Can the use of continuous cover forestry alone maintain silver fir (*Abies alba* Mill.) in central European mountain forests?

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Chronic browsing and inappropriate stand management are often discussed as causes for recruitment failure of tree species in temperate mixed uneven-aged forests. Continuous cover forestry is thought to produce conditions that are conducive to the recruitment of native shade-tolerant and browse-sensitive tree species such as silver fir (*Abies alba* Mill.). This study used density-dependent matrix population models parameterized for three main types of fir forests in Europe (53 048 measured trees from 3183 permanent sample plots) to project the effects of Business-As-Usual uneven-aged management (BAU) and three alternative management scenarios (Non-Intervention (NON), Profit Maximization (MAX) and stand management optimized for increasing recruitment (CONS)) on fir population dynamics over 100 years. BAU, MAX and, particularly, CONS improved the population parameters if natural recruitment was sufficient regardless of site, current and historical logging and transient and equilibrium growth rates under NON. In chronically browsed and recruitment-limited fir populations with transient and equilibrium growth rates <1 under NON, the demographic ageing of fir can only be halted temporarily if silviculture is optimized for conservation, but none of the scenarios can prevent fir from decline. Our results suggest that a number of uneven-aged silvicultural systems, including more profit-oriented, can improve the demography of fir in central European mountain forests. However, they are not a pragmatic method to conserve fir when a population suffers from limited recruitment that causes an unmanaged population to decline.

Keywords: conservation management, recruitment, simultaneous optimization, population growth, ungulate browsing, management strategies

Introduction

The survival of juvenile organisms and their recruitment is essential for maintaining population size. Chronic lack of recruitment leads to a decrease in species abundance, and when the mortality of juvenile organisms exceeds the natural rate of death for a long period, the species may ultimately become extinct (e.g. Morris and Doak, 2002; Brigham and Schwartz, 2003). Recruitment plays a crucial role in the population dynamics of tree species in temperate uneven-aged forests (Schütz, 1989; O'Hara, 2014). Continuous cover of trees in multi-aged stands provides unique patterns of dispersed light regimes and humid conditions favourable for the regeneration and recruitment of shade-tolerant and drought-sensitive tree species that regenerate in gaps and recruit individually or in cohorts when the microsite conditions become favourable (Mathews, 1999). The population dynamics of tree species in uneven-aged forests is regulated by continuous removal of individual trees or small groups of trees throughout the forest, thus maintaining distribution of regeneration and recruitment throughout the forest (Mathews, 1999).

One of the key tree species in European uneven-aged forests is silver fir (*Abies alba* Mill). Fir is native to Central European mountain forests, where it occurs in mixed fir–European beech (*Fagus sylvatica* L.)–Norway spruce (*Picea abies* (L.) Karst.) forests. The dynamics of this shade-tolerant and drought-sensitive conifer depends highly on favourable recruitment conditions. Fir requires high stand densities, longer partial rotation and regeneration periods and larger target diameters (Ellenberg, 1996). As it is less susceptible to insect attack than spruce and more resistant to avalanches or rockfall due to deeper rooting, it has long been considered as one of the most economically important tree species in Europe (Horndasch, 1993).

Humans have heavily impacted recruitment conditions, in particular by inappropriate regeneration regimes. Profit maximization forest management has favoured even-aged structures in many European mixed forests and an increased proportion of

commercially more valuable Norway spruce (Senn and Suter, 2003). Moreover, deforestation, livestock grazing in the forest and burning considerably reduced the competitiveness of fir in the regeneration (Horndasch, 1993). In the 1970s and 1980s, fir suffered severe crown dieback, a consequence of a combination of sulphur emissions, soil acidification and pathogen outbreaks, often coupled with inappropriate stand management (e.g. Kandler and Innes, 1995; Čavlović et al., 2015). Although its growth has recovered in most of its distribution range (e.g. Büntgen et al., 2014), drought-induced declines have been reported recently in the Spanish Pyrenees (Macías et al., 2006; Camarero et al., 2011) and south-eastern France (Cailleret et al., 2014a, b).

Apart from anthropogenic pressures, fir recruitment has also been influenced by chronic wild ungulate herbivory (Gill, 2006). As a palatable species, fir is the most heavily browsed conifer in central European mountain forests (Häsler and Senn, 2012), particularly by red deer (Cervus elaphus L.) (Gill, 1992; Côté et al., 2004), which have contributed to severe decline in several managed (e.g. Ammer, 1996; Motta, 1996; Senn and Suter, 2003; Klopčič et al., 2010a; Ficko et al., 2011; Kupferschmid et al., 2013; Schulze et al., 2014) and old-growth central European forests (Diaci et al., 2011; Šebková et al., 2011; Nagel et al., 2015).

