed forests of Central Europe, silver fir has been recognized as one of the most heavily browsed tree species (Motta 1996; Heuze et al. 2005), significantly affecting its population dynamics and the dynamics of forest stands in the short and long run (e.g. Didion et al. 2009; Klopčič et al. 2010; Cailleret et al. 2014).

Changes in the structure and composition of forest stands over past decades, centuries or even millennia have been well investigated with different methods (e.g. Swetnam et al. 1999), but projecting the future development of forest stands is an even more challenging task, especially in a changing environment (e.g. Clark et al. 2001). Projections are of great importance for forest policy and forest management. Empirical growth and yield models were the first tools developed for predicting tree growth at the individual tree and stand level (Pretzsch et al. 2008). They use site- and tree species-specific regression functions to project the growth of trees and stands using a set of ontogenic and abiotic predictors. Like matrix models (Buongiorno and Michie 1980), they are typically based on observation data and were initially developed for projecting growth and yield information for forest managers and for improving planning in commercial forests (Peng 2000). They may be suitable for investigating management alternatives and short-term yield, but they are generally inappropriate for projections beyond the historical range of climate variability and are thus not applicable under rapidly changing climate conditions (Fontes et al. 2010). Process based models (PBM) are another approach to simulate forest stand development by coupling demographic and ecophysiological models (e.g. Guillemot et al. 2014), which simulate the effects of (changing) climate and CO2 on tree functioning using a mechanistic approach. Their general applicability is rather limited because they require a large number of parameters and measurements for calibration and validation. Alternatively, forest gap models (Bugmann 2001) require a limited number of site-derived parameters, have broad applicability and have been widely used for investigating long-term forest dynamics across environmental gradients (Lindner et al. 1996; Bugmann and Solomon 2000). Some of them have been successfully calibrated and tested to simulate the impacts of harvesting interventions and forest management regimes under climate change in different forest types (Lasch et al. 2005; Pabst et al. 2008; Rasche et al. 2013), including mixed mountain forests (e.g. Didion et al. 2011).

Mountain forests cover approximately 23% of the globe and 40% of European forest land and provide humankind with a multitude of ecosystem services (Price et al. 2011), retention and provision of drinking water, protection against natural hazards, provision of timber and woody biomass, recreation, and provision of natural habitats to animal and plant species being only some of them. The diversity of mountain forests in their structure and composition differs significantly between regions. In Europe, coniferous tree species, mainly Norway spruce and silver fir, but also others (e.g. European larch *Larix decidua*, some *Pinus* sp.), are an indispensable component of mountain forests. Compared to broadleaves, their large amount and general good quality of timber designate their higher economic value, especially noteworthy being Norway spruce, which was extensively planted and favored in past centuries (Spiecker 2000). In Central, Southern and Southeastern Europe, mixed silver fir-European beech (*Fagus sylvatica*)-Norway spruce mountain forests are one of the prevailing forest types. Populations of both dominant coniferous species of these forests – Norway spruce and silver fir – have undergone significant changes in recent centuries. In the second half of the 20th century, the decline and decrease in proportion of silver fir due to various factors has been reported in several studies from many mountain regions (e.g. Oliva and Colinas 2007; Elling et al. 2009; Vrška et al. 2009; Camarero et al. 2011; Ficko et

al. 2011; Durand-Gillmann et al. 2014), while more recently many mountain regions across Europe have experienced a Norway spruce decline caused mainly by extensive bark beetle outbreaks closely related to changes in climate (e.g. Hlásny and Turčáni 2013). The decrease in the proportion of silver fir in stand stocking during several decades was reported to be as high as 80% in the Carpathians (Vrška et al. 2009) and around 20% in the Dinaric Mountains (Ficko et al. 2011). Following these facts and climate change projections (IPCC 2013), the future of Norway spruce and silver fir in the mixed mountain forests of Europe appears to be uncertain; moreover, in some areas even the preservation of these main native coniferous tree species may be in question. Therefore, questions arise about the possibility of maintaining both conifers in these forests in a sufficient amount to provide the desired ecosystem services, especially timber production and habitat provisioning related to biodiversity conservation. Accordingly, these are among the main management challenges in Central and Southeastern Europe, and are also of exceptional importance in Dinaric mountain forests. The study area seems appropriate to address such a study since it represents a narrow corridor in the distribution range of both studied tree species connecting Central European and Southeastern European populations (Euforgen 2015); the geomorphological features of the Dinaric Mountains induce high variability in site and climate conditions over a relatively small area, which may enhance the susceptibility of both coniferous species to climate change and related impacts.

Thus, our study aimed 1) to examine the prospects of the main native coniferous tree species – silver fir and Norway spruce – in Dinaric mountain forests; 2) to evaluate the impact of forest management, climate change and large ungulates on changes in the proportion of both species; and 3) to assess the options afforded by forest management to mitigate the possible negative (i.e. declining) trends in the proportion of conifers in the next century. Since silver fir is among the most threatened species in the mixed mountain forests of Central and Southeastern Europe, it was our primary focus.

Study area

The study was conducted in the Snežnik region of the Dinaric Mountains in Slovenia (45° 36'N; 14° 28'E), where mixed silver fir-European beech-Norway spruce mountain forests prevail. The forests are characterized by high stand volume (>400 m^3 ha^{-1}), and stands are mainly of an uneven-aged structure (i.e. 'plenter' and irregular shelterwood stands; Mathews 1999). The main tree species are silver fir (hereinafter fir), European beech (hereinafter beech), Norway spruce (hereinafter spruce) and sycamore maple (*Acer pseudoplatanus*), but many other species, such as wych elm (*Ulmus glabra*), rowan (*Sorbus aucuparia*), small-leaved lime (*Tilia cordata*), yew (*Taxus baccata*) and others, are sporadically present (SFS 2012). Extensive information on the analyzed forests and their past dynamics can be found in Klopčič and Bončina (2011).

Forest stands in the study area were categorized into representative stand types (hereafter stand types), defined as a unique combination of site conditions (i.e. elevation, aspect, soil properties), stand characteristics (i.e. stand structure, species mixture, developmental stage) and forest management type. We identified and simulated the development of 31 stand types (Appendix 1) covering a total of 4206 ha. Forest reserves in which no management takes place and spruce-dominated stand types resulting from a strong anthropogenic influence in the past were excluded from the simulations. We also excluded stands in the young growth phase, as available data (i.e. seedling and sapling density in height classes) were not suitable for initializing the forest model. The analyzed stand types extend between 600 and 1400 m a.s.l. and vary in slope and aspect (both were combined and categorized into three main categories: 1) south and 2) north facing slopes of >25°, and 3) flat terrain to gentle slopes of <25°.

Since elevation is usually the key factor controlling the microclimate in temperate mountain forests (Körner 2012), we stratified the stand types according to an elevation gradient (Table 1). Such categorization was also relatively effective in distinguishing the main stand types according to species mixture. The proportion of conifers decreases along the elevation gradient, while the proportion of beech increases. The reasons for this can partly be found in past forest management which promoted conifers at the expense of broadleaves (Perko 2002). Forest management was more intensive in low-elevation and mid-elevation stratum, considerably increasing the proportion of conifers, especially silver fir. The second reason is that altimontane forests and the upper forest limit in the sub-Mediterenean area have a different tree species composition from that of similar forests in Central Europe (Körner 2012); these forests are often composed of beech, as is the case in the Central Apennines in Italy and the Dinaric Mountains in the western Balkans.

Table 1. Characteristics of the elevation strata of stand types in the initial year of the stand development simulation

Strata of stand types	Elevation	Number of stand types included	Area (ha)	Main mixture type	Stand volume (mean ± SD in $m^3\ ha^{-1}$)	Fir proportion (mean % of SV ± SD)	Spruce proportion (mean % of SV ± SD)
low-elevation stratum	600-800	2	221	fir dominated	551 ± 58	60.6 ± 8.8	12.4 ± 5.1
mid-elevation stratum	750-1100	24	3458	fir dominated & mixed	510 ± 57	43.2 ± 9.0	16.6 ± 9.7
high-elevation stratum	1050-1400	5	527	beech dominated	455 ± 38	9.6 ± 6.6	11.1 ± 3.9

Methods

Data acquisition

Forest stand data

Data on the current state of forest stands were obtained from the databases of the Slovenia Forest Service (SFS 2012), comprising diameter distribution (i.e. number of trees per tree species by 5-cm diameter classes, the measurement threshold being 10 cm in dbh) and regeneration. For each stand type, the diameter distribution per tree species was obtained from a set of permanent sampling plots (grid 200×250 m, 500 m^2 each, measurement threshold dbh=10 cm) located in stands identified as an individual stand type and surveyed in 2004 (for details see Appendix 1); in total 823 permanent sampling plots were included in the calculation. Regeneration per tree species was surveyed on 42 temporary sampling plots located in different stand types. Due to the lack of plots in some stand types, regeneration data was additionally obtained from neighboring stands similar in stand and site characteristics. Regeneration data considered in AM3 were obtained from the fenced areas within the case study area. The regeneration was surveyed on 33 plots 4 m×4 m in size, placed in two fenced areas at 4-m intervals along transects located approximately 50 m from the fence (Klopčič et al. 2010).

