

Future ecosystem services from European mountain forests under climate change

Marco Mina^{1,2*}, Harald Bugmann¹, Thomas Cordonnier³, Florian Irauschek⁴, Matija Klopčič⁵, Marta Pardos⁶ and Maxime Cailleret¹

¹Department of Environmental Sciences, Forest Ecology, Swiss Federal Institute of Technology, ETH Zurich, Universitätstrasse 16, CH-8092 Zürich, Switzerland; ²Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland; ³Irstea-EMGR, 2 Rue de la Papeterie, BP 76, 38402 Saint-Martin-d'Heres Cedex, France; ⁴Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna (BOKU), Peter-Jordan-Straße 82, 1190 Vienna, Austria; ⁵Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Vecna Pot 83, 1000 Ljubljana, Slovenia; and ⁶Department of Silviculture and Forest Systems Management, INIA-CIFOR, Crtra Coruña Km 7.5, 28040 Madrid, Spain

Summary

1. Ecosystem services (ES) from mountain forests are highly relevant for human societies. ES with a direct economic support function (e.g. timber production), regulatory services (e.g. protection from natural hazards) and cultural services (e.g. recreation) are likely to be affected strongly by a rapidly changing climate. To evaluate whether adverse climate change effects on ES can be counteracted by adapting management, dynamic models and indicator-based assessments are needed.

2. We applied a forest dynamic model in case study areas of four European mountain regions and evaluated the future supply of four ES – timber production, carbon sequestration, biodiversity and protection against natural hazards – using state-of-the-art ES indicators. Forest dynamics were simulated under three management scenarios (no management, business-as-usual and alternative management) and five climate change projections for selected representative stand types in each region. We analysed potential trade-offs and synergies between ES and evaluated future changes among regions, forest stands, climate and management scenarios.

3. Impacts of climate change on the provision of multiple ES were found to be highly heterogeneous and to depend on the region, site and future climate. In the absence of large-scale natural disturbance (not considered), protection services, carbon stock and deadwood abundance (proxy for biodiversity) benefitted from no management in all regions. Negative impacts of climate change were evident for the provision of multiple ES but limited to the most severe climate scenarios and low-elevation stands. Synergies and trade-offs between the majority of ES were found to be sensitive to the choice of management strategy and – in some regions – to climate change.

4. *Synthesis and applications.* Management regimes in European mountain forests should be regionally adapted to stand and site conditions. Although in some cases alternative management regimes may be more suitable than current management for supporting multiple ecosystem services, adaptation options should be evaluated carefully at the local scale due to the highly different magnitude of the impacts of climate change in different regions and along elevation gradients.

Key-words: carbon sequestration, climate change scenarios, ecosystem service indicators, ForClim, forest dynamic modelling, forest management, silvicultural systems, synergies, timber production, trade-off

*Correspondence author. E-mail: marco.mina@wsl.ch

Introduction

The large array of ecosystem goods and services (ES) delivered by mountain ecosystems is fundamental for sustaining the well-being of people living in mountain and lowland areas (MEA 2005; Gret-Regamey, Brunner & Kienast 2012). Currently, about half of the global human population depends on benefits delivered by mountain ecosystems (Körner & Ohsawa 2005). In Europe, mountain regions cover more than 40% of the continent (Price, Lysenko & Gloersen 2004), of which about 40% is covered by forests (Price *et al.* 2011). These woodlands are key landscape elements that supply timber and non-wood forest products (Price & Butt 2000), offer habitat for many species of plants and animals (Estreguil *et al.* 2012), contribute to climate regulation, for example by storing carbon (Ciais *et al.* 2008) and have important recreational and cultural values (Peña, Casado-Arzuaga & Onaindia 2015). Furthermore, mountain forests protect the land against erosion and natural hazards such as rockfall and avalanches (Dorren *et al.* 2004). Thus, it is essential to understand and accurately predict whether mountain forests will be able to provide multiple ES in the future. In addition, since past and current resource management strategies were mainly driven by single objectives (e.g. timber production) that often lead to reductions or losses of other ES (Puettmann, Coates & Messier 2009), it is particularly important to investigate not only individual ES provision, but also the relationships between ES (i.e. trade-offs and synergies; Rodriguez *et al.* 2006).

This challenge is all the more important since climate models project strong increases of temperature and changes of precipitation amount and seasonality in mountain areas. In fact, temperature increase in mountain areas during the last 40 years was up to three times higher than the global average (Pepin *et al.* 2015). Recent temperature rise and changes in precipitation patterns have already induced changes in ecosystems (Nogues-Bravo *et al.* 2007), among others regarding tree regeneration (Smith *et al.* 2009), growth (Bowman *et al.* 2014; Pretzsch *et al.* 2014) and mortality (Allen, Breshears & McDowell 2015).

At the local scale, the effects of climate change on mountain forests can be expected to be heterogeneous due to the variability of (i) microclimatic conditions (Lindner *et al.* 2010; Engler *et al.* 2011), (ii) location-specific climate change and (iii) current stand properties that will strongly affect future forest trajectories (Bircher 2015). A range of options have been proposed for adapting silvicultural systems to novel conditions, such as increasing stand complexity (e.g. uneven-aged mixed forests; Bolte *et al.* 2010; Millar & Stephenson 2015). Due to the diversity of European forests and the different regional vulnerability to climate change, alternative management strategies may spatially vary substantially (Lindner *et al.* 2010). However, as high-resolution, long-term forest inventory and management data are usually not available for many locations, most regional-scale impact studies to date were

forced to draw conclusions based on a few sites only (Elkin *et al.* 2013; Hlasny *et al.* 2014). At the European scale, several studies have projected future changes of forest properties and ES provision, but without explicitly including management (Reyer *et al.* 2014) or ignoring the impacts of climate change (Biber *et al.* 2015).

Climate-sensitive models that simulate forest properties at local to regional scales are powerful to evaluate forest management strategies under an uncertain future (Elkin *et al.* 2013; Reyher *et al.* 2015). In mountain regions, stand-scale models have proven highly suitable (Rasche *et al.* 2011), particularly when management is simulated accurately (Mina *et al.* 2015). To date, however, there are only a few such studies, and they often did not assess future trade-offs and synergies between multiple ES across sites (Seidl *et al.* 2007; Ray *et al.* 2014).

We address three main questions: (i) What is the impact of climate change on multiple ES in European mountain forests? (ii) Will alternative management regimes be more suitable in providing multiple ES under climate change than current management? (iii) How would climate change and management alter the synergies and trade-offs between ES in different regions?

Materials and methods

STUDY AREAS AND REPRESENTATIVE STAND TYPES

We investigated four mountain regions: central Iberian Mountains (Spain), Western and Eastern Alps (France, Austria) and Dinaric Mountains (Slovenia; Fig. 1). These case study areas (CSAs) were selected in the context of the EU FP7 project 'ARAN-GE' to cover the key forest types and governance settings in the main mountain ranges of central and southern Europe and diverse climate regimes (see Tables 1 and 2 and Appendix S1, Supporting Information).

In each CSA, five representative stand types (RSTs) were selected to cover the most important site and stand conditions regarding species mixture, development stage and structure, management interventions, and site characteristics (i.e. topography and soil conditions) while keeping the simulation effort to a feasible level (Table 2). For the Iberian Mountains, we chose pure Scots pine stands since this species dominates >80% of the forest area in that region. Data for each RST consisted of detailed information on forest structure such as stem number by diameter classes or the proportion of tree species in the regeneration phase (i.e. density of trees shorter than 130 cm) and data on the abiotic environment (e.g. climate, available nitrogen, water holding capacity; additional information in Lexer 2013).