The establishment, growth and survival of the early life-history stages of tree species are predominantly influenced by microsite conditions and predation (Clark et al., 1999, p. 5), both of which can be controlled by silviculture and game management. However, there has been continued discourse between forest ecologists and wildlife ecologists on the significance of overabundant ungulates and mismanagement for the decline of browse-sensitive species (Reimoser, 2003; Côté et al., 2004). While the efficacy of deer reductions, exclosures and a variety of other techniques for regulating the effects of herbivory on the progression of browse-sensitive forest plant species has been well documented (e.g. Côté et al., 2004; Tremblay et al., 2007; Kuijper, 2011; Tanentzap et al., 2011; Jenkins et al., 2014; Kupferschmid et al., 2015), less is known about the capacity of silviculture for fir conservation. The promotion of native tree species and conservation of endangered plant species are among the main components of the contemporary international continuous cover forestry (CCF) debate (Pommerening and Murphy, 2004). CCF, broadly defined as the use of silvicultural systems whereby the forest canopy is maintained at one or more levels without clear felling (e.g. Mason et al., 1999), has been thought to be particularly beneficial for specialist tree species such as fir. Specialist species require a narrow range of understorey microclimate conditions that can be achieved by the appropriate stocking control (O'Hara, 2014). However, within the broad concept of CCF, a range of silvicultural systems are possible depending on site conditions, recruitment, past silvicultural practices and management objectives. Different silvicultural systems produce different horizontal and vertical structure of forest stands, resulting in more or less favourable conditions for natural regeneration and recruitment of species occurring in the stand (Mathews, 1999). Due to a decrease in fir occurrence in many areas across Europe, questions arise about the capacity of uneven-aged silvicultural systems prevailingly applied in central European mountain forests for fir conservation. Identifying the most efficient CCF management scenarios would enable managers to reshape their current practices.

The aim of the study was to investigate the capacity of CCF to halt the demographic ageing of fir in three contrasting types of fir forests. We compare the effectiveness of current management vs three alternative management scenarios. The forest types and management scenarios illustrate a variety of fir forests and management practices across Europe. We hypothesized that (1) CCF can reverse the negative demographic trend of fir in a wide range of uneven-aged forests and (2) stand management optimized for increasing recruitment is an effective solution for maintaining fir in heavily browsed forests.

Methods

Study area

Three forest types (hereinafter A, B and C, Figure 1) representing major fir habitats in Central and South-eastern Europe (Ellenberg, 1996) were selected in which group selection, single-tree selection and irregular shelterwood silvicultural systems (Mathews, 1999) have been practiced for at least 50 years (Bončina, 2011b). All forests were of uneven-aged structure but contrasted in recruitment rates, edaphic conditions and historical logging (Table 1; see also Ficko et al., 2011).

Management scenarios

We compared Business-As-Usual uneven-aged forest management (BAU) with Non-Intervention (NON), Profit Maximization (MAX) and Conservation (CONS) scenario. The CONS scenario was specifically designed for restoring the demography of populations exposed to chronic lack of recruitment.
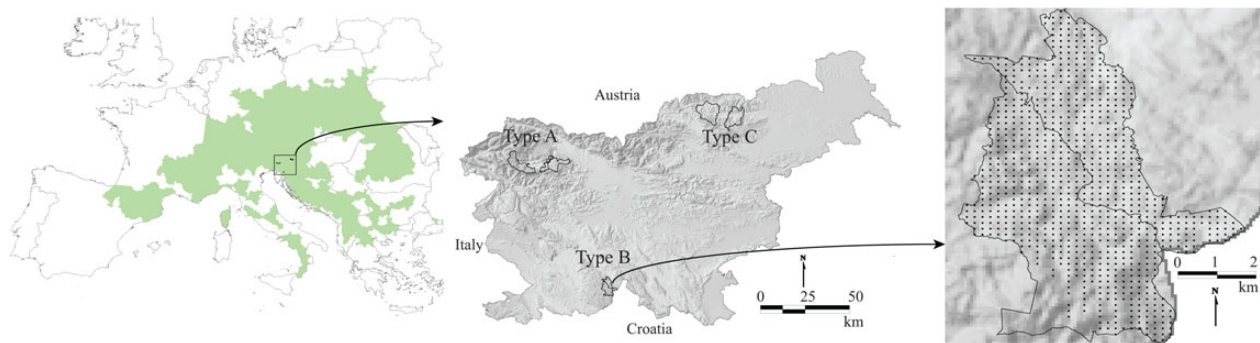
Figure 1 Indicated location of the three studied forest types with fir within the map of silver fir distribution in Europe (NatureServe and IUCN, 2014, left), detailed location of the study area (middle) and permanent sample plots in one of the studied types (type B, right).