Forest management data

Business-as-usual forest management regimes (hereafter BAU) were identified partly based on historic forest management records (1963-2010; Mina et al. 2017; Irauschek et al. in preparation) and partly on a questionnaire completed by local forestry practitioners. BAU represents the typical course of silvicultural measures over the entire rotation cycle of a stand. In the majority of stand types, a combination of small-scale irregular shelterwood, group selection and single tree selection silvicultural systems (Bončina 2011) is applied. In our study a small-scale irregular shelterwood system with a rotation period of 130-140 years was adopted as BAU. The main silvicultural interventions consisted of 4 thinnings (only 2 in the high elevation stratum) and 3 regeneration fellings with a regeneration period of 20-35 years using only natural regeneration (Table 2). In the model each intervention was scheduled to be carried out when the dominant trees in the stand reached a specific dbh threshold, which is similar to actual practice. Within each harvesting operation, the tree species composition of removals was defined to be equal to the initial tree species composition of the stand type.

In addition to BAU, we defined several alternative management strategies (hereafter AM) which were based on the following: 1) a questionnaire completed by forest owners and stakeholders in the case study area on their needs and demands, 2) experiences of local forestry professionals, 3) historical background information from archival material and 4) findings of previous research in the case study area. Data on AM regimes followed an identical structure as BAU, and their detailed description is given in the next section.

Simulation of forest development

Model description

We used the forest gap model ForClim, which is based on specific ecological assumptions, to capture the influence of changing environmental conditions on forest dynamics (Bugmann 1996). ForClim operates on small independent patches at the stand scale, where establishment, growth and mortality of tree cohorts are simulated based on species-specific responses to light availability, winter temperature, growing degree days and soil moisture. The establishment of different tree species also depends on browsing probability, which is calculated based on current browsing pressure in the stand – in our study derived from measurements of regeneration in sample plots and expert knowledge – and species-specific browsing palatability (Didion et al. 2011). The model is parameterized for 31 European tree species and has been successfully applied to several climatic regions worldwide (Bugmann and Solomon 2000; Shao et al. 2001; Busing et al. 2007). The management submodel (Rasche et al. 2011) allows for the implementation of a wide range of silvicultural treatments (e.g. thinning, shelterwood systems, plentering) and detailed harvesting regimes thanks to its scripting flexibility. A detailed description of the model can be found in Bugmann (1996) and Rasche et al. (2013); the latest version (v.3.3), which was used in this study, is documented in Mina et al. (2017). This study also includes a thorough evaluation of the behavior of ForClim in reproducing forest dynamics in mixed mountain forests of the Dinaric Mountains, and provides evidence that the expected natural stand dynamics can be accurately simulated by the model.

Simulation experiments

For each stand type we initialized 100 forest patches (default patch size 800 m^2) with the diameter distribution per tree species from the last forest inventory (SFS 2012). Data on site conditions such as slope, aspect, nitrogen availability and water holding capacity were used as inputs in the model (see Appendix 1). Subsequently, we simulated forest development for a century, i.e. until 2110. For simulations between 2100 and 2110, we assumed that climate would remain constant as simulated in 2100. Establishment settings (i.e. calibration of the establishment potential by species based on regeneration data) and harvesting interventions were adopted from Mina et al. (2017).

Stand development under BAU and AMs was simulated to assess the combined effect of forest management, climate conditions and the impact of large ungulates. Management strategies differed in the silvicultural system applied, regeneration density, its composition and origin, harvesting composition, nature conservation interventions, and large ungulate impact through selective browsing on regeneration (Table 2).

Table 2 Description of management strategies considered in the model simulations of stand types in the case study area

Strat-egy	Simulated area (ha)	Silvicultural system	Rotation period	Thinning frequency	Thinning intensity[c]	Regene-ration	regeneration period length	Regeneration harvests frequency & intensity[c]	Regeneration harvests species composition	Other guidelines	Browsing
BAU	4206	small-scale irregular shelterwood	130-140y	4 operations (only first 2 in high-elevation stratum) in stands of DBH_{dom}=15-50 cm	1: 22%, 2: 15%, 3 & 4: 10%	natural	20-35 y	1: 33%, 2: 40-70%, 3: 100%	proportional to stand mixture	-	on
NOM	4206	-	-	-	-	-					on
AM1[a]	3459	single tree selection	-	comprised in selection harvests		natural	-	15%	proportional to stand mixture lower proportion of fir	-	on
AM2	4206	small-scale irregular shelterwood	130-140y	same as BAU		natural + planting	20-35 y	1: 33%; 2: 40-70%, 3: ≈97%	& higher of beech and spruce than in stand mixture lower	fir conservation[d]	on
AM3[b]	881	small-scale irregular shelterwood	130-140y	same as BAU		natural (fenced)	20-35 y	1: 33%; 2: 40-70%, 3: ≈97%	proportion of fir & higher of beech and spruce than in stand mixture	fir conservation[d]	off

[a] AM1 was simulated only in mature and uneven-aged stand types because the model poorly supported the application of single tree selection forest management in pole stage stands and stands under regeneration;

[b] AM3 was simulated only in selected stand types since regeneration in the fenced areas corresponded only to these stand types;

[c] thinning and regeneration harvest intensity is given per operations (1-4 or 1-3, respectively), expressed in % of stand volume;

[d] silver fir <25 cm in dbh are retained in stands. In addition, 3% of stand volume in the final regeneration felling are retained in stands for general nature conservation purposes.

AM1 prescribed the application of the single-tree selection silvicultural system in all stand types; because of the specifics when applying this system (Mathews 1999), we simulated it only in mature developmental stages and in uneven-aged stand types, resulting in somewhat lower forest area simulated. In comparison to BAU, AM2 and AM3 assumed lower harvesting intensity on fir relative to beech and spruce (i.e. fir conservation strategies). In addition to this, AM2 assumed natural regeneration to be complemented with the planting of spruce (60 saplings per hectare), while AM3 eliminated 1) the past influence of large ungulates by using regeneration data from fenced areas within the study area (Klopčič et al. 2010) to calibrate the model and 2) their future influence by turning the browsing module of the model off. AM3 was simulated only in selected stand types (see Table 2 and Appendix 1) where regeneration data from fenced areas were available; thus the analysis of large ungulate impact was done by comparing the effects of BAU, AM2, AM3 and NOM only in these stand types, covering a total of 881 ha. For comparison reasons and to avoid confounding effects due to climate change and management induced effects (Lexer et al. 2002), we simulated stand development under a scenario of non-intervention (no management, hereafter NOM) under the current climate as well as under two climate change scenarios.

A baseline climate (C0) and two transient climate change scenarios (CC1 and CC2), each consisting of time series of mean daily temperature and precipitation sums, were developed for this study. Monthly temperature and precipitation data were derived from the climate data of the closest E-OBS 0.25 deg. grid point (45° 37′ 30″ N, 14° 22′ 30″ E, 877 m a.s.l.) for the period 1951-2011 (van den Besselaar et al. 2011). Climate data for the C0 scenario were processed in two consecutive stages. First, a 100-year time series with constant properties was generated using the stochastic weather generator LARS-WG (Semenov and Barrow 1997). Second, algorithms from Thornton et al. (1997) were used to derive climatic conditions for each stand type according to its elevation, slope and aspect. The climate change scenarios were derived from a combination of regional climate simulations with global climate models from the ENSEMBLES project (Hewitt and Griggs 2004) and based on the A1B greenhouse gas emission scenario. The two combinations, DMI-HIRHAM5_BCM and HadRM3_HadCM3Q16, were subsequently renamed as scenarios CC1 and CC2, respectively. Season-specific delta values for future climate (2070-2100) were calculated using the baseline climate (1951-2011) as a reference (Table 3).