Forest management data

We considered three management scenarios: a scenario of non-intervention (NM), Business-As-Usual (BAU) as a representation of current management practices and one alternative management regime (AM). Descriptions of silvicultural operations for BAU in each RST, as well as modifications to derive AM during a full rotation, were provided by local experts (Klopčič *et al.* 2013). Specifics of each intervention (e.g. thinning, regeneration felling),

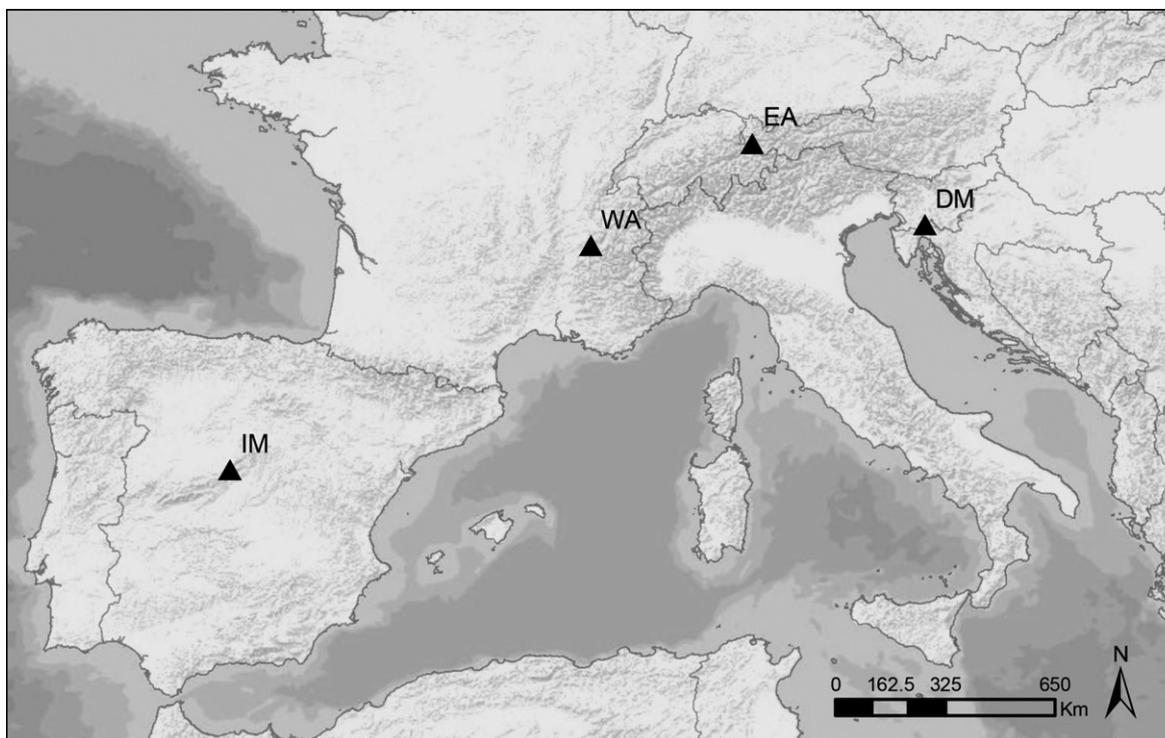


Fig. 1. Location of the case study areas (IM, Iberian Mountains; WA, Western Alps; EA, Eastern Alps; DM, Dinaric Mountains).

single-tree selection cuts) included data on removal percentages by tree species and removal structure in five relative diameter classes (RDCs). All RSTs were regenerated with natural recruitment. The AM scenario was modified and adapted from BAU to pursue similar or different management goals and provision of ES depending on the CSA (detailed description of management regimes in Appendix S1).

Climate change scenarios

Five climate change scenarios for the 21st century were selected from ensemble simulations generated by combinations of Global Circulation and Regional Climate Models run under the A1B emission scenario (van der Linden & Mitchell 2009). They represent a wide range of possible future climate conditions in each CSA and cover a reasonable amount of the uncertainty in climate projections. Scenarios were ranked based on the increase in mean annual temperature per CSA and subsequently renamed as 'CC1' (mildest) to 'CC5' (strongest). Taking baseline climate as a reference, we calculated season-specific anomalies for temperature (°C) and precipitation (%) for the period 2070–2100 as representative for future climate (all details in Appendix S1).

SIMULATION OF FOREST DYNAMICS

Model description

We used the climate-sensitive forest gap model ForClim, which simulates stand-scale dynamics of small independent forest patches containing mixtures of multiple tree species (Bugmann 1996). The model simulates establishment, growth and mortality of tree cohorts with an annual time step, based on species characteristics (e.g. shade and drought tolerance), environmental factors

(light availability, growing season and winter mean temperatures, soil nitrogen and water availability) and crown length. A flexible management submodel allows for the application of both analytical (e.g. thinnings in RDC) and empirically based harvesting interventions (e.g. single stem removals). ForClim has been evaluated under a wide range of environmental conditions in Europe, showing good performance in matching long-term forest inventory data (Rasche *et al.* 2011; Mina *et al.* 2015, 2016b), and it has also been used to assess climate change impacts (Didion *et al.* 2011; Elkin *et al.* 2013). We used model version 3.3, except in the Iberian Mountain CSA where we applied a variant of v3.3 that better captures the influence of summer drought on Scots pine growth (v3.3-LOC; see Mina *et al.* 2016b).

Simulation setup

For projecting future stand properties under the five climate change scenarios, we initialized ForClim for each RST using forest inventory data and simulated forest dynamics from 2010 until the end of each management cycle, which differed among CSAs, RSTs and management regimes (set to 2130 in the Iberian Mountains, 2100 Western Alps, 2110 Eastern Alps, and 2150 Dinaric Mountains; details in Appendix S1 and Table S1.1). Season-specific delta values for future climate calculated taking baseline climate as a reference were used as inputs in the simulations, assuming linear changes until 2100 followed by a constant climate until the end of the simulation. Management interventions under BAU and AM were simulated by removing species-specific percentages of basal area by RDC with the analytical harvesting algorithm described and tested in Mina *et al.* (2015). For the scenario of non-intervention (NM), we did not simulate any harvesting operation until the end of the rotation.

Table 1. Characterization of the case study areas (CSAs). Coordinates refer to the centre of the CSA

	Iberian Mountains	Western Alps	Eastern Alps	Dinaric Mountains
Name of the region	Valsaín	Vercors	Montafon	Snežnik
Country	Spain	France	Austria	Slovenia
Coordinates	40°50'N, 4°01'W	45°10'N, 5°32'E	47°04'N, 9°50'E	45°34'N, 14°24'E
Area (km ²)/forested (%)	100/90	500/55	75/90	50/97
Elevation range (m a.s.l.)	1200–2000	600–1900	600–2000	600–1500
Mean annual temperature (°C)	10.3	5.9	4.5	3.8
Annual precipitation sum (mm)	1116	1482	1448	1927
Range of soil water holding capacity (mm)	100–140	100–120	130–250	100–120
Main tree species	<u>Scots pine</u> , Pyrenean oak, Holm oak	<u>Spruce</u> , <u>Fir</u> , <u>Beech</u> , Maple	<u>Spruce</u> , Fir, Beech, Maple	<u>Fir</u> , <u>Beech</u> , Spruce, Maple

Annual mean temperature and precipitation sums are given for 1200 m a.s.l. in each CSA (1951–2011). Dominant tree species are underlined (Scots pine = *Pinus sylvestris*; Pyrenean oak = *Quercus pyrenaica*; Holm oak = *Quercus ilex*; Spruce = *Picea abies*; Fir = *Abies alba*; Beech = *Fagus sylvatica*; Maple = *Acer pseudoplatanus*).

