

Accurate modeling of harvesting is key for projecting future forest dynamics: a case study in the Slovenian mountains

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Abstract Maintaining the provision of multiple forest ecosystem services requires to take into consideration forest sensitivity and adaptability to a changing environment. In this context, dynamic models are indispensable to assess the combined effects of management and climate change on forest dynamics. We evaluated the importance of implementing different approaches for simulating forest management in the climate-sensitive gap model ForClim and compared its outputs with forest inventory data at multiple sites across the European Alps. The model was then used to study forest dynamics in representative silver fir–European beech stands in the Dinaric Mountains (Slovenia) under current management and different climate scenarios. On average, ForClim accurately predicted the development of basal area and stem numbers, but the type of harvesting algorithm used and the information for stand

initialization are key elements that must be defined carefully. Empirical harvesting functions that rigorously impose the number and size of stems to remove fail to reproduce stand dynamics when growth is just slightly under- or overestimated, and thus should be substituted by analytical thinning algorithms that are based on stochastic distribution functions. Long-term simulations revealed that both management and climate change negatively impact conifer growth and regeneration. Under current climate, most of the simulated stands were dominated by European beech at the end of the simulation (i.e., 2150 AD), due to the decline of silver fir and Norway spruce caused mainly by harvesting. This trend was amplified under climate change as growth of European beech was favored by higher temperatures, in contrast to drought-induced growth reductions in both conifers. This forest development scenario is highly undesired by local managers who aim at preserving conifers with high economic value. Overall, our results suggest that maintaining a considerable share of conifers in these forests may not be feasible under climate change, especially at lower elevations where foresters should consider alternative management strategies.

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Introduction

Forests provide a multitude of ecosystem services (ES) to humankind (EEA 2010), including direct economic support such as timber production, but also indirect benefits from the regulation of ecosystem processes (e.g., protection against natural hazards, regulation of biogeochemical

cycles) and cultural services (e.g., recreation, aesthetics). The provisioning of these ES has changed over the past decades and will continue to do so because of global change (Elkin et al. 2013). Although trees have developed mechanisms to cope with changes of environmental conditions (e.g., plasticity in functional traits; Nicotra et al. 2010), forests are particularly vulnerable to rapid environmental changes (Lindner et al. 2010) mainly due to the long lifespan of trees, which limits genetic adaptation. Temperature rise combined with higher nitrogen deposition positively influences tree growth in many boreal and temperate forests (Pretzsch et al. 2014a), but it may negatively affect tree vitality under increasing drought (Carnicer et al. 2011). Forest management can play a key role to mitigate these effects (Bravo et al. 2008). Several strategic options can be followed, from the promotion of more resistant and/or resilient tree species to the modification of forest structure using specific harvesting interventions to reduce competition (Elkin et al. 2015; Spathelf et al. 2014). Yet, an accurate evaluation of the potential effects, benefits and disadvantages of management measures is required.

Projecting the future properties of managed forests in a changing environment is challenging (Bugmann 2014). In forestry, this has traditionally been based on extrapolating past observations using expert knowledge. Empirical forest growth-and-yield models (GYMs) were the first quantitative tools predicting tree growth at the individual tree and stand level (Pretzsch et al. 2008). They typically derive from large field datasets and use site- and species-specific regression functions to simulate growth based on a combination of ontogenic and abiotic explanatory variables (Peng 2000). Although GYMs may be suitable for investigating management alternatives and short-term yield in a future where conditions are similar to the past for which they were calibrated (Kimmins et al. 2005), causal relationships between stand development and climate are not considered so they cannot be applied reliably for different climatic conditions (Fontes et al. 2010). Alternatively, forest dynamics can be simulated by coupling demographic and ecophysiological models (PBMs, e.g., Guillemot et al. 2014), explicitly considering physiological processes such as photosynthesis and respiration (Mäkelä et al. 2000). As PBMs simulate the effects of climate and CO₂ on tree functioning using a mechanistic approach, they are more appropriate than GYMs under changing environmental conditions. However, PBMs require a large number of parameters and measurements for calibration and validation (Shao and Reynolds 2006), which are often difficult to obtain for many sites and species, thus limiting their general applicability (Fontes et al. 2010).

An alternative approach is forest gap models (also called forest succession models; cf. Bugmann 2001; Shugart 1984). Over the past years, they have increasingly been

applied to investigate the impacts of management strategies (Kunstler et al. 2013) under climate change (Lindner et al. 2000; Rasche et al. 2013). As they are not fully mechanistic, the number of parameters they require is limited, and they generally have a broader applicability (Bugmann and Solomon 2000; Holm et al. 2012).

Many studies have reported accurate simulations of stand basal area, biomass or tree diameter distributions using forest gap models (Jiang et al. 1999; Pabst et al. 2008), but it is not clear at what level of detail the management has to be prescribed. Recent research has emphasized the better representation of ecological processes such as tree establishment (Wehrli et al. 2007), mortality (Bircher et al. 2015) or natural disturbances (Seidl et al. 2008). However, although several studies used different harvesting options and management interventions to simulate stand properties (Ditzer et al. 2000; Garman et al. 1992), the effects of specific harvesting functions on simulated forest dynamics have rarely been evaluated against long-term data (Pabst et al. 2008; Rasche et al. 2011). If we are to rely on gap models as decision support tools in forest management planning in the context of climate change, their ability to correctly capture management interventions is a key factor.

Thus, the goal of this study was (1) to evaluate the performance of a forest gap model with a focus on its sensitivity to specific harvesting functions, and (2) to assess the impact of current management practices and climate change on future forest dynamics in the Dinaric Mountains in Slovenia.

Materials and methods

Forest model

We used the model ForClim (Bugmann 1996; Rasche et al. 2012), which has been shown to represent silvicultural treatments well and has revealed high potential for investigating the impact of management scenarios under a changing climate (Rasche et al. 2013).

ForClim is a climate-sensitive forest gap model that has been developed to simulate forest dynamics over a wide range of environmental conditions (Bugmann 1996). It operates at the stand level and is based on specific ecological assumptions to capture the influence of climate and ecological processes on long-term forest dynamics. Diameter and height growth of every cohort (i.e., trees of the same species and same age) are calculated based on the principle of growth-limiting factors where a species-specific maximum growth rate is reduced depending on the extent to which environmental factors are at suboptimal levels (Bugmann 2001; Moore 1989). The management

submodel allows for the application of a wide range of silvicultural treatments such as clear-cutting, shelterwood felling, thinning or planting (Rasche et al. 2011). A detailed description of the model can be found in Bugmann (1996), Bugmann and Solomon (2000), Didion et al. (2009b), Rasche et al. (2012) and Bircher et al. (2015).