Table 1 Characteristics of three forest types with silver fir

	Forest type		
	A	B	C
Site characterization	Pre-alpine silver fir–beech forests on carbonate	Dinaric silver fir–beech forests on carbonate	Silver fir forests on non-carbonate
Study area	Jelovica and Notranji Bohinj (15 023 ha)	Sneznik and Leskova dolina (5051 ha)	Radlje desni breg and Lovrenc na Pohorju (19 643 ha)
No. of permanent sample plots	1556	898	729
Year of first/second inventory	1992/2002	1992/2003	1993/2003
Number of trees callipered in both inventories	35 208	9846	7994
Mean elevation (5th/95th percentiles) (m)	1110 (600/1400)	910 (750/1210)	800 (400/1370)
Mean annual precipitation (5th/95th percentiles) (mm)	2416 (2300/2900)	2099 (1900/2300)	1440 (1250/1700)
Mean annual temperature (5th/95th percentiles) (°C)	5.4 (5.0/5.7)	6.7 (5.0/7.0)	7.2 (5.0/9.0)
FAO soil types	Rendzic leptosols (64%), molic leptosols (31%), other (5%)	Chromic cambisol (95%), eutric cambisols (3%), rendzic leptosol (2%)	Dystric cambisols (74%), Dystric leptosols (24%), other (2%)
Mean pH (5th/95th percentiles)	5.2 (4.7/6.3)	4.8 (3.8/5.5)	4.0 (3.0/4.5)
European forest type ([Matijasic and Bončina, 2006](#)).	Illyrian mountainous beech forest	Illyrian mountainous beech forest	Nemoral spruce forest
Prevailing forest vegetation communities	*Homogyno sylvestris-Fagetum*	*Omphalodo-Fagetum*	*Dryopterido-Abietetum* syn.: *Galio rotundifolii-Abietetum*
Standing volume ($m^3 ha^{-1}$)	349	323	290
Tree species composition (% of standing volume)			
Silver fir	11.9	57.0	35.5
European beech	10.0	26.4	8.5
Norway spruce	78.1	16.6	56.0
Stand basal area ($m^2 ha^{-1}$)			
Silver fir	3.4	14.9	8.5
European beech	3.6	8.3	2.2
Norway spruce	21.0	4.7	13.2
Annual recruitment ($N ha^1$)			
Silver fir	2.0	0.5	2.7
European beech	3.6	2.4	1.0
Norway spruce	5.5	1.6	2.0
Annual mortality (% of trees that died or were cut for salvage reasons)			
Silver fir	4.0	6.0	4.2
European beech	3.7	1.1	0.1
Norway spruce	5.1	3.6	2.0
Red deer (*Cervus elaphus* L.) population density ($N km^{-2}$) ([Ficko *et al.*, 2011](#))	8.1	12.8	3.7
Roe deer (*Capreolus capreolus* L.) population density ($N km^{-2}$) ([Ficko *et al.*, 2011](#))	13.4	11.1	35.4

Regeneration and browsing rates for silver fir ([Bončina *et al.*, 2004](#))						
Height class	$N ha^{-1}$	% browsed	$N ha^{-1}$	% browsed	$N ha^{-1}$	% browsed
0–19 cm	5407	39.7	3352	18.1	21 453	No data
20–49 cm	2222	53.3	152	37.5	2051	No data
50–89 cm	1259	41.2	0		513	27.0
90–129 cm	1037	42.9	0		256	36.0
130–5 cm d.b.h.	3778	43.1	0		1282	No data

	A	B	C
Historical logging from the end of 19th century until 1950	Clear cutting and group sheltering	Single-tree selection	Uneven-aged forestry
Current silvicultural system	Irregular shelterwood, group selection	Small-scale irregular shelterwood, single-tree selection	Small-scale irregular shelterwood, freestyle techniques

In the BAU scenario, we extrapolated current logging intensities per tree species and diameter classes to 100 years after confirming that the observed logging intensities did not deviate substantially from typical intensities in the studied forests in the past 19 years (SFS, 2014). In the NON scenario, we simulated 100 years without management to ascertain the population trajectory in the event of a significant change in management objectives that can be best achieved by non-intervention. In the MAX scenario, we simulated population dynamics under the objective of the maximum net present value of all logged trees over a period of 100 years plus the value of the remaining stand at the age of 110 using a 2 per cent discount rate. A financial evaluation of single trees, logging costs and salvage cut was done by considering average timber prices and logging costs in the area (Roessiger *et al.*, 2016). In the CONS scenario, we optimized logging to create the stand density enabling the maximum number of recruits (i.e. firs in the smallest measured diameter class) over a period of 100 years. The objective function to be maximized was the mean number of firs in the diameter class 10–14 cm over a period of 100 years bearing in mind that the number of trees in the lowest diameter at breast height (d.b.h.) class is one of the most common indicators of recruitment sufficiency (Schütz, 2006). The CONS and MAX scenarios were determined by non-linear optimization of harvesting in the What's Best® package (Lindo Systems Inc., 2012).

Demographic indicators

We calculated transient and asymptotic population growth rate (λ_t and λ_1, respectively), relative abundance, stand density, proportion of small-diameter trees, standing volume distribution, recruitment and mortality of fir. λ_t, defined as the ratio of the number of trees at the end of the 100-year simulation period to the number of trees at the beginning of the simulation period, was estimated for all scenarios. λ_1, defined in the same way as the λ_t but for the period of oscillating dynamics until a convergence to stable stage structure is reached (Ezard *et al.*, 2010), was estimated only for the BAU and NON scenarios. Relative abundance was measured as the proportion of fir in the standing volume (in m^3 ha^{-1}). Stand density, defined as the sum of basal areas of all trees in a stand per hectare (ba), was used as an indicator of light conditions and sufficient number of seed trees (Schütz, 2006). We used the proportion of small-diameter trees (d.b.h. < 30 cm) in the standing volume and the distribution of standing volume per equidistant d.b.h. classes as two indicators of a balanced demographic structure (Schütz, 2006; O'Hara *et al.*, 2007). Fir recruitment was measured as the number of firs that pass the measurement threshold of 10 cm d.b.h. per decade. This 'sapling immigration view' on the role of recruitment (Clark *et al.*, 1999, p. 2) was used to gauge the factors affecting growth and mortality in the early life-history stages because no measurements of trees with d.b.h. <10 cm were available. Mortality was defined as the number of adult trees that die in a period or are harvested as salvage logging due to abiotic or biotic factors.