Table 2. Characteristics of the RSTs of the case study areas (IM, Iberian Mountains; WA, Western Alps; EA, Eastern Alps; DM, Dinaric Mountains), with their ID (decimal values denote stand development of the RST: 0 – uneven-aged; 1 – thicket; 2 – pole; 3 – mature; 4 – in regeneration phase), tree species composition at initialization (Ps, *Pinus sylvestris*; Pa, *Picea abies*; Aa, *Abies alba*; Fs, *Fagus sylvatica*; Ap, *Acer pseudoplatanus*; ordered from the most to the least abundant), development and structure of the stand (EA indicates even-aged), range of elevation, soil water holding capacity, slope and aspect (0: 0°–10°, 1: (10°–30°), 2: (>30°)) and plant-available nitrogen

CSA	RST ID	Elevation (m a.s.l.)	Initial stand		Site characteristics		
			Tree species	Stand development	Water holding capacity (mm)	Slope and aspect	Soil nitrogen (kg ha ⁻¹ yr ⁻¹)
IM	11.1	1375–1625	Ps	EA – Thicket	120	1 N	90
IM	11.4	1375–1625	Ps	EA – Mature	120	1 N	90
IM	13.2	1625–1875	Ps	EA – Pole	140	1 N	90
IM	13.3	1625–1875	Ps	EA – Mature	140	1 N	90
IM	14.4	1875–2000	Ps	EA – Overmature	100	1 N	60
WA	3.0	1200–1500	Pa/Aa	Uneven-aged	120	0.5 NW	60
WA	6.0	900–1200	Aa/Pa/Fs	Uneven-aged	100	0.5 SE	60
WA	8.0	1200–1500	Aa/Fs/Pa/Ap	Uneven-aged	100	0.5 SE	60
WA	13.0	1500–1800	Pa/Fs/Aa/Ap	Uneven-aged	100	0.5 NW	60
WA	19.0	1500–1800	Pa/Aa/Fs	Uneven-aged	100	0.5 SE	60
EA	10.0	1475–1825	Pa	Uneven-aged	170	2 N	90
EA	18.0	1125–1475	Pa	Uneven-aged	130	2 N	70
EA	35.0	1475–1825	Pa/Aa	Uneven-aged	250	2 S	100
EA	47.0	1475–1825	Pa/Aa	Uneven-aged	150	2 S	80
EA	53.0	1125–1475	Pa/Aa/Fs	Uneven-aged	250	2 S	100
DM	4.3	600–900	Aa/Fs/Pa	EA – Mature	120	0 flat	70
DM	5.3	710–1100	Aa/Fs/Ap	EA – Mature	120	0 flat	70
DM	8.3	760–940	Aa/Pa/Fs/Ap	EA – Mature	120	1 S	70
DM	17.0	790–1100	Aa/Fa/Pa	Uneven-aged	120	1 N	70
DM	23.0	1050–1360	Aa/Fs/Pa	Uneven-aged	100	1 N	70

The latter three parameters represent site characteristics in ForClim, whereas tree species composition and stand development characterize the forest stand at initialization. The complete list of RSTs identified in the context of the EU ARANGE project is available in Lexer (2013).

ECOSYSTEM SERVICE INDICATORS

From the simulation results (e.g. species-specific basal area, diameter distribution or leaf area index), we derived indicators for assessing four main ES provided by mountain forests: (i) timber production, (ii) carbon storage, (iii) forest biodiversity and (iv) protection against natural hazards. This latest ES is of particular importance in the Eastern Alps (Maroschek, Rammer & Lexer 2014) but is still of interest in the other three CSAs that are

characterized by stands with more gentle slopes (Table 3; e.g. Pardos *et al.* 2016; V. Lafond, T. Cordonnier, Z. Mao & B. Courbaud, in revision). First, we calculated annual values of 22 indicators that were averaged for the period 2080–2100, with the exception of timber volume harvested, which was calculated as the sum over the entire management cycle (complete list of indicators in Appendix S2). Secondly, we performed a multiple factor analysis (MFA) to establish cross-correlations between indicators and select a reduced number of them that best explained each ES

Table 3. F-values of the ANOVA on the multifunctionality index in each CSA

	d.f.	Iberian Mts	Western Alps	Eastern Alps	Dinaric Mts
CLIMATE	5	1.5	51.6	6.1	5.5
FM	2	987.8	1468.5	720.3	6011.2
RST	4	754.6	751.2	322.8	376.8
CLIMATE:RST	20	2.5	13.3	13.3	5.4
CLIMATE:FM	10	1.3	12.9	0.7	1.7
FM:RST	8	121.1	20.3	6.5	728.7
Key for P-values:		<0.001	<0.01	<0.05	>0.05

d.f., degrees of freedom. Cell colours represent the significance level of the respective and interactive effects of the climate scenario (CLIMATE), management scenario (FM) and RST. Residuals d.f.: 40.

(cf. Abdi, Williams & Valentin 2013). The analysis was performed with the software R (R Core Team 2014) using the package *FactoMineR* (Lê, Josse & Husson 2008). Finally, a total of five indicators were selected as follows: timber volume harvested for production (T), above-ground biomass for carbon storage (C), two indices that express protection against rockfall (P1) and avalanches (P2), and deadwood volume for biodiversity (B). Considering that deadwood pools are usually low in managed stands (Powers *et al.* 2012), ForClim did not simulate decomposition, which led to an accumulation of deadwood in the stand over time. The protection indices P1 and P2 were calculated on a scale between 0 and 1 (see Appendix S2). To enable the comparison between all indicators, T, C and B were standardized by dividing each value by the maximum obtained under the entire set of climate and management scenarios within each RST (i.e. standardized values range between 0 and 1).

A dimensionless index expressing the provision of all five ES (termed *multifunctionality index*, MFI) was obtained by calculating the mean of the standardized indicators. Within each CSA, an analysis of variance (ANOVA) was carried out to detect statistical differences in MFI between climate change and management scenarios and among the RSTs. To analyse trade-offs and synergies between ES, Spearman rank correlations were calculated on pairs of ES considering the two active management regimes, BAU and AM, since relationships between timber production and other ES could not be explored under NM. As ES time series are temporally auto-correlated, the calculation of Spearman correlation coefficients was based on the first and last years of the period 2080–2100 including all five RSTs in each CSA (i.e. 10 values were used to calculate each relationship between ES). For each pair, the change in correlation coefficients among climate change and management scenarios and among CSAs was assessed using ANOVA.

Results

PROJECTION OF FOREST ECOSYSTEM SERVICES

The projected future provision of ES differed considerably among CSAs and RSTs (Figs 2 and S3.2). Moreover, within each RST, we observed pronounced differences depending on the management regime, climate change scenario and ES. The ANOVA of the MFI showed

statistically significant differences ($P < 0.05$) among the RSTs and management regimes in all CSAs (Table 3). The effect of climate change on MFI was not consistent among the CSAs; it was not significant in the Iberian Mts but highly significant in the other CSAs.