Model improvements

Didion et al. (2009b) and Rasche et al. (2011) described the ability of ForClim to match time series data from long-term forest research plots. However, a series of simulation tests performed at multiple sites across the Alpine region (French Pre-Alps, Austrian Alps, Slovenian Dinaric Mountains) revealed a tendency of the model to underestimate stand basal area due to low simulated productivity (data not shown; cf. Bircher et al. 2015 for results on monospecific spruce stands). Further tests revealed that this is related to the link between simulated light availability and diameter growth, rather than to climate-related limiting factors (i.e., degree-day sum or drought). In addition, the management submodel does not allow for harvesting in selected diameter classes, which prevents the implementation of flexible interventions. These issues were addressed as described below.

Tree growth and light environment

Diameter growth in the current version of ForClim (v.3.3) is calculated as follows:

$$\frac{\Delta D}{\Delta t} = GRF * kG * D * \frac{1 - (H/gH_{MAX})}{(2 * H + f_H * D)} \tag{1}$$

where D and H are diameter at breast height and tree height (state variables), gH_{MAX} is the dynamically calculated site- and species-specific maximum tree height, f_H a function that distributes growth between diameter and height (Rasche et al. 2012), kG the species-specific maximum growth rate, and GRF the scalar reduction factor to determine realized growth. The latter is calculated with the following equation:

$$GRF = \sqrt[3]{ALGF * DDGF * SMGF * SNGF * CLGF} \tag{2}$$

where each factor ranges between 0 and 1 and expresses growth reduction due to available light (ALGF), degree days (DDGF), soil moisture (SMGF), soil nitrogen (SNGF) and crown length (CLGF), which are updated at each time step of the simulation (yearly). In the previous version of the model, reduction based on crown length (CLGF) acted as a separate multiplier in the diameter growth equation (Didion et al. 2009b, their Eq. 7). Since the effect of crown size on radial growth of dominant canopy trees is lower

than previously expected (Fichtner et al. 2013), and to prevent the underestimation of basal area increment in dense, productive stands, this effect was included in the overall growth reduction factor GRF in ForClim v.3.3 (Eq. 2). CLGF itself is calculated as follows:

$$CLGF = \text{MIN}\left(\frac{4}{3} * \frac{gA_1}{kA_{1diff}} * \frac{kLCP_s}{kLCP_{mean}}, 1\right) \tag{3}$$

where $kLCP_s$ is the species-specific light compensation point, $kLCP_{mean}$ the mean light compensation point for all the species parameterized in the model, gA_1 a relative measure of crown density, and $kA_{1diff} = kA_{1MAX} - kA_{1MIN}$. The value of gA_1 should vary between kA_{1MAX} and kA_{1MIN} , which represent the maximum and minimum envelope (95 %), respectively, of the relationship between tree diameter at breast height (DBH) and foliage mass (kg) of distinct species groups (Bugmann 1994; Wehrli et al. 2007). Earlier model versions did not include the influence of kA_{1MIN} in the calculation of the effect of crown length. Therefore, we adjusted the formulation of CLGF (Didion et al. 2009b, their Eq. 6) by adding the influence of kA_{1MIN} via kA_{1diff} (Eq. 3). Finally, the auxiliary variable gA_1 is still calculated as follows:

$$gA_1 = kA_{1MAX} - kA_{1diff} * gLAI \tag{4}$$

where $gLAI$ represents the leaf area index factor (LAI), which is a function of the LAI estimated at the top of the tree canopy ($gLAI_H$) and the maximum LAI in a patch ($kLAI_{MAX}$) that is achievable for the most shade-tolerant species:

$$gLAI = \text{MIN}[(gLAI_H/kLAI_{MAX}), 1] \tag{5}$$

Management

We complemented the management submodel by two harvesting functions that enhance model flexibility. The first function, labeled single stem removal (SSR), was developed for simulating removals of an exact number of stems for every tree species by diameter class (e.g., 5 or 10 cm bins) for each intervention. If the number of removed stems derives from inventory data or management plans for a specific plot size, their number was calculated in proportion to the size of the simulated area. We implemented a second function that allows removals of a percentage of stand basal area that is split into five relative diameter classes (RDC). These classes are calculated proportionally depending on the minimum and maximum simulated diameter in the stand in the current year (Seidl et al. 2005). This second function was primarily developed as a logical extension of SSR for running long-term simulations into the future, where prescribing removals of a

certain number of stems in static diameter classes is simply unrealistic. Following the classification by Soderbergh and Ledermann (2003), SSR can be categorized as an empirical function (i.e., based on observed data), while RDC was considered as an analytical harvesting algorithm such as the thinning functions previously implemented in ForClim (further below referred as GEN). As ForClim is a horizontally non-explicit forest model without interactions between individual simulated patches, tree removals are executed randomly within the patches.

Model evaluation: data and simulation settings

We evaluated the latest version of ForClim (v.3.3, as described above) against forest inventory data of five forest GYM plots in Switzerland and five forest compartments in the Snežnik area in southern Slovenia (Table 1; Online Resource 1). All plots are dominated by at least one of the three main species of European mountain forests, i.e., European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.), and are often associated with Sycamore maple (*Acer pseudoplatanus* L.), European larch (*Larix decidua* Mill.) or Swiss stone pine (*Pinus cembra* L.).

For each stand, forest dynamics was simulated under historical management and climatic conditions from the first to the last inventory (70–100 and 50 years in Switzerland and Slovenia, respectively). The stands were initialized using DBH data from the first inventory, allocating randomly each tree to the number of patches

obtained by dividing site area by the default patch size (i.e., 800 m²). We subsequently expanded this information to the standard number of patches (i.e., 200) by using replicates of these patches in order to reduce stochastic noise in the simulations (Didion et al. 2009b). Species-specific relationships between height and diameter were obtained from forest inventories at each site and were used to calculate initial tree height. In the absence of detailed local data, browsing pressure was set to 20 %. Interspecific difference of sensitivity to browsing is implemented in the model via species-specific browsing tolerance parameters (see Didion et al. 2009a for further details). The simulation settings for all sites are shown in Table 1 and in Online Resource 1.

For assessing the effects of the different harvesting approaches on simulated forest dynamics, we used two functions with the management submodel. We first ran simulations applying a *generic management* function (GEN), which removes a constant percentage of stand basal area in regular interventions during the management phase. It requires calculating the average number of years between management operations and the mean intensities of interventions (% of trees to harvest per patch). The algorithm automatically selects trees to be removed based on their DBH until a certain amount of basal area is reached using a stochastic Weibull function, which is determined from the current DBH distribution and a parameter controlling the type of thinning (for a detailed description see Rasche et al. 2011). All species present in the stand were assumed to be suitable for harvesting. Alternatively, we applied the *single*

Table 1 Main characteristics of the stands used to evaluate ForClim, their geographic region (CH = Switzerland; SLO = Slovenia), coordinates, elevation (in case of large compartments the mean elevation of the area is shown), mean temperature, mean annual precipitation,

area, simulation details on estimated water holding capacity (*BS* bucket size), soil available nitrogen, slope, aspect, simulation period with number of available inventory measurements (*n*) and share (% of basal area) of the different tree species at initialization