Table 3 Mean seasonal temperature (T) and precipitation (P) anomalies of predicted climate change scenarios (2070-2100) compared with the reference climate (1951-2011) shown along an elevation gradient. 600 m a.s.l. low elevation: mean annual T 8.3°C, mean annual P 1336 mm; 900 m a.s.l. mid elevation: mean annual T 6.1°C, mean annual P 1495 mm; 1200 m a.s.l. high elevation: mean annual T 3.8°C, mean annual P 1655 mm.

| Elevation | Variable | Unit | Scenario CC1 | | | | Scenario CC2 | | | |
			spring	summer	fall	winter	spring	summer	fall	winter
600	T	°C	+3.4	+1.3	+0.5	+3.1	+4.4	+5.0	+4.8	+5.4
	P	%	+3.5	-10.9	-7.9	+3.1	-5.9	-30.5	-13.6	+8.0
900	T	°C	+3.4	+1.4	+0.5	+3.1	+4.4	+5.0	+4.8	+5.4
	P	%	+3.4	-10.6	-7.7	+3.1	-5.7	-30.0	-13.4	+7.9
1200	T	°C	+3.3	+1.3	+0.5	+3.1	+4.4	+5.0	+4.8	+5.4
	P	%	+3.3	-10.3	-7.5	+3.0	-5.6	-29.4	-13.2	+7.8

Simulation outputs

In the analyses of simulated stand development, we focused on the proportion of targeted tree species in stand volume and their diameter distribution in order to obtain trends in their future dynamics. We assessed the influence of management strategies and climate change on the dynamics of coniferous tree species in the different stand types. We therefore aggregated simulation outputs for each stand type by the elevation stratum (Table 1) as well as for the entire case study area, calculating area-weighted mean values.

The impact of climate change was assessed through the analysis of projected development of stand types under the NOM scenario, while the combined effect of management and climate change was evaluated in the BAU and AM simulations. When comparing BAU, NOM, AM1 and AM2, the entire area simulated was included into the analysis. However, when comparing BAU, NOM, AM2 and AM3 to determine the impact of large ungulates, the results on all analyzed strategies were included only for those stand types for which AM3 was simulated (in total 881 ha). Differences between climate change scenarios or management strategies were statistically examined by the non-parametric Mann-Whitney test when two samples were compared, and the Kruskal-Wallis test with post-hoc pairwise comparisons when more than two samples were compared. The analyses were conducted in SPSS 21.0.

# Results

Simulations under the current climate and BAU

Under the current climate and BAU, the proportion of fir in the study area was simulated to drop substantially (Figure 1), from 52.7±17.3% (weighted mean ± SD) in 2010 to 44.1±21.4% in 2060 (p<0.01), until reaching only 24.6±13.2% in 2110 (p<0.01). In contrast, the decrease in spruce proportion between 2010 and 2110 was projected to be only minor (from 13.1±6.4% to 12.9±4.8%).
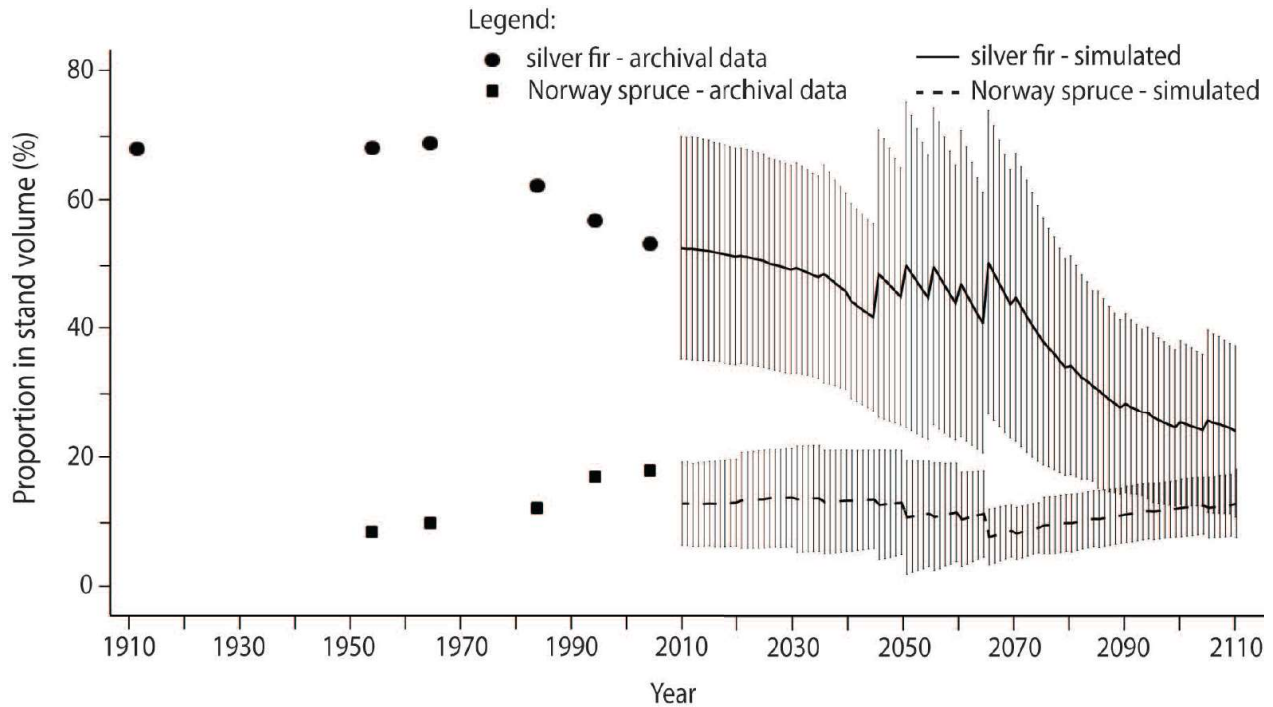
Fig. 1 Changes in fir and spruce proportions in the study area in the period 1912-2110. For the period 1912-2004, archival data are shown (adopted after Klopčič and Bončina (2011); for 1912, data for fir represents all conifers), while simulation results under the baseline climate scenario cover the period 2010-2110 (data displayed as weighted means with standard deviations).