Provision of ES under current climate

In the Iberian Mts, Eastern Alps and Dinaric Mts, MFI was higher in the absence of management (Fig. 3) owing to higher C storage, biodiversity and protective functions (Fig. 2a, b, e–h), despite the lack of any timber production. In the Western Alps, however, MFI was lower under NM, the rockfall and avalanche protection indices did not change markedly with management, and indicators of C storage and biodiversity were only slightly higher under NM.

AM exhibited significantly higher MFI values than BAU in the Iberian and Dinaric Mts. In all RSTs of the Iberian Mts, timber production under AM was slightly lower than under BAU, but the other indicators were higher (Figs 2a and S3.2). In the Dinaric Mts, timber production was nearly equal for both BAU and AM scenarios, but strong differences between the RSTs were found for the other indicators (Fig. 2g, h). For example, in even-aged RSTs (e.g. RST 5.3), C storage and both protective functions were projected to be higher under AM, while no differences between BAU and AM were observed for biodiversity. On the contrary, in uneven-aged RSTs (e.g. RST 23.0), a higher provision of C storage, biodiversity and protection would occur under BAU. In the Eastern Alps, highest timber supply was achieved with AM, but the highest MFI values were obtained in all RSTs under BAU. Finally, only in the Western Alps no significant differences ($P > 0.05$) were detected between BAU and AM, with the exception of a reduction in timber production in RSTs 13.0 (Fig. 2d) and 19.0 (Fig. S3.2).

Impacts of climate change

In the Iberian Mts, no effect of climate on MFI was detected, irrespective of the management scenario (Table 3, Fig. 3). Results for individual indicators showed a similar trend (Fig. 2). Under the mildest climate change scenario (CC1), nearly identical results were found as with baseline climate for RST 13.3 (Fig. 2i), while a slight increase in the biodiversity index was detected under NM and AM for RST 14.4 (Fig. 2j). Similarly, the strongest climate change scenario (CC5) induced only a minimal increase in the biodiversity index for RST 14.4 (Fig. 2r), and no changes were evident for RST 13.3 (Fig. 2q). By contrast, in the Western Alps, significant and generally strong climate-induced changes of MFI were simulated, their magnitude varying among RSTs and management scenarios. In this CSA, under the most severe climate scenario (but also under CC2, Fig. S3.2), a positive influence

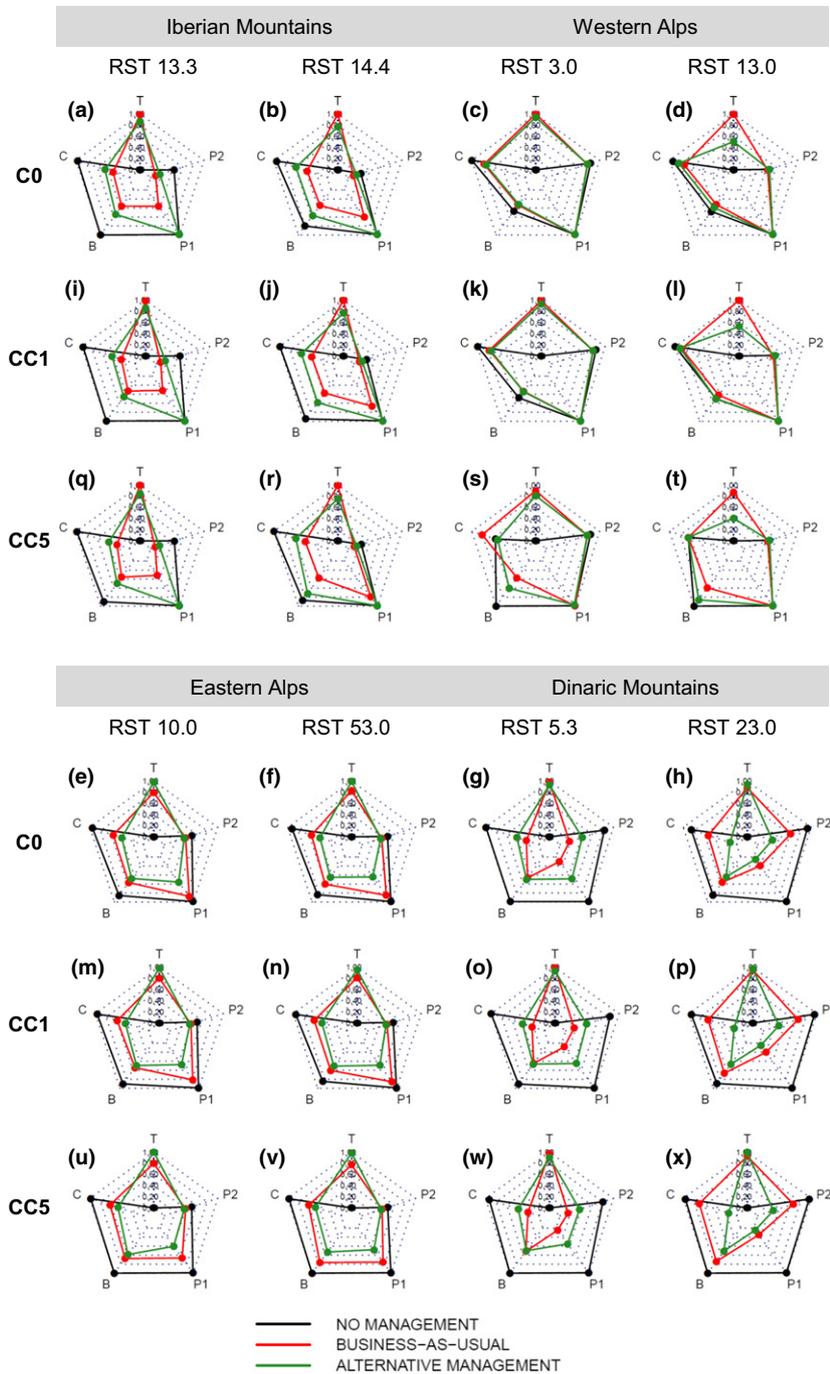


Fig. 2. Radar plots showing the projected future provision (2080–2100) of four ES (T: timber production; C: carbon storage; B: biodiversity; P1: protection against rockfall; P2: protection against avalanches) for selected RSTs in the four mountain regions (columns). Results for the different management regimes are shown as different lines for simulations under current climate conditions (C0; letters a–h) and two climate change scenarios (CC1 and CC5; rows; letters i–x). Results for all RSTs and climate scenarios are in Fig. S3.2. [Colour figure can be viewed at wileyonlinelibrary.com].

on the biodiversity index was evident, while C storage was affected negatively (Fig. 2s, t). Timber production exhibited a slight decrease in all RSTs, albeit under scenario CC5 only.

The ANOVA of MFI for the Eastern Alps showed significant differences due to climate. MFI was also statistically influenced by climatic effects depending on the RST. This is evident, for example, from the deviation of the indicators for C storage (decreased) and biodiversity (increased) for RST 47.0 under CC5 (Fig. S3.2). Overall, even under the most severe climate scenario, only minor changes were observed in this CSA, such as a small increase in the

biodiversity index and a slight reduction in rockfall protection (Fig. 2u, v).