Region	Site	Coordinates (°N; °E)	Elevation (m a.s.l.)	Temp (°C)	Precip (mm)	Site area (ha)	BS (mm)	Nitrogen (kg/ha * year)	Slope (°), aspect	Simulation period (n)	Pab/Aal/Fsy/Oth.
CH	Aarburg	47.33; 7.91	475	8.8	1130	0.25	100	80	0°	1890–1994 (18)	0/0/100/0
CH	Hospental	46.61; 8.58	1475	4.2	1513	0.40	100	80	20°, N	1933–2005 (10)	50/0/0/50
CH	Horgen	47.27; 8.56	630	8.5	1236	0.50	100	100	0°	1907–1999 (16)	14/3/77/6
CH	Morissen	46.74; 9.18	1630	3.6	1446	0.50	100	50	20°, S	1929–2002 (10)	69/0/0/31
CH	Zofingen	47.29; 8.00	510	8.7	1165	0.25	100	100	0°	1890–2001 (17)	0/0/98/2
SLO	1D	45.61; 14.45	968	6.3	1454	9.00	120	70	20°, E	1963–2013 (3)	10/77/12/1
SLO	2C	45.62; 14.46	825	7.3	1382	7.81	120	70	20°, N	1963–2013 (3)	16/72/11/1
SLO	7A	45.61; 14.48	965	6.4	1453	5.17	100	70	25°, NW	1963–2013 (3)	2/81/15/2
SLO	11B	45.60; 14.48	1205	4.7	1576	6.93	100	70	5°, N	1963–2013 (3)	24/55/19/2
SLO	40C	45.63; 14.46	815	7.4	1377	6.87	100	70	5°, S	1963–2013 (3)	8/80/11/1

Pab *Picea abies*, *Aal* *Abies alba*, *Fsy* *Fagus sylvatica*, *Oth* *Larix decidua* in Hospental, *Acer pseudoplatanus* in SLO, *Pinus cembra* in Morissen and Hospental, and *Quercus petraea* in Horgen

stem removal function (SSR) to simulate harvesting of the exact number of stems reported in the inventory for each species and DBH class (5 cm bin), matching the year of intervention.

Model outputs in terms of basal area, stem numbers, DBH distributions and volume harvested per hectare were compared with empirical data. For evaluating the goodness of fit between observations (obs) and simulations (sim) over n observations, we used the relative root-mean-square error (RMSE) and the percent bias (pbias):

$$\text{RMSE} = \frac{\sqrt{\sum(\text{sim} - \text{obs})^2 / (n - 1)}}{\sum \text{obs} / n} * 100 \quad (6)$$

$$\text{pbias} = \frac{\sum(\text{sim} - \text{obs}) / n}{\sum \text{obs} / n} * 100 \quad (7)$$

We further compared the simulated versus observed DBH distributions at the final simulated year using the Kolmogorov–Smirnov test and calculated the difference in percentage of the cumulative volume harvested at each site.

Model application

We selected mountain forests of the broader Snežnik area in the Dinaric Mountains in Slovenia as a case study (Fig. S1, right). Climate change has been and will be particularly pronounced in mountain regions (Christensen et al. 2007; Rebetez and Reinhard 2008), and thus, these forests and the ES they provide may be altered strongly. In the Snežnik area, forest management has a long tradition to promote timber production and nature conservation. Recent studies have highlighted increasing risks related to climate change (Boncina 2011; Diaci et al. 2010; Klopčič and Boncina 2011). Thus, there is high interest by local forest managers to assess future forest development under “Business-As-Usual” management and climate change, with implications at broader scales, i.e., for developing tools that provide decision support recommendations for adapting management plans for the future.

A total of 37 representative stand types (hereafter RST) were defined as a unique combination of site conditions, stand characteristics and forest management (FM) type. First, site conditions were assigned to each RST: elevation range, slope, aspect, nitrogen availability and water holding capacity. Second, forest structure data—tree species composition and DBH structure—were derived from a series of inventories for the period 1963–2003. Twenty-six RSTs were identified as even-aged stands with different development stages (i.e., pole, mature and regenerated stands), while the remaining 11 RSTs featured uneven-aged stand structures. Characteristics for each RST are reported in Table S4, Online Resource 3. We initialized the model for each RST at the year 2010 using data provided as the

number of trees by species per hectare in diameter classes of 5 cm. Simulation results are shown below for nine RSTs at three elevations only, as these RSTs represent the simulated diversity in stand structure and composition in the Snežnik area quite well.

Forest management data

To simulate future forest management, we used prescriptions representing the typical course of silvicultural measures over the entire rotation cycle of a stand (Business-As-Usual Forest Management, hereafter BAU-FM). BAU-FM data for each RST were gathered by local experts through questionnaires to forest practitioners. In even-aged RSTs, an irregular shelterwood system with rotation periods of 130–140 years was applied, and the main interventions consisted of 2–4 thinning operations and 2–3 regeneration fellings with a regeneration period of 20–30 years. Each intervention was executed when the stand reached a specific diameter (average of the 100 largest trees per hectare). Only natural recruitment was used for regenerating the stands. In uneven-aged RSTs, a combination of group selection, single-tree selection (“plentering”) and small-scale irregular shelterwood was used. Interventions occurred approximately every 10 years with harvesting intensities of typically 15 % of standing volume. Since data for future management scenarios for each intervention could not be anticipated in terms of single-tree removals for such long projections, we determined percentages of harvested basal area by tree species using the RDC approach.

Model settings and simulation experiments

For each RST, we generated a total of 100 model patches representing initial stand conditions using the methodology described in “[Model evaluation: data and simulation settings](#)” section. Harvesting was implemented using the RDC approach, with specification of harvesting percentages by species and RDC for each silvicultural operation, for both even-aged and uneven-aged RSTs. The minimum diameter for calculating RDC was set to 5 cm, with the exception of silver fir for which it was set to 25 cm in regeneration fellings (even-aged) and single-tree selection harvesting (uneven-aged) for conservation reasons. All stands were initialized in year 2010 and simulated until 2150, in order to simulate at least one full rotation period. We ran simulations under current and future climatic conditions (see Online Resource 2), assuming a constant climate after 2100. The establishment submodel was slightly modified for the model application, as explained in Online Resource 3.

We assessed the development of simulated basal area and species share for BAU management under current

climate and climate change scenarios for every stand as well as aggregated for the entire forested area (average values with their standard deviation indicating inter-site variability).

Results

Model evaluation

In the spruce-dominated subalpine plots of Morissen and Hospental (Switzerland), basal area, stem numbers as well as harvested volume and DBH distribution simulated with the single stem removal function (SSR) matched empirical data very well (Fig. 1; Table 2; Fig. S2 in Online Resource 1; bias in basal and stem numbers <5.5 %). With the generic function (GEN), however, basal area and stem numbers were generally underestimated (by ca. -15 and -30 %, respectively) due to an overestimation of the harvesting of large trees in the first four interventions. Still, simulated development of basal area and stem numbers converged with empirical data toward the end of the simulation, resulting in a good match with the observed DBH distribution (cf. Figure 1 for Morissen). As the GEN function removed a constant percentage of the stock at every intervention, harvested volume decreased over time proportionally to stand basal area. Similar patterns were obtained in Aarburg, except for a strong overestimation of stem numbers in the low DBH classes (+66 %; Table 2 and Fig. S2).