However, strong differences were forecasted along the elevation gradient (Figure 2, rows b-d and Figure 3, rows b-d). The largest relative changes were projected in stands at low-elevation, where the proportion of fir was projected to decline from 78.3±4.5% to 30.2±7.7% by 2060 and to 3.5±0.5% by 2110. In the mid-elevation stands, the decrease in fir proportion was simulated to be substantial as well, but its proportion was projected to remain at 24.1±10.7% in 2110. In the high-elevation stands, BAU simulations showed a strong rise in fir (from 17.4±13.0% in 2010 to 34.1±27.9% in 2060 and to 37.2±17.1% in 2110) together with a noticeable increase in spruce (from 14.9±6.7% in 2010 to 22.0±7.8% in 2110).
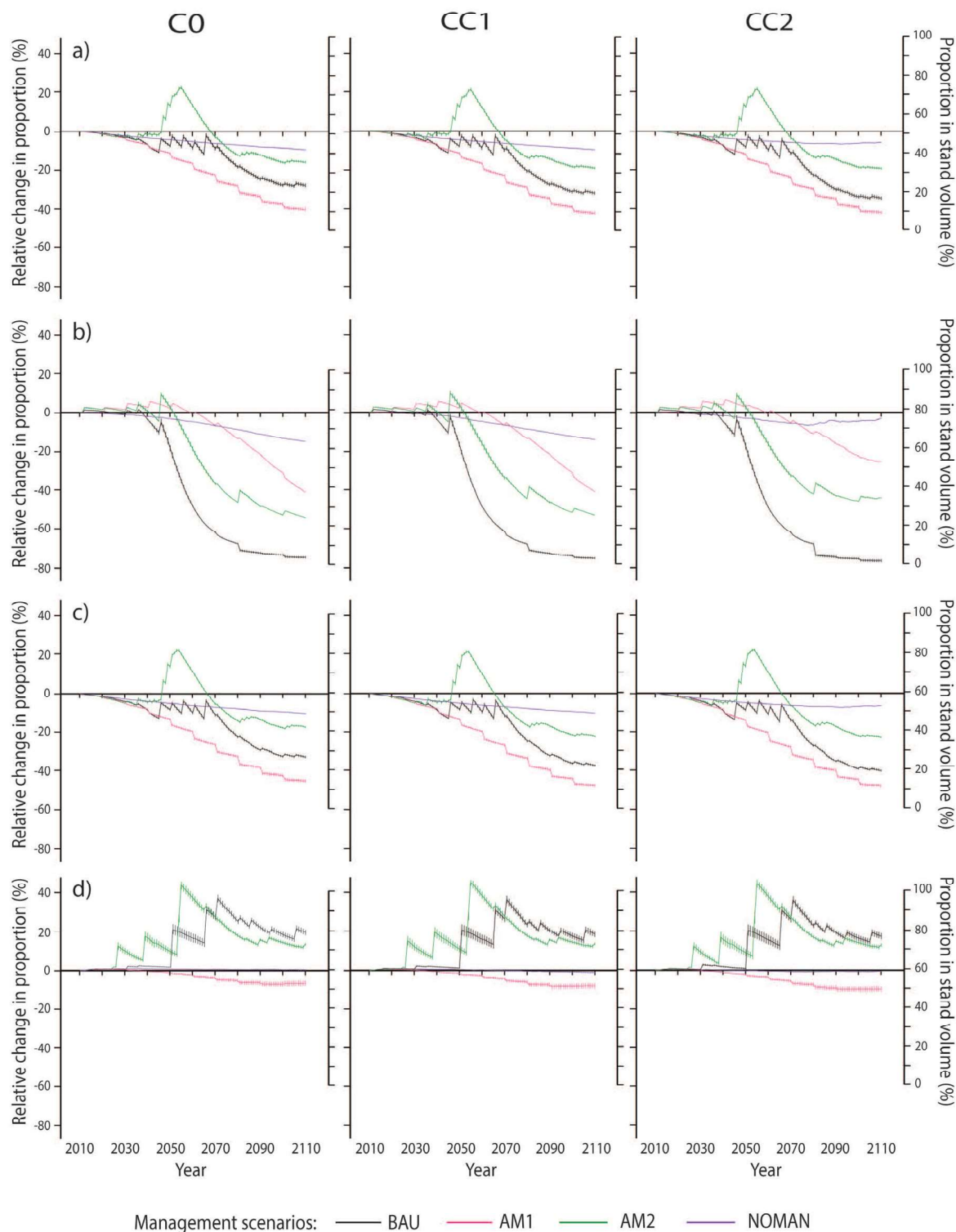
Fig. 2 Changes in fir proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in fir proportion in the stand volume (right axis in each chart) under different management strategies and climate scenarios: columns represent different climate scenarios (C0, CC1 and CC2) and rows different elevation strata: a) the entire study area; b) low-elevation stands; c) mid-elevation stands; d) high-elevation stands. Data are displayed as weighted means ± 1.96×SE

Simulations under "no management"

Simulations under NOM forecasted a steady decline of fir in the study area under all climate scenarios (Figure 2, row a), while spruce proportions were projected to rise until 2110 under C0 and CC1, but to decrease under CC2 (Figure 3, row a). The decrease in fir proportion under the CC2 scenario was slightly lower than that under the other two climate scenarios, but the decline in its volume was much higher due to a general reduction in total stand volume (results not shown). In the same period, the proportion of spruce was simulated to decrease significantly only under the CC2 scenario. Surprisingly, under the C0 and CC1 scenarios, its weighted mean proportion was projected to be statistically significantly higher at the end of the observation period than at the beginning (both $p<0.01$); however, the observed changes were small, making their ecological significance less prominent.

When the elevation gradient was considered, the most substantial impacts of climate change were observed in stands at low (Figure 2, row b) and mid elevations (Figure 2, row c), in which noticeable decreases in the proportion of both observed species were projected under the CC2 scenario. Surprisingly, in the second half of the simulation period (2070-2110), the rate of decrease in fir proportion was lower than in the first half (2010-2070). In the high-elevation stands, the decline in fir proportion under all climate scenarios was only minor (Figure 2, row d), although significant (all $p<0.05$), but its volume was simulated to increase substantially (by 19.2-28.2 m3 ha-1 between 2010-2110). In contrast, the increase in spruce proportion (Figure 3, row d) was noticeable under the C0 (5.1%) and CC1 scenarios (3.5%), while a slight decrease was projected under the CC2 scenario (-1.3%) (all $p<0.05$).

Comparison of BAU and alternative management strategies under current and climate change scenarios

Fir decline was projected under all management strategies and at low and mid elevations, with stands at the highest elevations being the exception (Figure 2). Under C0, BAU and AM1 resulted in a significantly lower proportion of fir at the end of the simulation period compared to the conservation-oriented AM2 strategy (KW(2) = 926,782, $p<0.01$; pairwise comparisons: all $p<0.01$). In contrast, BAU resulted in an increased proportion of spruce if comparing the starting and ending year of the simulation period (Figure 3, row a). The largest decrease in fir proportion was projected in stands at low elevation (-74.8 %, -41.0 % and -54.4 % for BAU, AM1 and AM2, respectively; Figure 2, row b) and was considerably lower in mid-elevation stands (-32.3 %, -44.8 % and -17.3 % for BAU, AM1 and AM2, respectively; Figure 2, row c). Also, the number of small-sized fir (10-15 cm in dbh) was projected to be much higher in the mid-elevation stands; in the low-elevation stands, small-sized fir = were nearly absent after 2030 (Figure 4). In the high-elevation stands, our results showed a general increase in the proportion of fir (Figure 2, row d); only simulations under AM1 exhibited its decline over time. In general, the simulation results under AM2 projected greater success in the preservation of fir than BAU and AM1; for spruce

the same was observed only in particular stand types (Figure 3, row d). The planting of spruce within AM2 did not increase its proportion as expected.
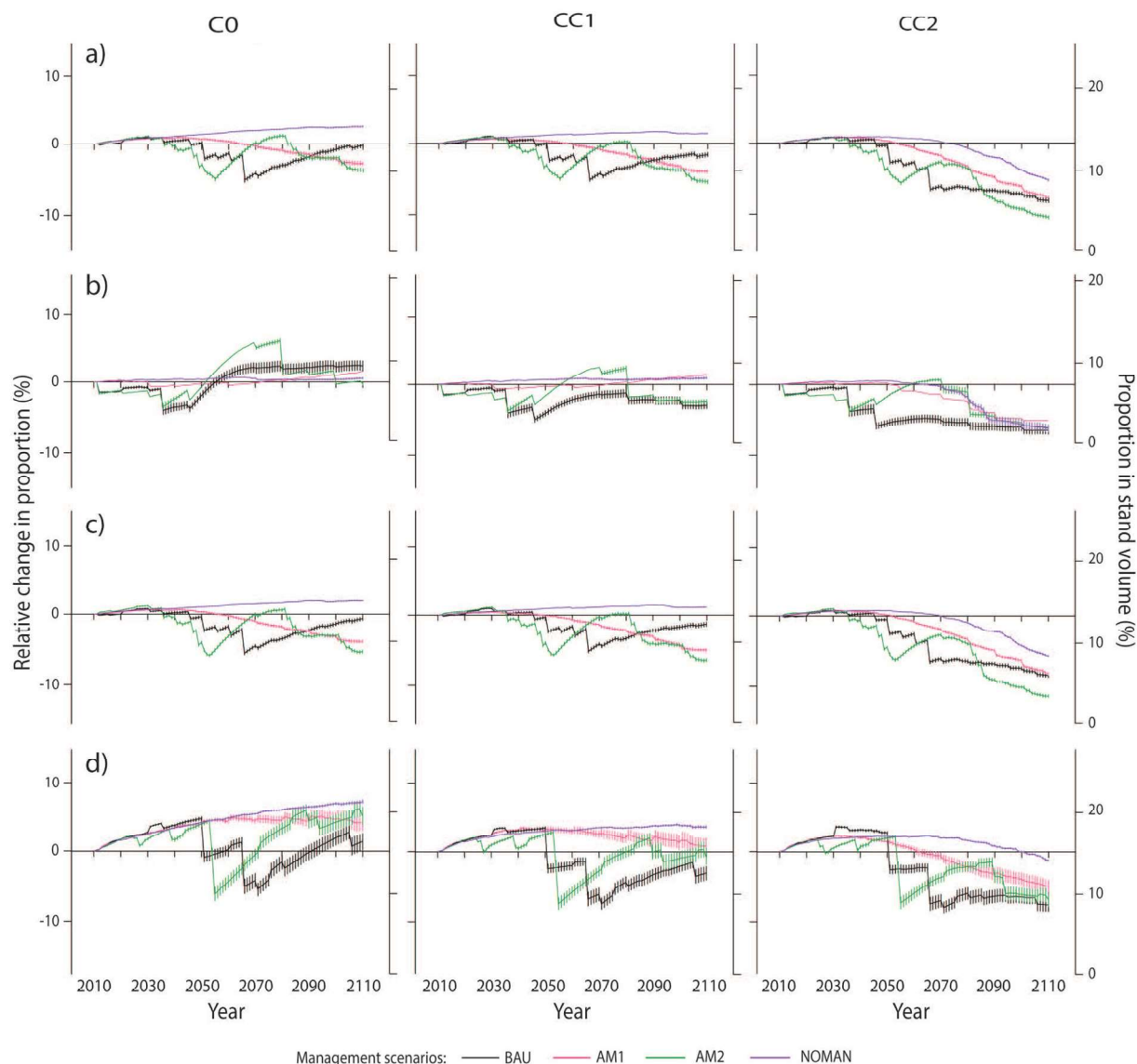