Stand development model

Density-dependent and growth variation-sensitive matrix model

We used Buongiorno and Michie's (1980) density-dependent matrix transition model for uneven-aged stands adapted by Roessiger (2014, p. 245–275) and further developed by Roessiger *et al.* (2016) to account for the growth variation between individual trees. Similar to the approach of Brienen and Zuidema (2007), trees of each species were segmented into slow-, medium- and fast-growing trees (i.e. trees with d.b.h. increment $\in$ [0, 2) cm, [2, 4) cm and [4, ∞) cm per decade, respectively), and the recruitment and transition probabilities were estimated separately for each growth class (i). For the recruits, we assumed that they maintain the same growth potential throughout their lifespan. The populations were

represented with 23 four-centimetre-wide d.b.h. classes (e.g. Tahvonen *et al.*, 2010). The lowest inventoried d.b.h. class thus included trees with d.b.h. $\in$ [10, 14) cm, and the highest d.b.h. class included trees with d.b.h. $\geq$ 98 cm. The model enabled stasis or transition of trees to the next d.b.h. class over time. The number of trees in a d.b.h. class in a decade was thus always dependent on the stand parameters of the previous period. The resulting matrix contained information about the number of remaining trees, trees to be logged and trees removed as salvage logging due to mortality, all per tree species, d.b.h. class and decade.

Vital rates

The ecology of tree species was considered by using tree species-specific and stand-density and d.b.h.-dependent non-linear functions for recruitment, transition and mortality. Recruitment probability of species j (R_j) was modelled with log-logistic distribution $R_j \sim LL(\alpha, \beta)$ as a function of ba where α and β were species- and forest type-specific scale and shape parameters and $\overline{ba}$ was mean stand basal area in the forest type. To account for the rapidly decreasing number of recruits with increasing stand density (Collet and Chenost, 2006) and to consider that no recruitment is possible at low stand densities unlikely to represent mature stands with seed trees (e.g. Ribbens *et al.*, 1994), we implemented the correction term and scaled the recruitment to a hectare by multiplying the recruitment per plot with the factor HF that depended on the plot size (equation 1, Supplementary Table 1):

$$R_j = \frac{\alpha\beta\left(\dfrac{ba}{\overline{ba}}\dfrac{\pi}{\beta \sin(\pi/\beta)}\right)^{(\beta-1)}}{\left(1 + \left(\dfrac{ba}{\overline{ba}}\dfrac{\pi}{\beta \sin(\pi/\beta)}\right)^{\beta}\right)^2}HF \tag{1}$$

The maximum recruitment of fir, beech and spruce thus happened at the ba of 26, 29 and 26 m^2 ha^{-1} in type A forests, 30, 28 and 25 m^2 ha^{-1} in type B forests, and 27, 25 and 25 m^2 ha^{-1} in type C forests. The recruits were allocated into one of the three growth classes by multinomial logistic regression as a function of ba and d.b.h. (equation 2). The probability of a recruit of the jth species being in growth class i was obtained as the quotient p_{ij} (equation 3):

$$MC_{ij} = \exp^{(u_{ij}+v_{ij}d.b.h._{-12}+w_{ij}ba_{t-10})} \tag{2}$$

$$p_{ij} = \frac{MC_{ij}}{\sum_{i=1}^{3} MC_{ij}} \tag{3}$$

where u, v and w are the coefficients specific for tree species, growth class and forest type (Supplementary Table 2).

The transition probability of slow-, medium- and fast-growing trees between d.b.h. classes, defined as the probability T_{ijk} that a tree of the ith growth class of the jth species grows from the $k-1$th to the kth d.b.h. class in 10 years, was calculated as the sum of constant transition probability (MI_{ij}) calculated from the mean increment of each growth class (Supplementary Table 3) and variable transition probability calculated by logistic regression using the d.b.h. and stand density (ba) as predictors (Roessiger, 2014, p. 63; Roessiger *et al.*, 2016; equation 4):

$$T_{ijk} = \frac{MI_{ij} - 0.5}{4} + \left(\left(\frac{1}{1 + \exp^{-(u+v\,d.b.h._{-d-4}+w\,ba_{t-10})}}\right)/4\right) \tag{4}$$

where u, v and w are the coefficients for the intercept, the mean of the $k-1$th d.b.h. class (d.b.h.$_{-d-4}$, in cm) and the ith growth class and the ba in the $t-10$ period (ba$_{t-10}$ in m^2 ha^{-1}), respectively (Supplementary Table 1).