In mixed submontane stands Horgen and Zofingen (Switzerland), there was a large difference in the simulation results between the two management functions. At initialization, these young stands (19 and 27 years, respectively) were characterized by a large number of small trees (>3000 ha⁻¹ with DBH <6 cm; Fig. 1 and Fig. S2). Using the GEN function, simulated basal area and stem numbers fitted well with empirical data, although there were slight differences in the final DBH distribution due to an overestimation of stem numbers in the 25–30 and 50–55 cm classes in Horgen and Zofingen, respectively. At both sites, harvested volume over the entire simulation period was 20.4 and 41.7 % higher than empirical data suggest (Table 2). In contrast, the SSR function clearly underestimated total harvested volume in Horgen (-46 %), leading to a strong overestimation of basal area (+68 %) and stem numbers (+124 %), especially in the DBH classes <40 cm. In Zofingen, simulated basal area and stem numbers were higher than observed as well (+68.3 and +50.6 %, respectively) due to a strong underestimation of harvested stems for the first two interventions (ca. -750 and -500 stems/ha in 1892 and 1898, respectively; cf. Fig. S3 in Online Resource 1).

Fig. 1 Change over time of stand basal area (m²/ha), stem numbers (per ha) and volume harvested (m³/ha/year) based on inventory data (black) and simulated by ForClim using the GEN (blue) and SSR (red) functions. Diameter distributions (5-cm bins) at the last inventory and at the end of the simulations are shown in the bottom panel; the color-shaded areas show the 2.5th and 97.5th percentile of the simulations

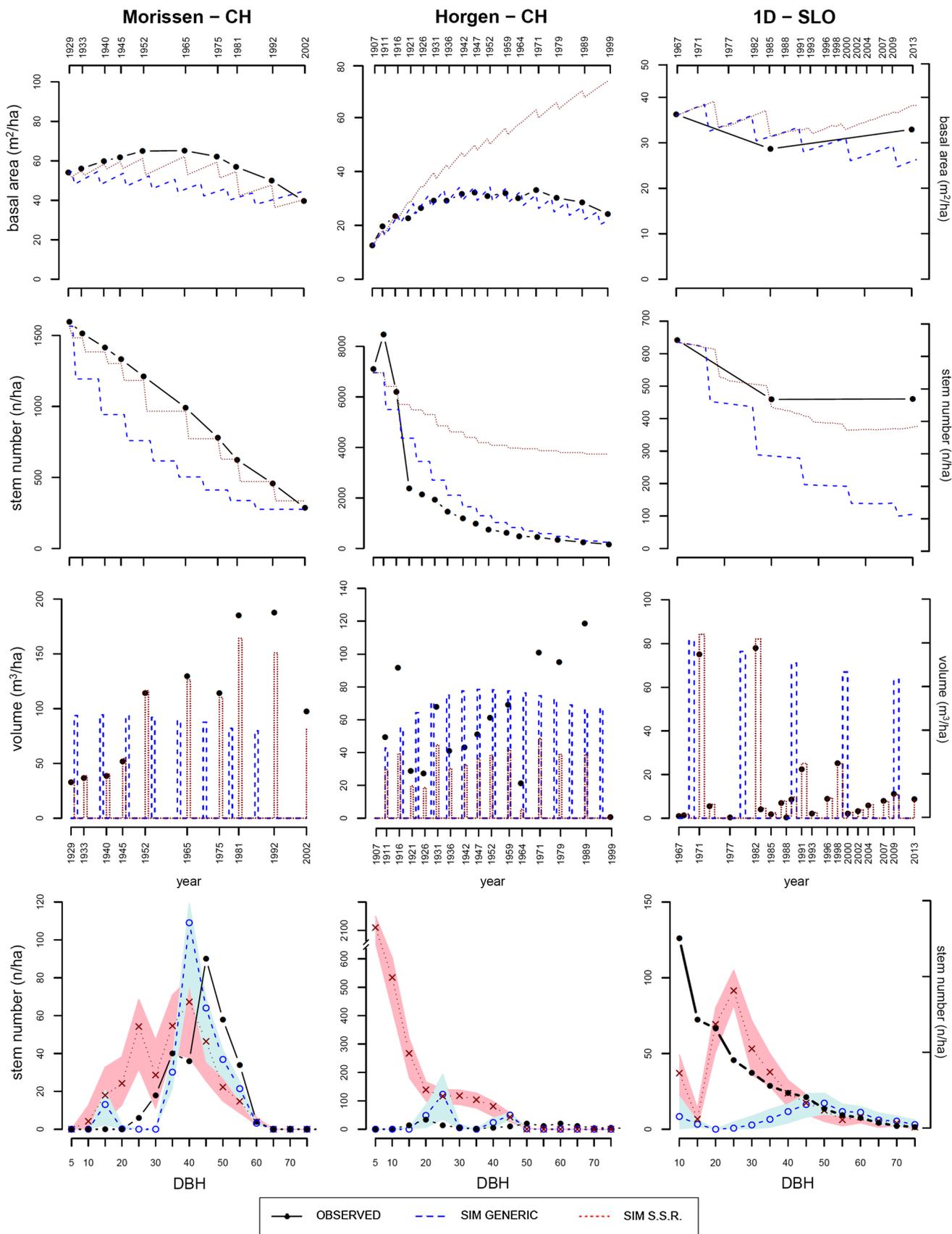
Finally, consistent results were obtained for the Slovenian sites, but the SSR algorithm typically led to more realistic results than the GEN function (Table 2). Using five thinning interventions executed at ten-year intervals, the GEN function underestimated stand basal area (e.g., -5 % for site 1D; Fig. 1) and, to a higher extent, stem numbers (between -25.8 and -42.7 %). Due to the strong overestimation of harvesting in the low and medium diameter classes (10–45 cm), this bias increased over time leading to a significantly different DBH distribution at the last inventory (Fig. 1; Fig. S2; Table 2). However, the lack of empirical data for trees <10 cm at initialization (see Online Resource 1) resulted in a general underestimation of stem numbers in the low diameter classes, independent of the harvesting function. Still, the SSR function yielded a better match between observed and simulated basal area and stem numbers (bias <10 % except for stem numbers at site 11B). Moreover, volume harvested in the years of intervention corresponded remarkably well with management records, and the DBH distribution at the end of the simulation period was quite close to observations (excluding the 10 cm DBH class).