Similarly, climate change significantly affected MFI in the Dinaric Mts, with variations by RST along the elevational gradient. For example, at high elevations where tree growth benefited from higher temperatures, the indicator for C storage increased – although to a small extent – along with the biodiversity indicator (e.g. RST 23.0, Fig. 2h, p, x). At mid-elevations (RST 5.3; Fig. 2w), the strongest climate change scenario induced a reduction in rockfall protection and an increase in biodiversity, but only under BAU and AM. At low elevations (RSTs 4.3 and 8.3, Fig. S3.2),

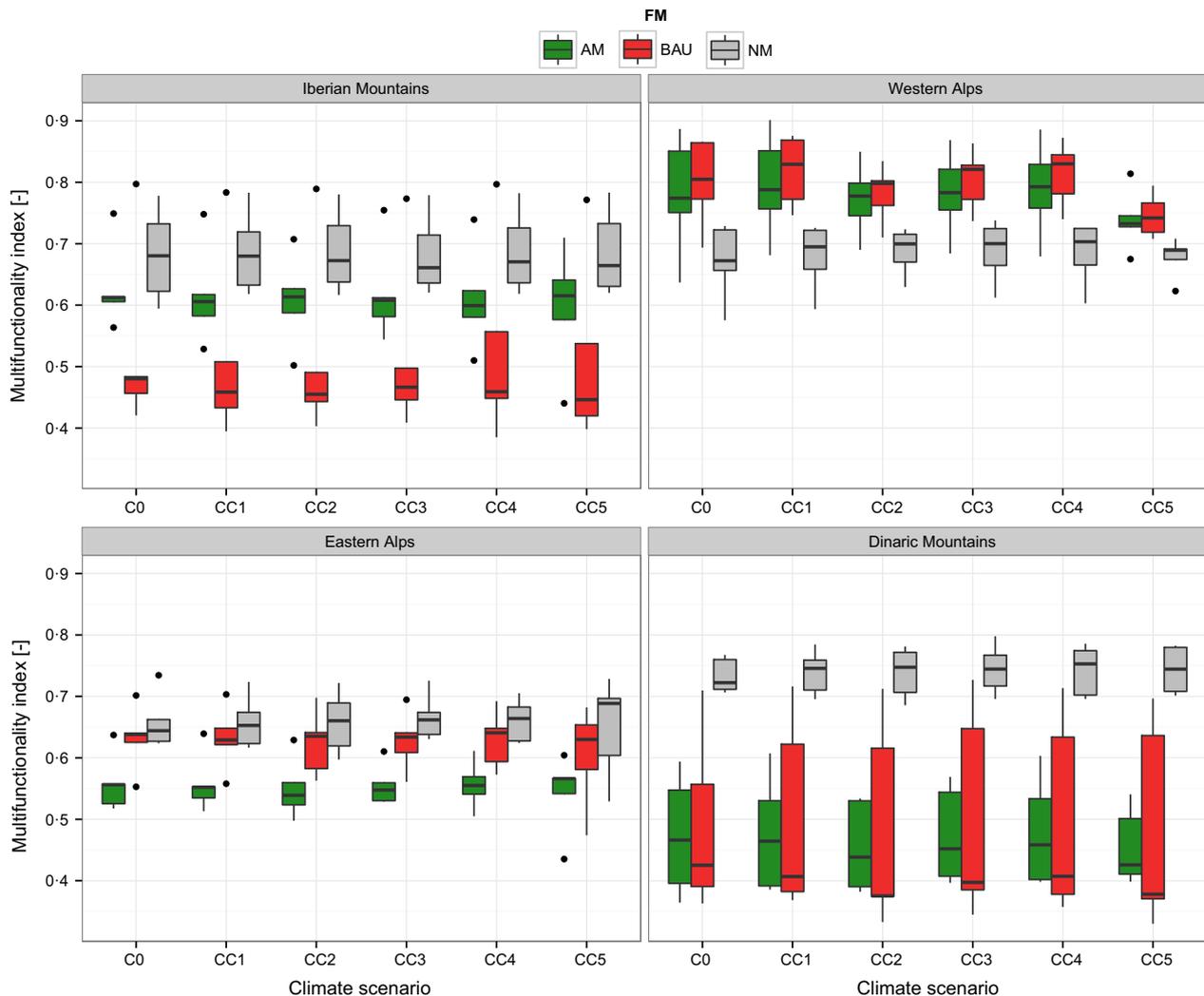


Fig. 3. Change in the multifunctionality index MFI in each CSA as a function of management and climate scenario. The range of MFI within a scenario represents the differences between RSTs. [Colour figure can be viewed at wileyonlinelibrary.com].

however, a decrease in C storage and an increase in the biodiversity index was found, due to high mortality of Norway spruce and Silver fir caused by the increase in summer temperature and drought. In all RSTs, timber production was generally unaffected by climate change.

TRADE-OFFS AND SYNERGIES BETWEEN ECOSYSTEM SERVICES

A large fraction of the ES pairs showed synergies (i.e. positive correlations), not trade-offs (Table 4). For example, synergetic relationships were identified between C storage and biodiversity and between the protective functions and C storage. Although there were a large number of non-significant relationships, the biodiversity indicator was often positively related to protective functions as well. Large variability was observed in certain ES pairs (e.g. timber vs. C storage) while others exhibited a consistent pattern across CSAs and management scenarios (e.g. biodiversity vs. avalanche protection).

The ANOVA on each ES pair revealed that the primary source of variability was the CSA, as its effect was significant on all ES pairs (Table 4). Except in the Western Alps (Table 5), ES correlations were more frequently impacted by changes in forest management (BAU vs. AM) than climate, with eight and six out of the ten pairs being significantly different, respectively (Table 4). Significant variations due to climate change were typically limited to climate scenario CC5, whereas only minor differences were observed between baseline climate and the other climate scenarios (Fig. 4) and were observed in all CSAs except in the Dinaric Mts, where it was significant under AM only (Table 5; Fig. 4).

Discussion

The simulation results demonstrate that the impacts of climate change on forest ES vary strongly among and within European mountain regions due to the high variability of environmental and stand properties. However, in all

Table 4. Top: F-values of the ANOVA on Spearman's rho for each pair of ES

	d.f.	T-C	T-B	T-P1	T-P2	C-B	C-P1	C-P2	B-P1	B-P2	P1-P2
CLIMATE	5	4.6	1.3	8.9	2.5	12.9	0.9	10.3	8.2	1.7	24.9
FM	1	0.4	63.6	3.4	458.3	7.7	5.0	31.9	8.5	88.2	46.9
CSA	3	231.3	358.9	156.9	1818.9	16.4	26.3	114.2	22.0	99.1	68.9
CLIMATE:FM	5	0.6	1.4	0.5	0.5	0.5	1.3	1.5	1.2	0.8	2.7
CLIMATE:CSA	14	1.4	3.4	2.3	2.0	4.3	1.2	5.6	3.4	1.8	15.9
FM:CSA	3	39.8	57.8	11.4	199.2	23.1	6.5	83.9	11.5	148.9	67.9
Positive		5	24	2	19	24	22	22	5	36	8
Negative		6	2	11	6	0	0	0	0	0	0
Non-significant		37	22	35	23	24	26	26	43	12	40
Key to P-values:		<0.001		<0.01		<0.05			>0.05		

d.f., degrees of freedom. Shades of grey represent the significance level of the respective and interactive effects of the climate scenario (CLIMATE), management scenario (FM) and CSA. Bottom: Number of positive, negative and non-significant correlations for each ES pair. Residuals d.f.: 15.