Fig. 3 Changes in spruce proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in spruce proportion in the stand volume (right axis in each chart) under different management strategies and climate scenarios: columns represent different climate scenarios (C0, CC1 and CC2) and rows different elevation strata: a) the entire study area; b) low-elevation stands; c) mid-elevation stands; d) high-elevation stands. Data are displayed as weighted means ± 1.96×SE

Under CC1 and CC2, the decline of fir was projected to be faster than in the current climate. Simulations under BAU and AM1 again showed a significantly lower proportion of fir at the end of the simulation period compared to the conservation-oriented AM2 strategy (CC1: KW(2) = 4676.2, p<0.01; pairwise comparisons: all p<0.01; CC2: KW(2)=4871.5, p<0.01; pairwise comparisons: all p<0.01). However, two exceptions need to be mentioned. Firstly, in the low-

elevation stands, the AM1 scenario under CC2 resulted in the highest proportion of fir at the end of the simulation period (Figure 4b). In the high-elevation stands, BAU simulations showed an increase in fir proportion, similar to the AM2 strategy under both the CC1 and CC2 scenarios. Here, climate change was projected to exacerbate the decline of spruce.

The number of small-sized fir (10-15 cm in dbh) was projected to increase in the middle of the simulation period, but drop afterwards (Figure 5). This indicated that after 2080 fir recruitment was hindered by climate-related factors, although differences between stands at different elevations were detected. In the low-elevation stands, fir recruitment was projected to be almost absent, resulting in a declining number of small-sized fir. On the other hand, in the high-elevation stands, fir recruitment was projected to be quite abundant, resulting in a substantially higher number of small-sized fir in the second half of the simulation period than at its beginning.
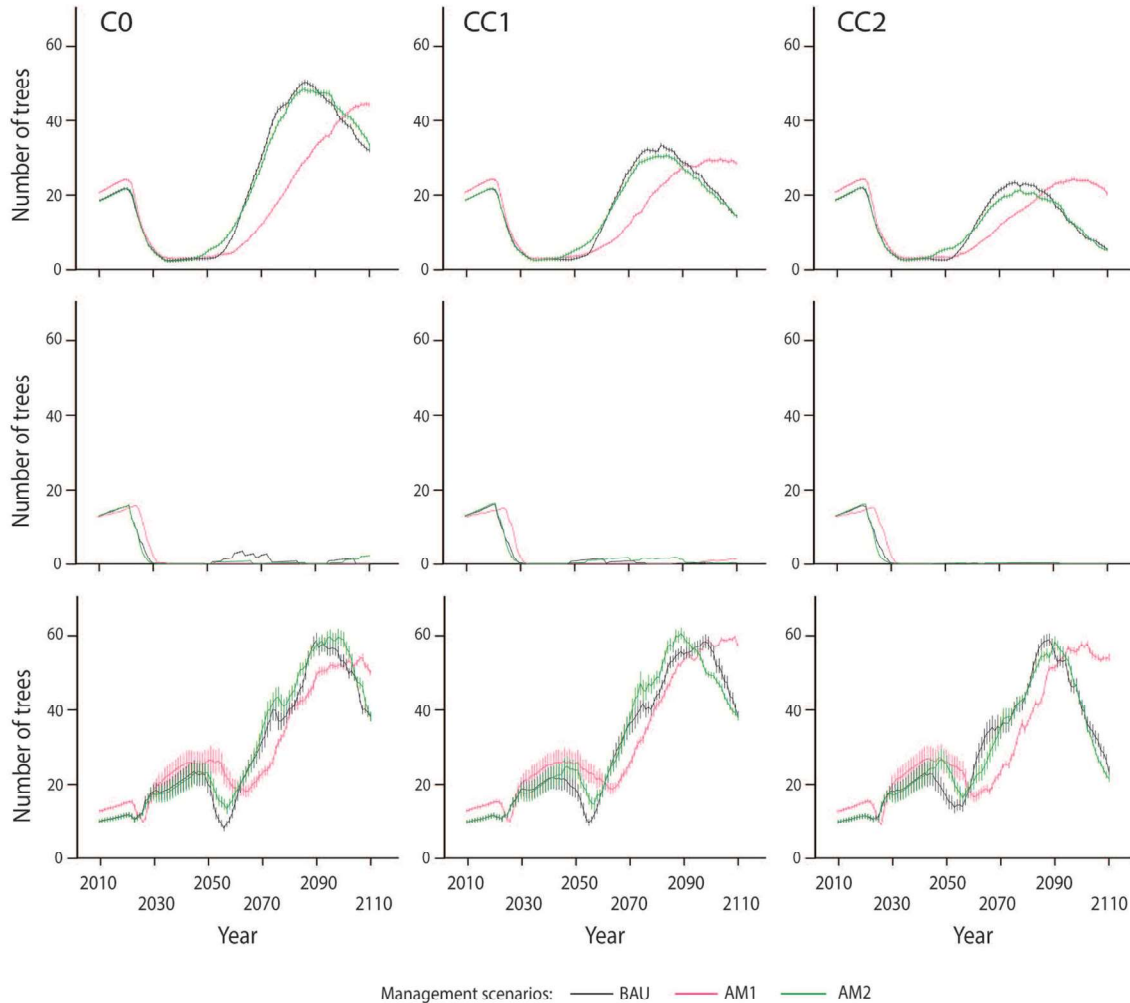
Fig. 4 Number of small-sized fir (10-15 cm in dbh) indicating its recruitment in the simulation period 2010-2110 in the study area (upper row), low-elevation stands (middle row), and high-elevation stands (bottom row). Data displayed are weighted mean values ± 1.96×SE

Impact of large ungulates

Compared to BAU and AM2, simulations of AM3 showed higher proportions of fir under all climate scenarios (Figure 5). This was expected since the regeneration potential of fir in fenced areas was much higher. When omitting the past and future impact of large ungulates, the simulation under C0 showed a significantly higher proportion of fir in the second half of the simulation period than under BAU or AM2 (both p<0.01). In contrast, AM3 did not result in a higher proportion of spruce compared to BAU and AM2 (6.1 % vs. 13.1 % and 4.6 % in 2110, respectively). The AM3 simulation also resulted in a significantly higher number of small-sized trees below 15 cm in dbh compared to BAU or AM2 (Figure 6). However, during the first decades of simulation, the absence of saplings 5-10 cm in dbh can be observed, followed by a drop in the number of trees 10-15 cm in dbh. This happened because, when initializing the model, seedlings and saplings below the measurement threshold of 10 cm in dbh were not considered although they were present in stands. Nevertheless, the proportion of fir in the total number of trees 10-15 cm in dbh was projected to increase from 24.3% in 2010 to 26.5% in 2110, while the final proportion under BAU and AM2 would be only 13.0% and 14.2%, respectively. Furthermore, between 2010 and 2110, the fir proportion on the observed area would decrease by only 4.0% instead of 18.0% or 30.7% as in AM2 and BAU, respectively.
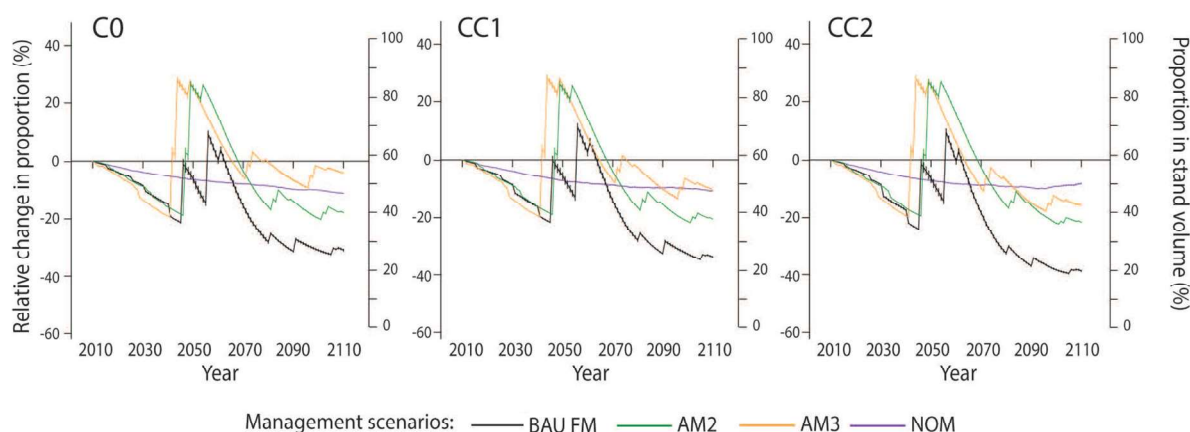
Fig. 5 Changes in fir proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in fir proportion in the stand volume (right axis in each chart) under different management strategies and different climate scenarios in selected mid-elevation stand types. Data displayed are weighted mean values ± 1.96×SE