Model application

Simulated forest dynamics under current climate and BAU-FM

For the entire Snežnik area, the average stand basal area projected for the end of the simulation period did not differ substantially from initial conditions (i.e., 38.3 ± 7.8 m²/ha in 2010 vs. 39.8 ± 11.1 m²/ha in 2150). However, there were strong differences with elevation, showing an increase in basal area at medium elevations and a decrease at higher elevations (Fig. 2a, d). The higher stand basal area at medium elevations was due to a strong increase in the share of beech (from 33.5 ± 23.0 to 75.8 ± 17.1 %) across the entire area (Fig. 2f). In contrast, the basal area of silver fir was simulated to decrease irrespective of elevation (Fig. 2b, e). In 2010, it had a mean value of 41.4 ± 23.8 % and reached >60 % in medium-elevation stands, but its share did not exceed 15 % for most RSTs in 2150 (10.2 ± 8.9 %, Fig. 2e).

At high elevations and in even-aged RSTs, simulations indicated a development from typical upper montane beech-dominated to mixed beech-fir-spruce stands (e.g.,



for RST 1E: Fig. 3, upper panels). Concerning uneven-aged stands, RST 1Ua, which initially was dominated by beech, featured a reduction in beech basal area over time combined with a slight increase in spruce and a nearly constant amount of silver fir. For the mixed beech–fir–spruce RST 1Ub, we observed a decline of silver fir and spruce associated with a strong increase in beech basal area over time. Most of the stands located at medium elevations showed a similar trend in forest composition, slightly modified by the management approach. In the RSTs 2Ea, 2Eb and 2U, which were dominated by silver fir and beech (Fig. 3), simulations projected a clear decrease in silver fir and promoted a strong rise of the proportion of beech, which was the prevailing species at the end of the management cycle. This was especially important in uneven-aged RSTs (e.g., RST 2U), for which harvesting was simulated with a stronger intensity on silver fir rather than on beech (and on spruce), which in turn replaced silver fir as the dominant species. The replacement of silver fir and spruce by beech was even more apparent at low elevations (Fig. 3: RSTs 3Ea, 3Eb, 3U). Eventually, the simulation under current climate resulted in nearly pure beech stands with a high basal area (40–55 m²/ha). Simulated forest development for the remaining RSTs is shown in Fig. S6.

Effect of climate change

Changing climate conditions—i.e., warmer and drier climate, especially during summer (Table S3, Online Resource 2)—induced a reduction in average basal area when considering all RSTs (Fig. 2). However, the decline was not very strong, as it averaged 33.1 ± 10.8 and

29.7 ± 11.2 m²/ha in 2150 for the CC1 and CC2 climate scenarios, respectively (Fig. 2g, l). The simulated share of silver fir was even lower than under current climate (5.2 ± 6.1 % under the CC2 scenario; Fig. 2m). In contrast, climate change further promoted beech dominance over the whole area (mean share 89.6 ± 9.3 % under the scenario CC2; Fig. 2n). In high-elevation stands, temperature rise was highly beneficial for beech and to the detriment of spruce and silver fir, resulting in a decline of the share of conifers irrespective of the BAU-FM variant used (Fig. 3, upper panels). No positive effect of higher temperatures on beech was found at medium elevations. However, combined with the decrease in precipitation, it impacted spruce strongly negatively and to a lesser extent also silver fir in the long term (i.e., after ca. 2080). At low elevations, climate change exacerbated the decline of conifers such that they were nearly absent toward the end of the management cycle (Fig. 3, lower panels). Interestingly, a reduction in growth was observed for beech as well, as the development of its basal area over time diverged from the simulation under the current climate after ca. 2080, especially for the CC2 scenario, for which the difference in beech basal area in 2150 was close to 30 m²/ha (e.g., stand 3Ea. Figure 3).

Discussion

General model performance

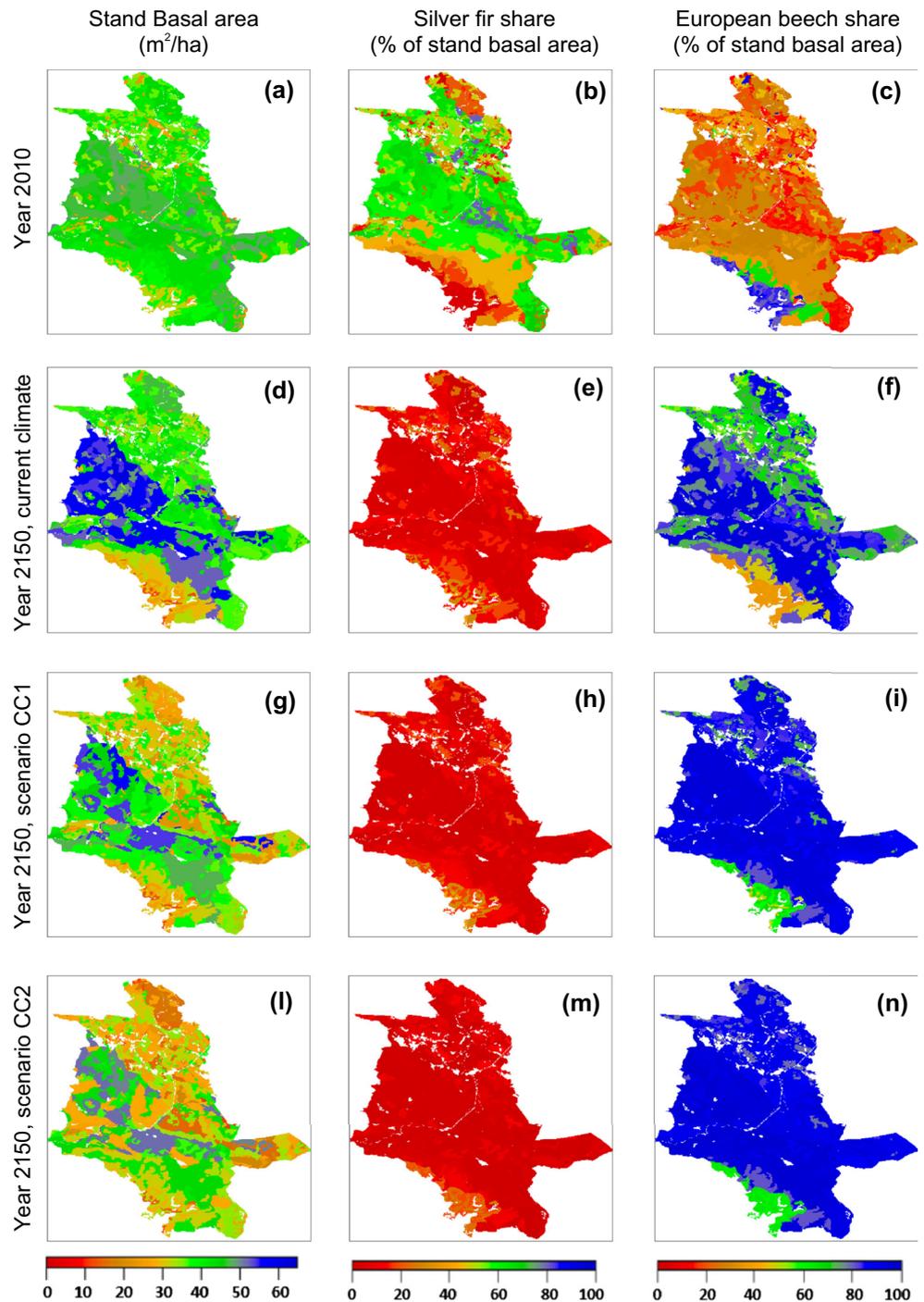
For model evaluation, we used relatively long inventory periods (50–104 years) and multi-species stands, in