The mortality probability of a species (M_j), defined as the proportion of trees in a given d.b.h. class that die in 10 years, was calculated by logistic

regression (equation 5) using d.b.h. as a regressor (Supplementary Table 1).

$$M_j = \frac{1}{(1 + \exp^{(u + v\,d.b.h.)})} \qquad (5)$$

Data

Tree diameters measured by a calliper with rounding down to the nearest centimetre were acquired from two consecutive forest inventories on 3183 permanent circular sample plots. Since the plot size differed between forest types (all trees with d.b.h. $\geq$ 10 cm measured on a 400-m^2 circular plot in the type A forest *vs* all trees with d.b.h. $\geq$ 10 cm measured on an inner circle of 200 m^2 and trees with d.b.h. $\geq$ 30 cm measured on a 300-m^2 outer circle in type B and C forests), we weighted the hectare values of stand parameters by the area of the circles.

Since the permanent sample plot data provided no information on the cause of harvesting, we calculated the mortality rates per tree species and d.b.h. classes proportionally to the salvage logging rates in the salvage logging register (SFS, 2014) for a comparable time period (1995–2004). The mortality was assumed to be a function of d.b.h. because no information on stand density (ba) was available in the logging register.

Results

Business-As-Usual

By continuing current forest management, most of the fir population parameters can be improved in type A and C forests. The projection suggests a 1.9- and 1.4-fold transient increase of the fir population in type A and type C forests after 100 years, respectively (Figure 2a). Current management practice in type A forests (irregular shelterwood system and group selection) will double the ba of fir from 3.4 m^2 ha^{-1} (Table 1) to 7.1 m^2 ha^{-1} (Figure 2b) and increase its proportion in the standing volume from 11.9 to 25.0 per cent (Figure 3). A similar trend is projected for type C forests. Conversely, BAU is not effective for fir conservation in type B forests, where one fir per hectare will recruit every 2 years (Table 1) while the mortality will remain higher than 5 per cent (Figure 3), resulting in a 40 per cent of the size of initial population after 100 years. As a consequence, beech and spruce will gradually substitute fir (Table 1, Figure 2b).

Non-intervention

In the case of a significant change in management objectives that can be best achieved by non-intervention, the fir population will almost double in type A forests after 100 years, slightly decrease in type C forests, but more than halve in type B forests (Figure 2a). The relative abundance of fir is projected to increase on average from 11.9 to 21.1 per cent in type A forests and decrease from 35.5 to 30.0 per cent in type C forests. In type B forests, NON will slow down the decline of fir in the short run ($\lambda_t = 0.48$), which appears to be the most effective strategy for maintaining fir in the next 100 years (Figures 2a and 3). However, the asymptotic growth rate $\lambda_1 = 0.10$ suggests drastic decline of fir if forests are not managed (Figure 2a), indicating that NON is not an advantageous strategy for conserving fir in forests with recruitment failure. Moreover, non-intervention will decrease recruitment and increase the mortality of fir in all forest types, e.g. in type A forests, only 12.5 per cent of small-diameter firs will be left and fir mortality will be 1.6 times higher than the current one (Figure 3). Stands left to natural development are expected to transform to predominantly beech old-growth structures (Figure 2b).
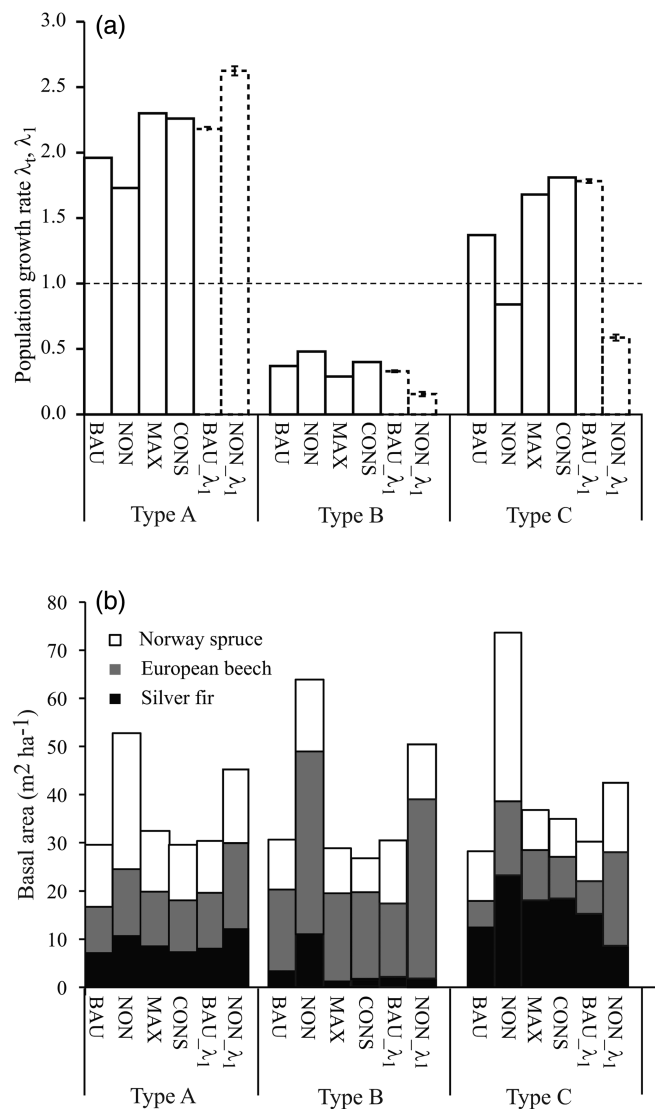
Figure 2 (a) Growth rates for silver fir populations in three forest types (A–C) under 100 years of different management scenarios (Business-As-Usual uneven-aged forest management (BAU), Non-Intervention (NON), Profit Maximization (MAX) and Conservation (CONS)). The long-term equilibrium growth rates for Business-As-Usual (BAU_λ_1) and Non-Intervention (NON_λ_1) are shown with dashed histograms. The dashed horizontal line represents a population with no growth, and growth rates below 1.0 indicate a declining population. (b) Projected stand basal area per species after 100 years and at the equilibrium (the first four columns and the last two columns in each type, respectively).