Climate change may accentuate the impact of large ungulates. In the last decades of simulations under C0 and CC1, the proportion of fir was projected to be the highest under AM3 and significantly higher than that under NOM. But under the extreme CC2 scenario, the proportion of fir under AM3 dropped significantly and below NOM, indicating the substantial influence of large

ungulates under extreme climate change. The lower number of small-sized fir confirmed the significant influence of climate change and large ungulates on the fir population.
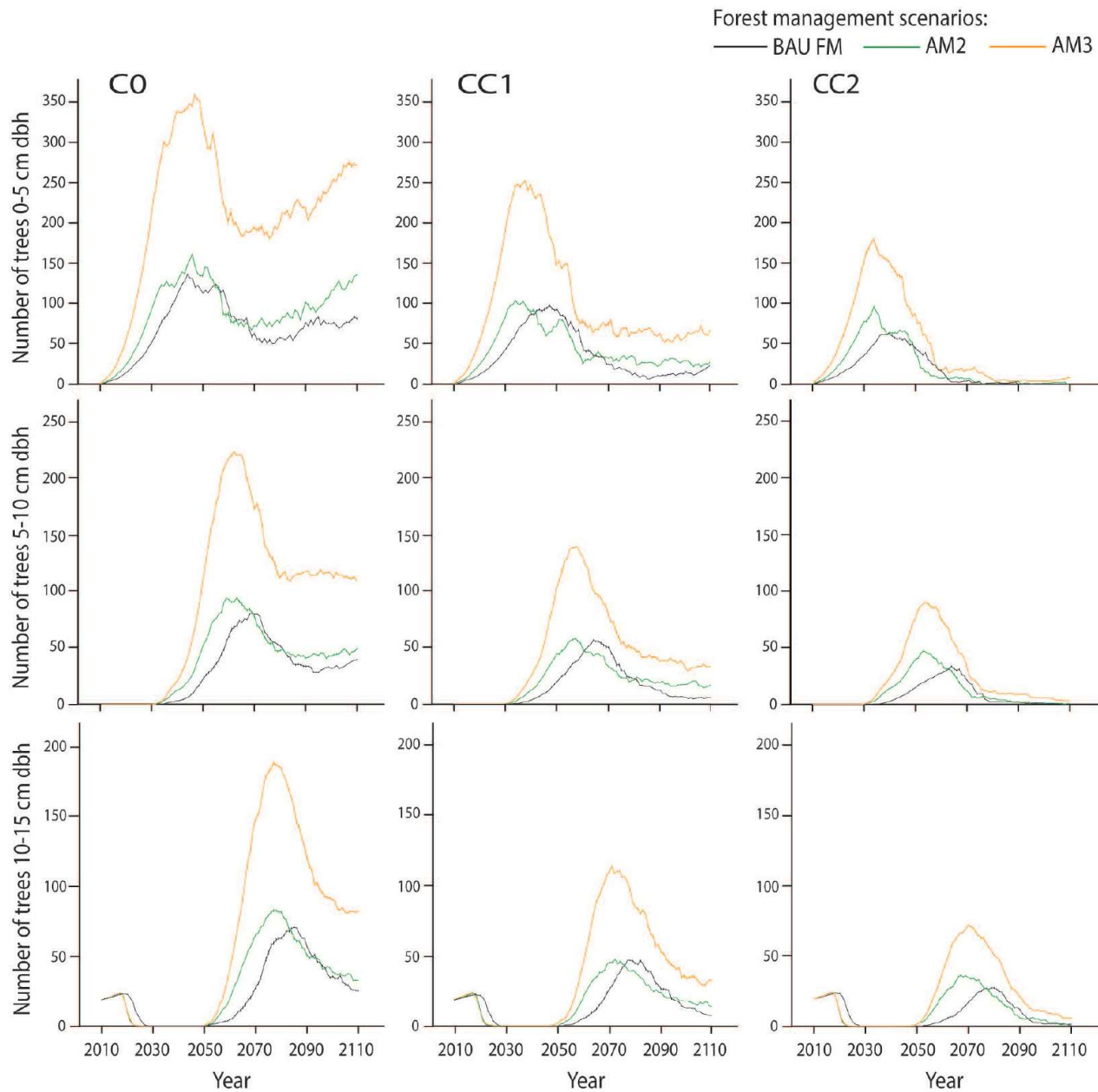
Fig. 6 Number of fir saplings (0-5 cm dbh; upper row) and small-sized trees (5-10 cm dbh; middle row; 10-15 cm dbh; bottom row) simulated under BAU, AM2 and AM3 and climate scenarios C0, CC1 and CC2 (columns). Data displayed are weighted mean values ± 1.96×SE

Discussion

Both native coniferous tree species in the mixed mountain forests of the Dinaric Mountains silver fir and Norway spruce were projected to experience substantial changes in the next century. The decline of fir was simulated to be prominent, while a perceptible decline in spruce was obvious only under the climate change scenarios.

When interpreting the simulation results, we need to be aware of several methodological constraints. The results of this study are based on the use of the dynamic forest gap model ForClim, which has been extensively evaluated in multiple studies (e.g. Didion et al., 2009; Rasche et al. 2013; Mina et al. 2017). Several studies have indicated it as a useful tool for studying forest composition along environmental gradients and for decision support in forestry (e.g. Bugmann and Solomon 2000; Rasche et al. 2011). ForClim, however, does not include a module for simulating stochastic natural disturbances that might be of high relevance in the study area (i.e. bark beetle infestation, wind throw events). In addition, possible invasion of exotic species and seed dispersal between the stands, as well as migration of tree species or species provenances more adapted to new climatic conditions were not considered. To take such processes into account, modeling at the landscape scale (e.g. Temperli et al. 2013) would be required, which was beyond the scope of our stand-focused study.

Furthermore, simulated stand development contains a bias originating from the simultaneous application of management strategies on the entire area of each stand type, which might be slightly unrealistic and (co-)contributed to obvious 'peaks' and 'depressions' in our simulations. In reality, forest management operations would be scheduled in time and space to fulfill forest management goals and take into account the logistical constraints of the area. Moreover, BAU was not defined in complete accordance with applied interventions in forests, as the proportion of tree species in harvesting was set to be constant throughout the simulation period, while in reality it may change considerably even between two consecutive harvesting interventions within a stand.

It is also noteworthy that an unspecified number of trees below 10 cm in dbh were present in stands at the time of model initialization, but they could not be taken into account when running the simulations. Since in ForClim new trees are established as saplings with 1.27 cm in dbh, they, and the new cohorts they compose, require more than a decade to several decades until they reach the measurement threshold of 10 cm. This resulted in an underestimation of tree numbers in the lowest diameter classes and must be considered when interpreting the obtained results.

In addition, when simulating ungulate pressure, we did not consider possible oscillations of browsing intensity, which may occur due to changes in ungulate density within the study area (cf. Didion et al. 2009). Evaluating multiple browsing scenarios or the implementation of a mechanistic model of deer density and impacts (Millington et al. 2013) would be advantageous for better assessing the long-term effects of large ungulates on forest dynamics. Lastly, the model itself is subject to a certain degree of uncertainty given that some processes rely on species-specific pa-

rameters. For example, it is possible that the projected decline of fir at low-elevations may have been overestimated due to uncertainties in the parameter expressing the maximum winter temperature tolerated for regeneration (for more details see Morin et al. 2011).