Table 2 Relative root-mean-square error (RMSE; in %) and percentage bias (pbias; in %) of basal area and stem numbers simulated by both GEN and SSR scenarios with regard to observed values for the evaluation sites

Region	Site	Basal area				Stem numbers				Volume harvested		DBH distribution	
		GEN		SSR		GEN		SSR		GEN	SSR	GEN	SSR
		RMSE	pbias	RMSE	pbias	RMSE	pbias	RMSE	pbias	Diff	Diff	Stat	Stsat
CH	Aarburg	4	−3.4	3	2.4	48	45.0	70	66.0	−40.0	−17.7	0.25	0.44
CH	Hospental	17	−14.9	6	−5.3	37	−32.9	3	2.8	−20.2	−4.8	0.31	0.25
CH	Horgen	2	−1.6	73	68.2	16	15.3	132	124.1	20.4	−46.5	0.63	0.63
CH	Morissen	19	−17.3	4	−3.4	33	−29.4	1	−1.1	−28.0	−7.1	0.13	0.19
CH	Zofingen	16	15.3	73	68.3	0	0.5	54	50.6	41.7	11.5	0.63	0.69
SLO	1D	7	−4.6	12	7.9	51	−34.3	11	−7.4	28.0	8.1	0.57	0.14
SLO	2C	15	−10.1	7	5.0	47	−31.4	12	−8.4	−2.9	−22.2	0.57	0.29
SLO	7A	23	−15.5	6	−4.3	39	−26.1	5	−3.5	1.0	1.9	0.71	0.36
SLO	11B	30	−20	12.8	−8.5	64	−42.7	33	−22.3	26.9	4.5	0.64	0.29
SLO	40C	9	−6.1	2.8	1.9	39	−25.8	2	1.3	−25.8	−6.5	0.43	0.29

The difference of cumulative volume harvested between observed and simulated data (diff; in %) is also indicated. The last two columns represent the sample statistics calculated with the Kolmogorov–Smirnov test to compare the cumulative DBH distribution at the final observation year; values in bold indicate that distributions significantly differ with a p value <0.05

Fig. 2 Current (in 2010) and projected (in 2150) stand basal area and share of silver fir and beech (in percentage of basal area) extrapolated to the entire Snežnik area. Simulations into the future were run using three climate scenarios: current climate, CC1 and CC2. The maps were generated by plotting RST-level simulation data into raster polygons (migration of species and large-scale external disturbances are not considered, in contrast to landscape-scale, spatially explicit models; details on the methodology in Online Resource 3)



contrast to many earlier studies (e.g., Lasch et al. 2005; Seidl et al. 2005). It is pleasing to see that at Slovenian sites, for which ForClim had never been applied to date, the model produced reasonable results compared with inventory data. This confirms the observations of Didion et al. (2009b), who demonstrated a good applicability of the model under a broad range of environmental conditions.

In contrast to ForClim 3.0 (Rasche et al. 2011), no systematic underestimation of basal area was observed any more with ForClim 3.3 (the percentage bias over all inventory sites averaged: -18.34 ± 9.6 and -7.8 ± 10.3 with the models ForClim v3.0 and ForClim v3.3, respectively), particularly at subalpine, conifer-dominated sites (see Fig. S4 and Table S1 in Online Resource 1). We suggest that the reduction in diameter growth due to short