Profit maximization

The MAX scenario will have positive short-term effects on the fir populations in type A and C forests but should be avoided in type B forests. This is because of stronger reductions of ba as a result of increased harvesting of financially over-mature large-diameter firs in first decades (Figure 2b). This will lead to a sharp decrease in recruitment to only 0.2 firs ha^{-1} per year (Figure 3) with no recovery within 100 years. The long-term effectiveness of MAX, however, remains unclear. The estimation of asymptotic growth rate under the MAX scenario was not possible due to the finite optimization period of 100 years.
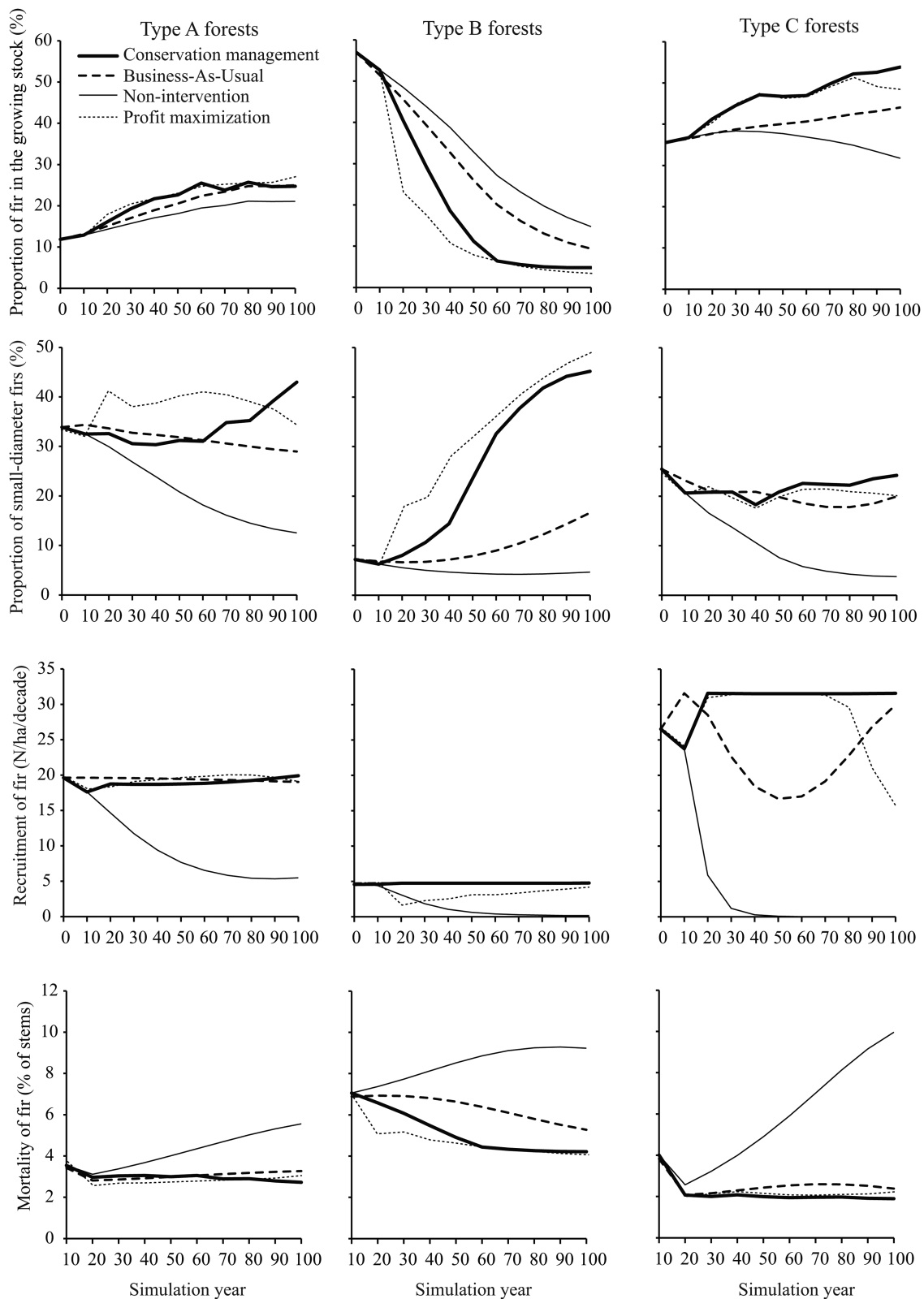
Figure 3 The projection of demographic indicators in three types of silver fir forests for the next 100 years under Business-As-Usual and three alternative management scenarios.