The prospects of silver fir and Norway spruce

The decline of conifers was clearly sensitive to elevation, which is closely related to climate conditions; a similar pattern was projected for the Austrian Alps (Lexer et al. 2002). The decline was simulated to be strongest in low-elevation (between 500 and 800 m a.s.l.) and mid-elevation stands (between 750 and 1100 m a.s.l.), especially on south-facing sites (results not shown). In low-elevation stands the continuation of BAU may cause fir to vanish from stands in which it has played a dominant role for a century and a half (Klopčič et al. 2010); the possible disappearance of fir in low-elevation stands was also reported at Mont Ventoux, France (Cailleret and Davi 2011). Moreover, our results indicate an upward shift of fir, as at Mont Ventoux, France (*ibid.*) and in the Swiss Alps (Didion et al. 2011). At higher elevations, fir can take advantage of higher carbon assimilation due to higher temperatures and a longer growing season (Cailleret and Davi 2011), which may increase its growth rate also in the younger life stages and thus enhance its recruitment rate. As long as browsing pressure is not excessively high, this may result in an increased proportion of fir in the long term. The projected decline of conifers will obviously trigger a shift in species dominance in these forests: the low- and mid-elevation fir-dominated stands were projected to shift into beech-dominated stands or those having an even mixture of the three main tree species, while the high-elevation beech-dominated stands were projected to transform into mixed stands with significantly higher proportions of both fir and spruce.

The decline of both coniferous species can be attributed to the interrelated impact of several factors: 1) forest management strategy; 2) the impact of large ungulates through selective browsing on regeneration; and 3) climate change. The latter two are closely related to i) the lower regeneration potential of fir and spruce as compared to European beech and ii) altered growth rate of both conifers. In addition to these, a higher probability of pest and insect infestations may be an important influential factor of the future dynamics of mixed mountain forests (Hlásny and Turčáni 2013), although these were not simulated in our study.

Forest management can be an important predisposing factor that leads to a decline process (Oliva and Colinas 2007), but it can also be an inciting factor of fir decline (Camarero et al. 2011), as found in our study. Our simulations show that there would be a dramatic drop in the proportion of silver fir in the region during the next century if BAU were to continue; in low-elevation stands fir might even disappear. Simulations of alternative management strategies did not demonstrate any strategy as being significantly beneficial for the abundance of fir. Nevertheless, the conservation oriented strategy AM2 yielded the most promising results, although there was still a significant decline in fir's proportion in the stand volume. The higher proportion of fir was directly influenced by two measures applied in AM2: 1) fir trees under 25 cm in dbh were retained and 2) the proportion of fir in harvests was lower than its proportion in the stand volume. Similar pat-

terns were found by Ficko et al. (2016), who studied fir dynamics in Dinaric mountain forests using matrix modeling. Both studies showed that the potential of silviculture is limited in terms of maintaining fir in these forests at the target amount (i.e. 30-50 %; FMP 2011). Prior to this study, we expected a decline of fir in the growing stock in the next decades for two main reasons. The first is related to the genesis of the current stands. The overstorey firs germinated mainly in the mid-19th century and were afterwards substantially promoted by the practice of cutting out European beech, resulting in a much higher proportion of fir in the stand volume (> 70%; Perko 2002) than would be the case in near-natural forests (30-50%; Veselic and Robic 2001). The second reason concerns recruitment failure (Ficko et al. submitted), which coincided with a strong loss of vitality (Elling et al. 2009; Čavlović et al. 2015). Both factors contributed crucially to the decline of fir and the subsequent reduction in its proportion, starting in the 1970s. The decline of spruce, however, was not that prominent in our simulations. Simulations of management strategies with artificial planting of spruce did not increase its proportion as expected. A higher density of planting than that simulated in AM2 would surely result in a higher proportion in the long run, but this would also increase management risks (cf. Hlásny and Turčáni 2013).

Large ungulates may seriously impact the forest ecosystem through selective browsing on regeneration (Motta 1996), and in the long run large ungulates may even cause large compositional shifts in forests. In our study, the impact of large ungulates was recognized as being substantial for fir. When past and future browsing pressure were eliminated and the current climate was considered in the simulations, the decrease in fir was 25% lower than that in BAU and 9% lower than that in the fir conservation-oriented AM2. Due to the slow growth of fir in the young life stages, the number of trees 10-15 cm in dbh (i.e. the lowest dbh class inventoried) is a pertinent indicator of future fir dynamics (Klopčič et al. 2015). Our simulation results showed that under AM3 the proportion of fir in the total number of trees 10-15 cm in dbh would remain rather constant between 2010 and 2110, which is promising for fir conservation, while it would drop significantly under BAU and AM2. The combined effect of climate change and large ungulates on fir proportion suggested the dominance of a non-compensatory effect (Didion et al. 2011), meaning that an increase in browsing pressure may enhance the shift in dominance of certain tree species. In contrast to fir, spruce is usually significantly less impacted by large ungulates. Their impact on spruce dominated forests in the Bavarian Forest National Park was reported to be negligible compared to that of forest management and climate change (Cailleret et al. 2014) since the trajectory of stand development was not significantly altered by browsing.

Climate, in close relation to elevation and topography, seems to play a role in retaining fir and spruce in the studied forests, but not as significant as was expected. In fact, forest management and large ungulates seem to have a much greater impact than climate change. In general, climate change induced alterations in tree regeneration and growth rates of several species in different bioclimatic regions (e.g. Jolly et al. 2005; Bošel'a et al. 2014) and increased tree mortality events (Allen et al. 2015). The combined effect of high temperature and low precipitation during the summer (combined with the study area's carbonate bedrock and shallow soils with low water

holding capacity) facilitates drought and its negative influence on fir and spruce growth and vigor (Levanič et al. 2009; Cailleret et al. 2014; Čavlović et al. 2015). In ForClim the establishment of fir and spruce is parameterized to require the mean temperature of the coldest month below -3°C and -1°C, respectively, representing the chilling requirements derived by regressing the degree day sum at the southern range limit of the species (for details see Morin et al. 2011). In the low-elevation sites, these requirements were often projected to not be met for fir under all climate scenarios, thus preventing its establishment, and were only partly met for spruce, whose establishment was projected to be limited in 40% of the years within the observation period under the current climate. In addition, climate change may significantly reduce the growth rate of both conifers at low and mid elevations, while it may increase it at high-elevation sites (e.g. van der Maaten-Theunissen et al. 2013). It is possible that species perform differently along an elevational gradient depending on how site conditions buffer the effects of regional climate change; Villa et al. (2008) reported such a pattern for *Pinus sylvestris* and *Pinus halepensis* in France and Jolly et al. (2005) for fir, spruce and beech in Switzerland. Drought is often exposed as the key climatic factor controlling the decline of fir (Camarero et al. 2011). Hence, conifers in low- and mid-elevation mountain forests may be replaced by more drought tolerant tree species (e.g. European beech, oak species) as shown in our simulations and reported for mountain forests at Mont Ventoux, France (Cailleret and Davi 2011). Although not considered in our study, a higher probability of pest infestations is another potential negative impact of climate change on both conifers in the area (Temperli et al. 2013). Climate change may increase the frequency of extreme events such as droughts and storms (IPCC 2013), which would increase the amount of breeding material for insects (e.g. bark beetles) and substrate for other pests and indirectly increase the vulnerability of the remaining stands to subsequent biotic disturbances, or it may increase the number of generations and the probability of summer swarming of bark beetles *Ips typographus* on spruce (Jönsson et al. 2007) or *Pityokteines spinidens* on fir.

Conclusions and implications for forest management

Mixed forests are recognized for providing high habitat diversity, resulting in a higher diversity of animal and plant species (Cavard et al. 2011), as well as for simultaneously providing multiple ecosystem services at higher levels as the number of species increases (Gamfeldt et el. 2013). Thus, to maintain both conifer species in the forest stands of the Dinaric Mountains in an adequate proportion is of enormous economic and ecological significance. Our simulations showed that both conifers might be in large part replaced by European beech, which might change provisioning of ecosystem services; for example, timber production might differ due to different productivity of mixed stands and pure beech stands (Pretzsch et al. 2010). However, it is also true that climate change may induce the immigration of certain tree species, especially those from the nearby sub-Mediterranean area (e.g. Meier et al. 2012), thus increasing the diversity of these forests.