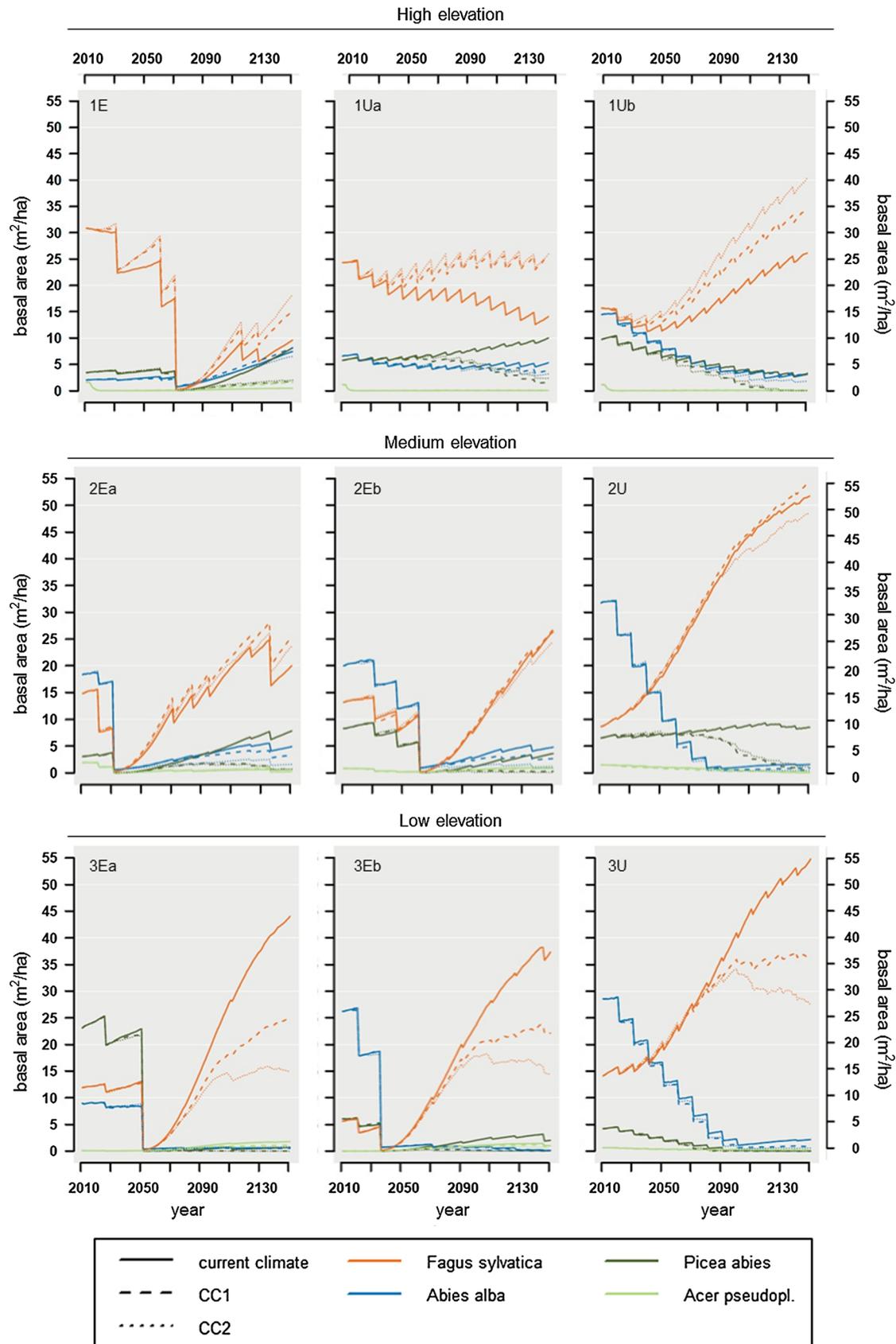


Fig. 3 Simulated change in basal area of *Fagus sylvatica*, *Abies alba*, *Picea abies* and *Acer pseudoplatanus* under current climate and two climate change scenarios for nine RSTs of the Snežnik area. These RSTs were selected at three elevations to represent the diversity in stand structure, species composition and BAU-FM. Symbols for different panels indicate the elevation (1 = high; 2 = medium; 3 = low), structure and management system (*E* even-aged; *U* uneven-aged) of the RST. Simulation results for the other 28 RSTs are available in Online Resource 3

tree crowns as implemented by Didion et al. (2009b) was too strong, being an artifact of the need to consider multiple growth-reducing factors (Eq. 1; cf. Bugmann 2001). In accordance with Fichtner et al. (2013), we reduced the dependency of the radial growth of dominant canopy trees on crown length and thus the impact of CLGF on simulated diameter increment (cf. “Tree growth and light environment” section). However, we are aware that the new equation may be improved further and that studies devoted to a better representation of crown characteristics and the impact of plant morphology and the light regime on tree growth would be highly welcome so as to reduce bias and uncertainties in simulations (Ligot et al. 2014).

In addition, the modeling of tree mortality and establishment in managed stands could be improved as well. Mortality functions in forest gap models (Keane et al. 2001) mostly fail to match natural mortality in GYM plots, and consequently, their growing stock (Bircher et al. 2015) as mortality rates (and deadwood pools) is usually lower than under unmanaged conditions (Powers et al. 2012). Regarding establishment, the concept of a constant seed rain without dispersal limitation and without feedback from canopy trees (Price et al. 2001) may be rather inappropriate, especially in intensively managed forests (e.g., Snežnik RSTs in this study; details in Online Resource 3), in which harvesting intends to favor the regeneration of the most economically valued species (Wagner et al. 2010).

Performance of the two harvesting functions

Several studies have evaluated the effects of harvesting intensities on simulated forest properties, yet they did not analyze the consequences of using different algorithms (Lindner 2000; Taylor et al. 2008). Although the reliability of gap models for forest management has been criticized (Monserud 2003), ForClim proved to be suitable for investigating different harvesting techniques and analyzing how they impact future forest development. Rasche et al. (2011) suggested that detailed settings for management functions can be substituted without harm by generic ones; we therefore examined whether the model was capable to capture forest dynamics and timber volume harvested by using an analytical harvesting algorithm (generic; GEN) versus an empirical one (single stem removal; SSR).

Interestingly, our analysis across multiple sites revealed a trade-off in the performance of these approaches, depending on stand structure.

In mature plots at initialization (e.g., Morissen, Hospental and the Slovenian sites), SSR performed better than GEN in terms of simulated stand basal area, stem numbers and harvested volume. By removing a constant percentage of the growing stock at every intervention, GEN generally underestimated basal area somewhat (Rasche et al. 2011). The better performance of SSR over GEN at these sites reflects the sensitivity of the harvesting function to the initialized stand structure: Model projections across decades depend strongly on the initial state (Temperli et al. 2013). When the simulation starts from a mature stand, the model calculates initial canopy height and biomass, which influence available light at the forest floor. In this case, forest dynamics are much less subject to stochastic processes of the model (which influence mortality and establishment) compared to simulations starting from young stands or even from bare ground (Wehrli et al. 2005), and the chance that growth is neither under- nor overestimated is much higher. As a consequence, SSR was able to capture harvesting very well, as the number of stems to be removed in the specified DBH classes was easily identified in every intervention.

By contrast, in young forest stands that feature a large number of small trees (e.g., Horgen and Zofingen), simulations carried out using GEN were closer to observations, while basal area and stem number were strongly overestimated with SSR due to the large underestimation of harvesting. As SSR removed a preselected number of stems within diameter classes with static bins, a mismatch between simulated and observed growth rates induced a divergence in the harvesting. This problem cannot occur with GEN, since the thinning algorithm automatically calculated the number of stems to harvest in each diameter class based on the probability distribution associated with the silvicultural operation.

We conclude that the implementation of empirical harvesting algorithms, such as SSR, in forest gap models (or, as a matter of fact, in any other dynamic forest model) may fail to represent forest dynamics properly when the simulated diameter structure diverges from real conditions. Approaches such as SSR are promising to assess model behavior when single-tree data from historical records are available or to investigate the impacts of harvesting in the short term (i.e., <50 years). However, we are less confident in their relevance for long-term projections, especially since they require a priori knowledge of the number of stems to harvest in each diameter class, irrespective of future forest structure (Arii et al. 2008). Thus, analytical algorithms are likely to be more suitable due to the stochasticity in distributing stem removals (e.g., thinning

algorithms such as in Lin and Paro 2011; or relative diameter classes as in Seidl et al. 2005). In addition, since they better mimic actual silvicultural decisions and are easily adjustable by the user, they should be preferred when models are used as decision support tools by forest practitioners (Soderbergh and Ledermann 2003).

Implications of Business-As-Usual forest management in Snežnik, Dinaric Mountains

We used the RDC harvesting approach to simulate future forest dynamics under BAU-FM in the Snežnik area. As discussed above, this analytical algorithm was the best approach we could use to avoid possible model failures in capturing the characteristics of the harvesting interventions based on available management prescriptions. However, since our intent was to correctly capture the management regime rather than mimicking empirical removal interventions where species-specific removal percentages might be adjusted depending on the current species proportions, this could have induced large, possibly unintended changes in the share of individual species.

Simulated forest dynamics under current climate and BAU-FM

Although stand basal area simulated for 2150 did not change significantly compared to initial conditions (2010), species composition differed strongly. In the majority of the RSTs, we observed a drastic reduction in silver fir basal area, followed by an expansion of beech. These changes were due to (1) the higher establishment potential of beech and (2) the direct impacts of harvesting on silver fir.