Conservation management

Most of the population parameters will improve after 100 years of CONS in type A and C forests but only some in type B forests. In type A forests, CONS will double the ba of fir from 3.4 to 7.5 m^2 ha^{-1} (Table 1, Figure 2b), increase the proportion of small-diameter firs by a factor of 1.3, maintain the current recruitment rate at ~20 firs ha^{-1} in a decade and reduce the annual mortality of fir below 0.3 per cent (Figure 3). In type C forests, the already abundant fir will gradually become the dominant species, reaching 53.9 per cent of the growing stock (Figure 3) and a 1.5-fold increase in the ba (Table 1, Figure 2b). CONS will also increase the proportion of small-diameter firs and recruitment from 26.5 to 31.6 firs ha^{-1} per decade (Figure 3). After 100 years of CONS, fir mortality in type C forests is expected to be the lowest among all three forest types (1.9 per cent dead firs, Figure 3).

However, CONS will not compensate for recruitment failure in type B forests. In the next 100 years, the ba of fir will decrease from the current 14.9 to 1.6 m^2 ha^{-1} (Table 1, Figure 2). The relative abundance of fir is also expected to decline, but at a rate similar to other management scenarios, from the current 57.0 per cent in standing volume to 9.4, 14.7, 3.9 and 4.8 per cent in the BAU, DN, MAX and CONS scenarios, respectively (Figure 3). However, CONS will increase the proportion of small-diameter firs in the standing volume from 7.2 to 45.2 per cent and lower mortality to 4.2 per cent, which rates CONS as the best performing scenario in mortality reduction in forests suffering from poor recruitment (Figure 3). Despite these conservation measures, the recruitment will remain at the current level of 0.5 firs ha^{-1} per year, which is insufficient for replacing the population over the average lifespan of a fir, although the survival rate at the age when firs on average begin fruiting is high (Figure 4).

Discussion

The capacity of CCF

Using matrix transition models, we simulated the life history of fir under four management scenarios in three types of fir forests in Europe in which CCF has been practised for more than 50 years. We showed that in general CCF can improve the population
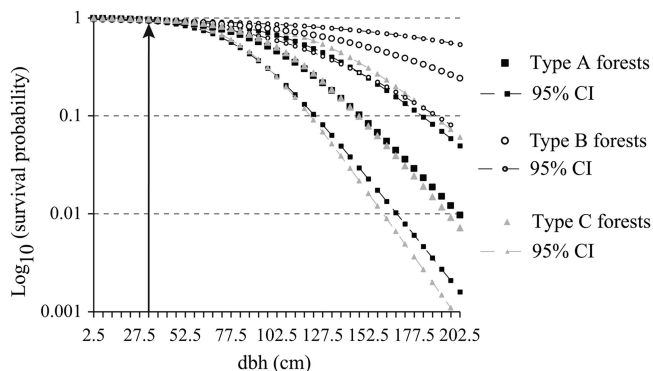
Figure 4 Expected survivorship and the corresponding 95% confidence intervals for silver fir in three forest types. The vertical arrow indicates the average d.b.h. corresponding to the average age of fir in the stands with densities 20–30 m^2 ha^{-1} (Klopčič *et al.*, 2010b) at which fir starts producing viable seed.

parameters of fir more than passive conservation (NON). However, CCF proved efficient only if recruitment is not the limiting factor in the population dynamics. In two study areas with sufficient recruitment (type A and C forests), two alternative management scenarios (CONS and MAX) were even more efficient for fir conservation than current forest management, which can be explained by the same tool both strategies use, i.e. the intensification of felling while maintaining stand densities favourable for the regeneration of shade-tolerant fir (de Andrés *et al.*, 2014; Kupferschmid *et al.*, 2015). If the unmanaged population is declining, which is the case in type B forests, none of the active management scenarios can prevent decline, not even stand management optimized for increasing recruitment. In large areas of type B forests, recruitment of fir has almost come to a halt (Klopčič *et al.*, 2010a; Ficko *et al.*, 2011) due to high red deer densities. Evidence of deer population reduction effects on the progression of browse-sensitive species (e.g. Côté *et al.*, 2004; Tremblay *et al.*, 2007; Jenkins *et al.*, 2014) implies that forest practitioners should focus more on reducing chronic herbivory. Recovery from herbivory is a protracted process during which tree regeneration may continue to decline despite a reduction in browsing pressure (e.g. Tanentzap *et al.*, 2011), so instant restoration actions are needed in herbivory-induced declining populations.