To maintain fir in the target proportion (30-50 %; FMP 2011), adequate forest and wildlife management interventions would need to be carried out. The goal of keeping conifers at such a high proportion is understandable when considering the fulfillment of the provisioning ecosystem services (i.e. timber supply), but it may be unrealistic given the anticipated extent and impact of climate change. Simulations of alternative management strategies did not produce the expected results in mitigating the decline of fir; on the contrary, one of them even accelerated it compared to BAU. We thus conclude that silviculture has only limited options for preserving fir in an adequate proportion in mixed mountain forests experiencing both climate change and browsing pressure. Nevertheless, if we consider the highest proportion of fir at the end of the simulation period as being the best possible outcome, preserving all thin fir (dbh<25 cm; as reflected in AM2) in the stands would be a promising solution in the short term; in some areas of the Dinaric Mountains, this strategy is already being practiced and the results are encouraging. The enrichment planting of fir seedlings of local or more drought-resistant provenances (Brang et al. 2014) sporadically or in small patches should be considered as another possibility to maintain an adequate proportion of fir in these forests. However, to warrant fir preservation in the long term, a "window of opportunity" needs to be given to fir once in a while (cf. Sage et al. 2003). Fir would be the main beneficiary of a reduction in large ungulate density in the area. However, their impact would have to be diminished to the extent that would enable ample fir regeneration and recruitment into larger size classes in adequate abundance (Heuze et al. 2005; Ficko et al. submitted).

Spruce has a large potential in these forests, especially at high elevations, as long as bark beetle and wind throw disturbances do not prevail. Its proportion may rise above current shares if the climate does not change drastically. However, our simulations of BAU and alternative management strategies in mid-elevation stands showed that spruce cannot replace the declining silver fir. Sporadic planting of spruce in patches (AM2) did not increase its proportion as expected, but it may have other benefits, for example, protection of sycamore maple saplings against browsing (local forest managers, personal communication). Moreover, climate change may induce even more drastic reduction in spruce than modelled since natural disturbances were not considered in the simulations. A similar caveat may apply also to fir, which may beside the changed disturbance regime suffer from a climate change induced fir decline.

Overall, our results suggest that serious efforts in both forest and wildlife management need to be made in Dinaric mountain forests if the current tree species mixture with the desired proportion of conifers is to be preserved in the future. Divergent development in stands at different elevations suggests that a standardized silvicultural system should not be generally prescribed and applied in these mixed mountain forests. The employment of uneven-aged, 'freestyle' silviculture (Bončina 2011; O'Hara 2014), which combines measures of different silvicultural systems, including those of enrichment planting and the application of regeneration processes differing in longevity and spatial arrangement, would make it possible to consider site- and stand-specifics on a micro- and meso-spatial scale. Such an approach would enable us to effectively cope with pos-

sible hazards for future stand dynamics as well as to implement temporally varying forest management goals, while maintaining the key priority of preserving all native tree species.

Acknowledgments

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Appendix 1

Determination of stand types and acquisition of input data for model initialization

Stand types were defined via several stand characteristics: 1) species mixture, 2) stand development stage, 3) site type (considering elevation, slope and aspect, and soil type and depth), and 4) stand structure (i.e. even-aged or uneven-aged) (for details see Lexer 2013). Each stand in the study area (comprised in the GIS stand map and database, n=1438, mean area=3.5 ha) was categorized into one of the 47 defined stand types, but only 31 of them were included in our study (for details see the Study area description and Table A1). Afterwards, stand types were attributed to three main elevation strata based on their elevation range: 1) low- (the prevailing elevation range 600-800 m), 2) mid- (750-1100 m), and 3) high-elevation stands (1050-1400 m). Since the elevation ranges of stands and consequently stand types were broadly defined, stand types cannot be unambigously categorized to a certain elevation stratum and some overlaps in elevation range occurred.

Two basic datasources to determine the initial diameter distribution of each stand types were used (SFS 2012): 1) permanent sampling plots (PSP) on a fixed grid (200×250 m, n=823, 500 m^2 each), comprising data on individual trees with registered location within the plot (i.e. azimuth and distance to the plot centre), tree species, 5-cm diameter class, social and health status, quality, and some other individual tree characteristics, and 2) forest stand map and database, comprising polygons delineating individual stands and data on main stand characteristics (i.e. area, stand volume, volume of each tree species, volume increment, allowable cut) for each polygon/stand. The procedure to acquire the initial diameter distribution was conducted in two steps. First, when stand type was defined for all stands, we overlapped the GIS layers of i) forest stands and ii) PSP in order to identify PSP located in particular stand type. Second, we extracted PSP per stand type and calculated the average diameter distribution in 5–cm diameter classes, starting at the measurement threshold of 10 cm in dbh. The number of PSP per stand type varied between 4 and 109, but only in 7 stand types out of 31 the number of plots were less than 10. The calculated average diameter distribution was a direct input for initializing the ForClim model.
Another input for the ForClim model were the regeneration data. The detailed data on the density of seedlings and saplings per height classes (i.e. 0-15 cm, 15-30 cm, 30-60 cm, 60-130 cm, 0-10 cm in dbh) per each tree species were acquired from 33 regeneration inventory plots located in the study area. For initializing AM3, the data acquired in the regeneration survey in the fenced areas were used (for details see Klopčič et al. 2010).

Table A1 The main characteristics of stand types included in our analysis.

Stand type	Elevation stratum	Development al stage	Area (ha)	Slope (°) & aspect	WHC* (mm)	N** (kg/ha/y)	Stand mixture	Simulated management strategies				
								BAU	AM1	AM2	AM3	NOM
1.2	mid-elevation	pole	16.1	<25°	98	68	mixed	×		×		×
1.3	mid-elevation	mature	164.1	<25°	98	68	mixed	×	×	×		×
1.4	mid-elevation	regeneration	104.0	<25°	98	68	mixed	×		×		×
2.2	high-elevation	pole	28.7	≥25°, N	85	66	beech	×		×		×
2.3	high-elevation	mature	91.8	≥25°, N	85	66	beech	×	×	×		×
2.4	high-elevation	regeneration	97.4	≥25°, N	85	66	beech	×		×		×
4.3	low-elevation	mature	176.5	<25°	98	68	fir	×	×	×		×
4.4	low-elevation	regeneration	44.2	<25°	98	68	fir	×		×		×
5.3	mid-elevation	mature	98.9	<25°	98	68	fir	×	×	×		×
5.4	mid-elevation	regeneration	59.1	<25°	98	68	fir	×		×		×
6.2	mid-elevation	pole	10.2	<25°	98	68	fir	×		×		×
6.3	mid-elevation	mature	347.3	<25°	98	68	fir	×	×	×		×
6.4	mid-elevation	regeneration	187.1	<25°	98	68	fir	×		×		×
7.3	mid-elevation	mature	132.9	≥25°, N	98	68	fir	×	×	×		×
7.4	mid-elevation	regeneration	106.8	≥25°, N	98	68	fir	×		×		×
8.3	mid-elevation	mature	81.5	≥25°, S	98	68	fir	×	×	×		×
8.4	mid-elevation	regeneration	36.5	≥25°, S	98	68	fir	×		×		×
11.2	mid-elevation	pole	7.7	<25°	98	68	mixed	×		×		×
11.3	mid-elevation	mature	100.5	<25°	98	68	mixed	×	×	×		×
11.4	mid-elevation	regeneration	49.0	<25°	98	68	mixed	×		×		×
12.0	high-elevation	uneven-aged	148.8	≥25°, N	85	66	beech	×	×	×		×
14.0	mid-elevation	uneven-aged	129.6	<25°	98	68	fir	×	×	×		×
15.0	mid-elevation	uneven-aged	135.6	<25°	98	68	fir	×	×	×		×
16.0	mid-elevation	uneven-aged	100.4	<25°	98	68	fir	×	×	×		×
17.0	mid-elevation	uneven-aged	226.8	≥25°, N	98	68	fir	×	×	×		×
18.0	mid-elevation	uneven-aged	88.6	≥25°, N	98	68	fir	×	×	×	×	×
19.0	mid-elevation	uneven-aged	409.7	≥25°, S	98	68	fir	×	×	×	×	×
20.0	mid-elevation	uneven-aged	382.5	≥25°, N	85	66	fir	×	×	×	×	×
21.0	mid-elevation	uneven-aged	373.3	≥25°, N	98	68	mixed	×	×	×		×
22.0	mid-elevation	uneven-aged	97.7	≥25°, N	85	66	mixed	×	×	×		×
23.0	high-elevation	uneven-aged	142.5	≥25°, N	85	66	mixed	×	×	×		×

* water holding capacity (in mm of water column which can be stored in a soil profile)
** soil nitrogen availability (in kg/ha/y)

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