First, the modification of the establishment potential of beech in ForClim according to currently observed natural regeneration strongly favored this species at the expense of conifers. As beech is currently the dominant species in the understory, our simulations suggested that its proportion would increase in the future. This trend was especially strong at low elevations, where spruce originates from planting. In dense spruce plantations, beech regeneration is generally limited due to the lack of seeds (Poljanec et al. 2010). However, considering that planted stands in the Snežnik area are small, thus allowing seed influx from surrounding stands, and that some beech trees were initially present in these stands, there was no reason to exclude beech establishment in the model. This resulted in nearly pure beech stands after the simulated regeneration fellings. In ForClim, silver fir and spruce are parameterized to require a mean temperature of the coldest months below -3 and -1 °C, respectively (Bugmann and Solomon 2000). At low elevations in Snežnik, however, the average temperature of the coldest months is above the chilling

requirements for silver fir (i.e., establishment was not possible at any time) and partly for spruce (establishment limitation in 40 % of the years), while it was not limiting for beech in the model. Above 1200 m a.s.l., stands were not dominated by beech in the simulations as its growth was limited by low temperature during the growing season. Here, BAU-FM promoted a higher proportion of conifers (Fig. 3, RSTs 1E & 1Ua), which agrees with empirical studies where a decline of beech in Slovenian subalpine forests was observed during the last 40 years (Poljanec et al. 2010).

Second, simulated harvesting intensity for silver fir was too high to maintain a sustainable amount of its growing stock over time and to cope with competition by beech. As a result, the strong silver fir decline observed during the twentieth century in these forests (Klopčič et al. 2010) and in other forest types across Slovenia (Ficko et al. 2011) may continue. Numerous authors have anticipated a decline of silver fir in the Dinaric Mountains (Diaci et al. 2010; Klopčič and Boncina 2011; Poljanec et al. 2010). Our simulations confirm this expectation. As silver fir is highly sensitive to natural and human disturbances (e.g., wildfires or harvesting; cf. Tinner et al. 2013), harvesting intensities such as the ones prescribed in BAU-FM seem to be inappropriate to warrant its conservation. In addition, as silver fir's regeneration is the most sensitive to browsing among the other tree species (Cailleret et al. 2014; Klopčič et al. 2010), its decline could be further amplified in case of increased ungulate density in the area.

Effect of climate change

Our study revealed that climate change would have strongly varying impacts on basal area and species composition in Dinaric mountain forests, mainly depending on their elevation. This broadly confirms the findings of a range of studies from other mountain areas (Cailleret et al. 2014; Elkin et al. 2013). In high-elevation stands, climate change improved growing conditions for beech compared to the current climate. Soil water availability is barely limiting in these forests, and thus, the rise of temperature and the extension of the growing season favored beech growth, as demonstrated by several empirical and modeling studies (Pretzsch et al. 2014b; Tegel et al. 2014). As a consequence, the higher leaf area index had a negative effect on spruce, whose regeneration was hindered by low light availability (Stancioiu and O'Hara 2006). At medium elevations, conditions for beech were already quite favorable under current climate, and thus, an increase in temperature did not further promote its growth. The slight reduction in summer rainfall did not have a negative effect on beech increment, as simulated drought did not exceed the tolerance of the species. However, in low-elevation

stands, the increase in summer temperature associated with a decrease in summer rainfall led to severe constraints on tree growth, and it caused drought-induced tree mortality as revealed by the reduction in beech stand basal area after ca. 2080, which was even stronger under the scenario CC2 than under CC1. Drought-induced mortality also occurred at low and intermediate elevations in silver fir and spruce (e.g., RST 2U), whose drought resistance is lower than that of beech (Morin et al. 2011). This dieback phenomenon was all the more important since nearly no regeneration of either conifer species took place due to the anticipated increase in winter temperatures (at low elevations >-1 °C from the year 2024 for CC1 and 2016 for CC2, respectively), thus leading to a nearly complete absence of conifers after the final regeneration felling.

Methodological aspects and limitations of the study

Our simulation results provide a comprehensive assessment of future forest development in the Dinaric mountain forests under BAU-FM and climate change. However, they represent an evaluation of possible future *trends* rather than definite *forecasts* of forest properties (cf. Bugmann 2014). We only considered harvesting and changes of climatic conditions as influencing factors on forest productivity. Other changes may also impact forest dynamics. For example, the rise of CO₂, nitrogen deposition and changing air pollution (Elling et al. 2009) as well as natural disturbances such as windthrow or pathogen outbreaks (Seidl et al. 2014) may need to be considered. In addition, our simulations disregarded possible migration of species that are potentially more adapted to future climatic conditions (e.g., drought-tolerant oaks or pines). Furthermore, we acknowledge that the decline of silver fir may have been overestimated (Ruosch et al. 2015). Although many studies that have investigated past and current forest conditions agree on the future decline of this species (Heuze et al. 2005; Klopčič and Boncina 2011; Oliva and Colinas 2007), recent paleoecological studies suggest that silver fir is probably more drought tolerant than previously thought, as it was quite abundant in the Mediterranean area as long as the disturbance regime was low (Tinner et al. 2013). Based on these new observations, a re-parameterization of this species in the model may be appropriate. Lastly, we acknowledge that in our study we investigated the effects of climate change based only on two climate scenarios that were selected from a wide—if not infinite—range of possible climate projections.

Implications for forest management and conservation

In the Snežnik area, timber production continues to be the most important ES, followed by biodiversity conservation.

Our simulation results support future timber production, albeit not of conifers, although these are preferred by forest owners and managers for their economic value. The main consequence of BAU-FM would thus be that timber production *per se* could be maintained, as climate change would have detrimental effects on growth in the long term and at low elevations only. Although the interest for beech has been growing in the last decades (Hahn and Fanta 2001), managers and scientists need to consider alternatives to BAU-FM if they want to preserve a considerable amount of conifers in these mountain forests. Moreover, forests entirely dominated by beech, as they were present some centuries ago (due to anthropogenic disturbances and grazing; cf. Diaci et al. 2011; Klopčič et al. 2010), would likely be less resistant and resilient to natural disturbances compared to mixed forests (Knoke et al. 2008; Neuner et al. 2015), especially to spring frosts (Cailleret and Davi 2011) and snow damage while leaves are still present (Nykanen et al. 1997). It would therefore be desirable to preserve a considerable share of conifers in these forests to maintain their economic value and to reduce vulnerability to major disturbance events (Vuletić et al. 2014).

Conclusions

Our study documents the high flexibility of the forest gap model ForClim to reproduce forest dynamics and specific management regimes in two different mountain areas of Europe. However, the success of gap models to capture the drivers of tree growth in managed stands depends strongly on the accuracy of the harvesting regime. Detailed empirical algorithms can be helpful for evaluating model performance over short time scales, but they are at risk of failing if growth is not simulated in a highly accurate manner. Therefore, analytical algorithms are most likely more promising for projecting the impacts of future forest management on forest structural patterns in the long term.

Based on a set of representative stands in the Snežnik mountain forests, we determined that BAU-FM combined with climate change would (1) maintain current growing stocks except at low elevations and (2) strongly impact species composition by favoring beech at the expense of silver fir and spruce. Further research is required to investigate potential *adaptive* management measures that aim at maintaining conifer timber production while also preserving tree species diversity in Dinaric mountain forests.

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