The urgency of restoration actions before a population declines to a critical level can be illustrated by calculating the survival probability of recruits at the age when fir begins to produce viable seed. By comparing the number of successors, each fir still alive at the age when it began to produce viable seed should produce to replace itself (e.g. Chien *et al.*, 2008) with the current recruitment per number of fructifying trees, we can estimate whether the current recruitment is sufficient for population maintenance. Survival probability of recruits at the age when fir begins to fruit (i.e. >60 years, Brus, 2012) was over 90 per cent in all three forest types (Figure 4, the vertical arrow), implying that on average each fructifying fir would need to produce slightly more than one recruit in its entire reproductive period to maintain the population size. At the current recruitment rate, the populations in type A, B and C forests would need 24–65, 477–1273 and 44–117 years, respectively, to be replaced, assuming fructification every 3–8 years (Brus, 2012). CONS, which increases recruitment negligibly, can shorten the replacement periods only up to 5 years. Clearly, this does not represent a solution for fir in forests with recruitment failure.

The context of fir population decline

The decline of a common tree species due to factors other than pathogens is challenging for applied ecologists since the scale of the decline may vary from the local to the metapopulation. Since tree species are declining and disappearing as a part of long-term changes in ecosystem dynamics (White and Pickett, 1985), the local decline or even extinction of fir may not be problematic because the overall fir population trend is stable (Farjon, 2014). To mitigate the negative biological and financial effects of fir decline in type B forests, conservation regimes could be established in the other two types of forests. In Central Europe, however, the integration approach to nature conservation is preferred over segregation (Bončina, 2011a). Moreover, such an off-reserve conservation strategy may be hard to implement in type B forests given the expected trajectory towards beech domination in the case of

non-intervention, which is similar to projections for the declining Pyrenean fir forests at mesic sites (Camarero *et al.*, 2011) or mixed *P. abies – A. alba – F. sylvatica* forests in the Bavarian Forest National Park (Cailleret *et al.*, 2014a, b). Our projections are consistent with the observed dynamics of mixed old-growth forests in Eastern and South-eastern Europe in the last 50 years (Diaci *et al.*, 2011), which show that in most old-growth *P. abies – A. alba – F. sylvatica* forests, air pollution and overbrowsing are the key factors for the shift from patchy changes in species mixture to a synchronous fir decline. Where these two stressors have been insignificant, fir has experienced no growth reductions (Castagneri *et al.*, 2014), but repeated canopy openings due to periodical spruce bark-beetle outbreaks have contributed to the higher competitiveness of beech *vs* fir (Keren *et al.*, 2014).

The conservation of conifers in forests with recruitment failure in an era of rapid global warming is challenging due to limitations in latitudinal range shifts (e.g. Kroiss and HilleRisLambers, 2015). However, Tinner *et al.* (2013) consider that the future geographic range of fir may not contract even if the climate becomes significantly warmer as long as precipitation does not fall below 700 – 800 mm per year and anthropogenic disturbance does not become excessive. This is consistent with the analysis of the world's largest dendrochronological dataset for fir (Büntgen *et al.*, 2014) and several distribution models (e.g. Falk and Mellert, 2011; Serra-Diaz *et al.*, 2012), which imply that fir may benefit from warmer (but not drier) climate in mesic areas, whereas in southern habitats, it may be exposed to increasing stress and an increased risk for decline (Gazol *et al.*, 2015; Vicente-Serrano *et al.*, 2015). However, when the joint effects of climate change and browsing are considered, a climate change-induced increase in growth may not compensate for browsing-induced reductions in ba (Didion *et al.*, 2011). Cailleret *et al.* (2014a, b) showed that 100 years of browsing can change tree species composition more than changing climate. However, empirical studies on the joint effects of climate change and browsing are still scarce. The study on growth of selected temperate tree species at their upper range limit exposed to high browsing pressures (Fisichelli *et al.*, 2012) demonstrated that browsing can eliminate positive responses of growth to warming and severely threaten migration. From the perspective of conservation and uncertainty related to local climate change, conserving fir in type B forests (and elsewhere) is a pragmatic undertaking. Allowing fir to decline significantly in the coming 100 years, whatever the climate will be, reduces financial benefits, decreases species richness and consequently reduces the opportunity to have fir in the future tree species portfolio in changing but perhaps locally favourable climatic episodes.

Conclusions

We showed that continuous cover silvicultural systems can improve the demographic parameters of declining browse-sensitive tree species without additional conservation measures and profit loss. However, in forests chronically suffering from insufficient recruitment, CCF is inadequate for preventing species decline, although negative demographic trends can be reversed temporarily if silviculture is optimized for conservation. We conclude that forest management is not the major tool for the conservation of browse-sensitive and shade-tolerant tree species in mixed uneven-aged forests with recruitment failure. Based on the simulations and

management optimizations in three different types of fir forests in Europe, we argue that recruitment failure is a serious factor limiting the long-term persistence of fir in European forests and that factors other than silviculture, such as browsing, are incomparably more critical for conserving fir in mixed uneven-aged forests.

Supplementary data

Supplementary data are available at *Forestry* online.

Conflict of interest statement

None declared.

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