Table 5. F-values of the ANOVA on Spearman's rho calculated for the four CSAs

	d.f.	Iberian Mts	Western Alps	Eastern Alps	Dinaric Mts
CLIMATE	5	4.4	237.9	27.1	0.6
FM	1	85.3	0.9	68.7	122.6
ES	9	48.6	58.6	143.3	209.2
CLIMATE:FM	5	4.5	1.6	3.4	0.5
CLIMATE:ES	44	1.0	14.1	3.6	0.7
FM:ES	7	7.5	2.1	11.6	78.7
P-value		<0.001	<0.01	<0.05	>0.05

d.f., degrees of freedom. Cell colours represent the significance level of the respective and interactive effects of the climate scenario (CLIMATE), management scenario (FM) and ES pairs (ES). Residuals d.f.: 45.

regions, human-induced 'disturbances' (silvicultural interventions) have a larger influence on ES than climate change, at least for the time horizon considered here and in the absence of large natural perturbations (Thompson *et al.* 2011; Lal *et al.* 2013).

FUTURE PROVISION OF ES IN THE FOUR MOUNTAIN REGIONS

Our simulation results in the Iberian Mts indicate that forest management, rather than climate change, is responsible for a reduction in C storage and biodiversity. This CSA features a continental Mediterranean climate that is characterized by summer drought (Fig. S1.1). We found no changes in ES provision with climate change, which was counter-intuitive, particularly since the model was calibrated to reflect this regime (cf. Mina *et al.* 2016b), and several authors have reported negative impacts of recent climate change on Scots pine at dry sites (Martínez-Vilalta & Piñol 2002; Rebetez & Dobbertin 2004; Sánchez-Salguero *et al.* 2015). According to our projections, however, Scots pine growth would not be impacted strongly by increased summer drought as long as spring precipitation remains sufficient (Eilmann *et al.* 2011). Although the projected increase in winter

temperatures strongly limited Scots pine establishment in the simulations (regeneration not possible in 90% of the years under CC5 due to warming conditions and the absence of a chilling trigger), this did not have a major impact on the 100-year simulation because simulated forest dynamics were driven mainly by initial stand conditions, not by the newly established trees. Nevertheless, higher winter temperatures and spring droughts are likely to strongly hamper the regenerative capacity of these forests in the longer term (Castro 2006).

By contrast, our projections for the Western Alps indicate that climate change induces large alterations in the supply of some ES. Under CC5 and CC2, ForClim simulated a higher biodiversity index (which is linked to the amount of coarse woody debris) due to the intensification of drought-induced tree mortality, affecting in particular drought-intolerant Norway spruce. This is consistent with other studies where the dominance of Norway spruce was projected to decrease under the warmest climate scenarios (Elkin *et al.* 2013; Falk & Hempelmann 2013; Bircher 2015). The protection functions were not particularly affected in this CSA, as all RSTs are characterized by gentle slopes, and thus, rockfall and avalanche protection were always high, irrespective of stand structure and management.

In the Eastern Alps, all ES would benefit from the absence of management, with the obvious exception of timber production. No negative influences of climate change were detected except for one south-exposed RST with a low water holding capacity where a drought-induced dieback of Norway spruce was simulated under the driest scenarios (CC2 and CC5; Figs S1.2 and S3.1). These outcomes generally agree with other studies reporting that upper montane forest stands in the Eastern Alps would not be significantly affected by climate change unless natural disturbances such as bark beetle infestations or wind-throw are considered (Seidl, Rammer & Lexer 2011; Irauschek, Rammer & Lexer 2015).

In the Dinaric Mountains, climate change would strongly affect ES, albeit differently depending on elevation, thus highlighting the necessity to consider the

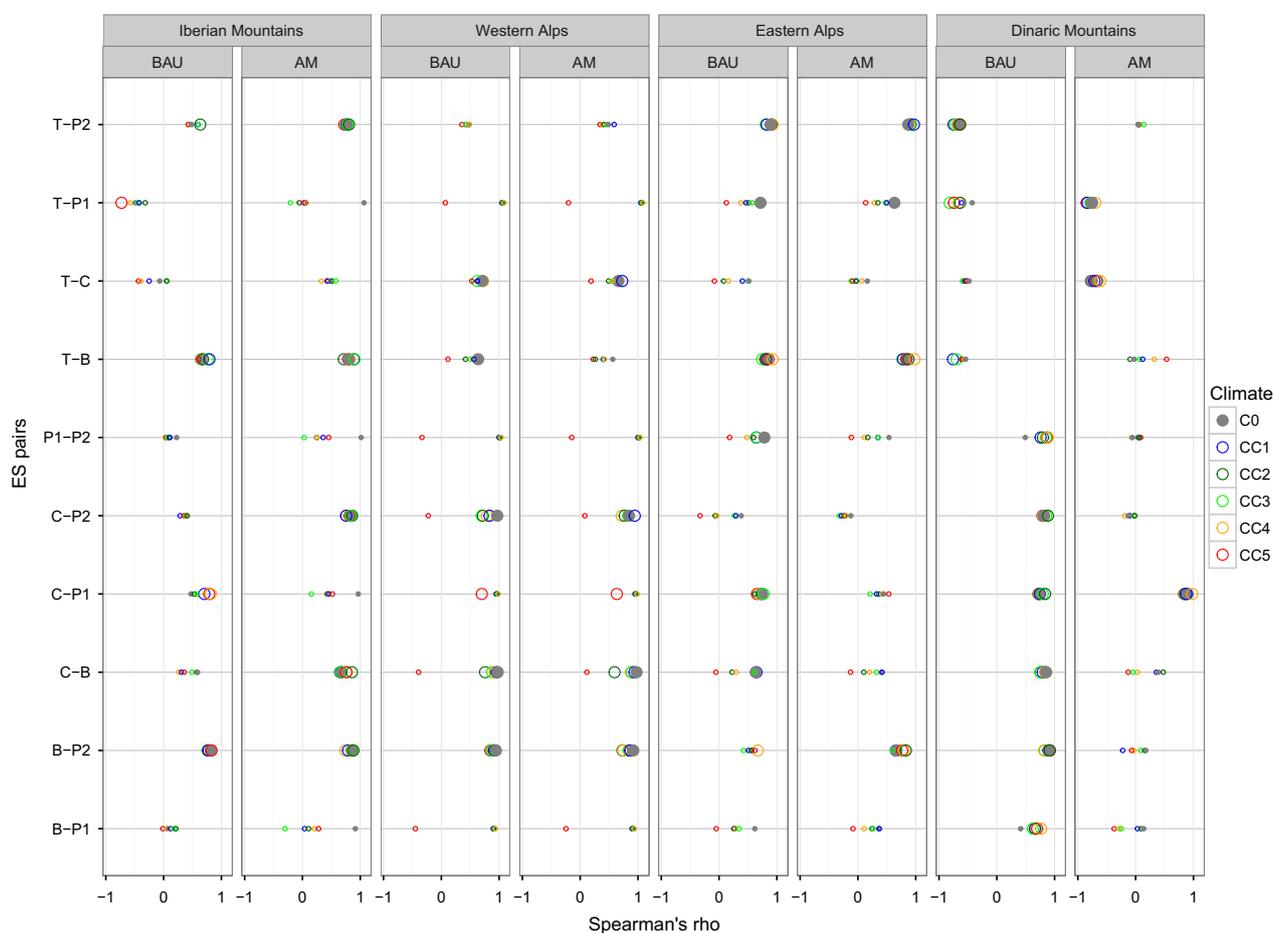


Fig. 4. Trade-offs and synergies between the five ES expressed as Spearman's rho in the four CSAs and for the two active forest management scenarios. Non-significant correlations ($P < 0.05$) are shown with smaller circles. [Colour figure can be viewed at wileyonlinelibrary.com].

heterogeneity of local climate (as induced by elevation and topography) when projecting regional-scale forest development (Bircher 2015). At low elevations, the simulated increase in tree mortality rates of Norway spruce and Silver fir induced by the increase in summer temperature and drought was coherent with the shift from conifer to broadleaved forests projected by Kutnar & Kobler (2011) and confirms the pattern observed for a broader range of RSTs in the same region (Mina *et al.* 2015).

TRADE-OFFS AND SYNERGIES BETWEEN ECOSYSTEM SERVICES

Several studies have focused on synergies and trade-offs between forest ecosystem services (Seidl *et al.* 2007; Lafond, Cordonnier & Courbaud 2015; Lutz *et al.* 2016), but only a few of them have evaluated differences between regions (Biber *et al.* 2015), within a landscape (Duncker *et al.* 2012), or under different climate and forest management scenarios (Temperli, Bugmann & Elkin 2012). We addressed these four components simultaneously, focusing on the relationships between timber production, C storage, biodiversity and protection against rockfall and avalanches.

First, we found that each relationship between two ES differs significantly depending on the CSA, which was the main source of variability in our analysis. Similar results were reported in a model intercomparison by Biber *et al.* (2015), although there this trend was valid for particular ES pairs only. The relationships may also differ within a CSA (i.e. among RSTs), but this could not be assessed here as the correlations between ES were calculated considering all RSTs.

Secondly, we were able to show that the large majority of ES relationships are highly sensitive to management. The differences between BAU and AM were considerable in all CSAs except in the Western Alps, confirming that both management strategies had similar impacts on forest development and ES provision in this region. In the Eastern Alps, ES relationships changed significantly only under the strongest climate change scenario and for one south-exposed RST (cf. above).

Thirdly, we also found that climate change is likely to induce changes in the relationships between some ES. Such modifications were simulated in the Iberian Mts, Western and Eastern Alps, but not in the Dinaric Mts. The high heterogeneity among CSAs in the respective and

combined impacts of climate change and management (Duncker *et al.* 2012) may have strong implications for management regimes that try to cater for a distinct set of ES today (Ray *et al.* 2014).

The model did not simulate the traditional trade-off between timber production and biodiversity (Dickie *et al.* 2011; Lafond, Cordonnier & Courbaud 2015), but suggested synergies for most RSTs, although they differ significantly according to the management regime (see also Biber *et al.* 2015), due to the fact that the model did not simulate deadwood decomposition (see section *Methodological aspects*), and thus deadwood volume, which was used as the biodiversity indicator, increased over time. This also explains the synergetic relationship between C storage and biodiversity (i.e. above-ground living and deadwood volume) that was lower in the case of climate change in the Western Alps and in one RST of the Eastern Alps. Often, C storage and biodiversity are thought to be conflicting objectives (Burton *et al.* 2013), as higher C storage diminishes light availability and thus reduces plant species richness. However, the nature of this relationship obviously depends strongly on its definition. Since the C sequestration potential and its sensitivity to forest management is of high interest in the context of climate change mitigation (Bellassen & Luyssaert 2014), we recommend further investigations on this relationship (e.g. Schwenk *et al.* 2012).

The synergy between the protection function (rockfall and avalanches) and C storage confirms the key role of forest cover for reducing the risk of natural hazards (Wehrli *et al.* 2006). Not only C storage, but also the biodiversity indicator was related positively to avalanche protection, indicating that deadwood may have an important role in protection forests (Fuhr, Bourrier & Cordonnier 2015). The fact that the protective function was typically higher under NM than under BAU or AM scenarios should not be interpreted to imply that forest management is not needed to guarantee protection against natural hazards *continuously* in time and space (cf. Krumm *et al.* 2011): managing forest stands to protect human infrastructure (e.g. roads, settlements) from rockfall or avalanches remains a key challenge.

IMPLICATIONS FOR FOREST MANAGEMENT

To assess whether the cessation of management would promote forest ES compared to managed stands, we included a non-intervention scenario. For some RSTs, no management may be sought for environmental conservation reasons (e.g. foundation of forest reserves), but also simply due to their low accessibility (Klopcic *et al.* 2013). Nevertheless, since no management implies no commercial timber production, which continues to be perceived as the most important ES in many European mountain forests (Klopcic *et al.* 2015), this scenario may not find application to the extent implied here. Yet, by comparing the three management scenarios, it is evident that no single

management strategy would be appropriate to maximize the provision of multiple ES across European mountain forests, as our simulations indicated contrasting results between and within the CSAs. The most advantageous management scenario in terms of ES provision clearly depends on the specific needs for ES in the different regions, and thus, management must be regionally adapted to the prevailing stand and site conditions. In this context, studies that aim at maximizing ES provision based on stand-specific optimized planning schedules would be highly welcome in the future (e.g. Härtl *et al.* 2015).

In the Iberian Mts, for example, AM would achieve higher multifunctionality than BAU, although our simulations showed that AM is not urgently needed. Since C storage and biodiversity are strongly linked to the presence of deadwood and to timber stock, we suggest that modifications to BAU (e.g. lowering removals and promoting canopy cover) or converting selected stands to forest reserves could help achieving higher provision of these ES while maintaining timber production and protection (but see Vayreda *et al.* 2012). In the Western Alps, AM would not counteract the projected negative impact of climate change with similar future ES provision as under BAU. However, since most of the negative impacts were found in RSTs with a high proportion of Norway spruce, a suitable adaptation measure would be to favour species diversity and particularly species that are more drought-tolerant (e.g. European beech), which would foster resistance and resilience to extreme climatic events (Knoke *et al.* 2008) and sustain a wider array of ES (Gamfeldt *et al.* 2013). In the Eastern Alps, where BAU was found to be more appropriate than AM for achieving multifunctionality, we suggest similar adaptive measures especially on drought-prone south-facing sites. In the Dinaric Mts, RST-specific silvicultural systems were applied in BAU, and thus the recommendations cannot be generalized for the entire CSA. In this region, uneven-aged approaches seem to be more successful in providing ES than even-aged regimes (Boncina 2011), confirming that management systems supporting continuous canopy cover have a higher capacity to supply ES (O'Hara & Ramage 2013), in particular C storage and biodiversity. In even-aged stands, however, we found that the AM strategies investigated here would be suitable to ensure a higher provision of multiple ES.

METHODOLOGICAL ASPECTS

The model applied in this study does not consider external, large-scale disturbance that may be quite important for future forest dynamics in the four CSAs, such as bark beetle infestations in the Alps (Seidl *et al.* 2008), wildfires in the Iberian Mountains (Vazquez *et al.* 2015) or wind-throw across most of Europe (Gardiner *et al.* 2010). Also, exotic invasive species (Richardson *et al.* 2014) and the migration of species and provenances that

are more adapted to the novel environmental conditions (Taeger *et al.* 2013) have not been considered. Since large-scale disturbance events are likely to increase under climate change (Neuner *et al.* 2015) and may have strong impacts on carbon storage (Seidl *et al.* 2014), vulnerability of mountain forests could in part be counteracted by management interventions, such as establishing appropriate stand structures and species compositions (Millar & Stephenson 2015; Metz *et al.* 2016). Thus, the simulation results presented here need to be interpreted within these limitations of the approach and should not be taken as comprehensive 'predictions' of the future. Nonetheless, owing to its ability to capture management regimes and predict environmental impacts on species composition and stand structure, we are confident that ForClim provides robust results that should be useful for decision support in European mountain forest management.

In addition, we decided to select one individual indicator that best explains each ES, rather than using a broad set of indices, which may have led to different results. This is especially true for the indicator of 'biodiversity conservation', where we used deadwood volume as a key proxy of biodiversity (Stokland, Tomter & Söderberg 2004; Lassauce *et al.* 2011), instead of other options such as tree size diversity or elements of structural diversity that are important, for example for bird habitat. Therefore, depending on what element of 'biodiversity' is targeted, different indicators are required and may lead to vastly different results. Also, ForClim does not simulate wood decomposition. Although deadwood pools are usually low in managed stands (Powers *et al.* 2012), we recognize that there may have been an overestimation of deadwood volume which could have led to biased quantification of the biodiversity indicator, and consequently of the multifunctional index, under the non-intervention scenario and in stands with high simulated mortality rates. Additional discussion on methodological aspects can be found in Appendix S4.

CONCLUSIONS

The simulated impact of climate change on the provision of multiple forest ecosystem services in four European mountain regions is highly heterogeneous and depends on the specific site and climatic conditions. Generally, negative impacts on ES were detected at low elevations, especially in Norway spruce stands due to increasing drought, while at higher elevations, the effects were mostly positive due to higher temperatures and thus more favourable conditions for tree establishment and growth.

Climate change and different management strategies are likely to induce shifts in the synergies and trade-offs between ES, and their effects are not consistent across mountain regions. Nonetheless, negative impacts of a changing climate on the provision and relationships between ES are likely to occur under severe climate projections only, which hinders conclusive statements as long

as anthropogenic emission paths are uncertain. Yet, this sensitivity indicates that emission abatement policies are highly needed so as to guarantee that ecosystem trajectories remain within boundaries that avoid severe climate-induced damage.

Alternative management regimes have the capacity to increase ES provision under climate change, but shifts in management must be assessed carefully, considering the large differences between mountain ranges across Europe and the contrasting effects of climate change on forest stands along gradients of elevation and species composition. Adaptations and modifications of business-as-usual regimes may be sufficient in some mountain forests for enhancing multiple ES provision, especially for C storage and biodiversity functions, whereas other regions would face considerable deterioration of ES provision independent of the management regime.

Acknowledgements

This study was financially supported by the project 'Advanced Multifunctional Forest Management in European Mountain Ranges (ARANGE)' within the European Commission's 7th Framework Program (Grant Agreement No. 289437). We are grateful to local foresters in each case study region who made the forest management data available and to Manfred J. Lexer for coordinating the ARANGE project.

Data accessibility

The data used in this study (ES indicators calculated with ForClim for each simulated year) are archived in Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.21sj8> (Mina *et al.* 2016a).

References

- Abdi, H., Williams, L.J. & Valentin, D. (2013) Multiple factor analysis: principal component analysis for multitable and multiblock data sets. *Wiley Interdisciplinary Reviews: Computational Statistics*, **5**, 149–179.
- Allen, C.D., Breshears, D.D. & McDowell, N.G. (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, **6**, 1–55.
- Bellassen, V. & Luysaert, S. (2014) Managing forests in uncertain times. *Nature*, **506**, 153–155.
- Biber, P., Borges, J.G., Moshammer, R., Barreiro, S., Botequim, B., Brodrechtova, Y. *et al.* (2015) How sensitive are ecosystem services in European forest landscapes to silvicultural treatment? *Forests*, **6**, 1666–1695.
- Bircher, N. (2015) *To Die or Not to Die: Forest Dynamics in Switzerland Under Climate Change*. Ph.D. Thesis, Swiss Federal Institute of Technology (ETH).
- Bolte, A., Ammer, C., Lof, M., Nabuurs, G.J., Schall, P. & Spathelf, P. (2010) Adaptive forest management: a prerequisite for sustainable forestry in the face of climate change. *Sustainable Forest Management in a Changing World: A European Perspective*, **19**, 115–139.
- Boncina, A. (2011) History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. *Forestry*, **84**, 467–478.
- Bowman, D.M.J.S., Williamson, G.J., Keenan, R.J. & Prior, L.D. (2014) A warmer world will reduce tree growth in evergreen broadleaf forests: evidence from Australian temperate and subtropical eucalypt forests. *Global Ecology and Biogeography*, **23**, 925–934.
- Bugmann, H.K.M. (1996) A simplified forest model to study species composition along climate gradients. *Ecology*, **77**, 2055–2074.
- Burton, J.I., Ares, A., Olson, D.H. & Puettmann, K.J. (2013) Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecological Applications*, **23**, 1297–1310.

- Castro, J. (2006) Short delay in timing of emergence determines establishment success in *Pinus sylvestris* across microhabitats. *Annals of Botany*, **98**, 1233–1240.
- Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J. et al. (2008) Carbon accumulation in European forests. *Nature Geoscience*, **1**, 425–429.
- Core Team, R. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Dickie, I.A., Yeates, G.W., St John, M.G., Stevenson, B.A., Scott, J.T., Rillig, M.C. et al. (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, **48**, 926–934.
- Didion, M., Kupferschmid Albisetti, A.D., Wolf, A. & Bugmann, H. (2011) Ungulate herbivory modifies the effects of climate change on mountain forests. *Climatic Change*, **109**, 647–669.
- Dorren, L.K.A., Berger, F., Imeson, A.C., Maier, B. & Rey, F. (2004) Integrity, stability and management of protection forests in the European Alps. *Forest Ecology and Management*, **195**, 165–176.
- Duncker, P.S., Raulund-Rasmussen, K., Gundersen, P., Katzensteiner, K., De Jong, J., Ravn, H.P. et al. (2012) How forest management affects ecosystem services, including timber production and economic return: synergies and trade-offs. *Ecology and Society*, **17**, 50.
- Eilmann, B., Zweifel, R., Buchmann, N., Pannatier, E.G. & Rigling, A. (2011) Drought alters timing, quantity, and quality of wood formation in Scots pine. *Journal of Experimental Botany*, **62**, 2763–2771.
- Elkin, C., Gutierrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L. et al. (2013) A 2 degrees C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biology*, **19**, 1827–1840.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., AraÚJo, M.B. et al. (2011) 21st Century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330–2341.
- Estreguil, C., Caudullo, G., de Rigo, D. & San-Miguel-Ayanz, J. (2012) Forest Landscape in Europe: Pattern, Fragmentation and Connectivity. JRC Scientific and Policy Report EUR 25717EN.
- Falk, W. & Hempelmann, N. (2013) Species favourability shift in Europe due to climate change: a case study for *Fagus sylvatica* L. and *Picea abies* (L.) Karst. based on an ensemble of climate models. *Journal of Climatology*, **2013**, 18.
- Fuhr, M., Bourrier, F. & Cordonnier, T. (2015) Protection against rockfall along a maturity gradient in mountain forests. *Forest Ecology and Management*, **354**, 224–231.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P. et al. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, **4**, art. 1340.
- Gardiner, B., Blennow, K., Carnus, J.-M., Fleischer, P., Ingemarson, F., Landmann, G. et al. (2010) Destructive storms in European forests: past and forthcoming impacts. Cestas. available via <http://ec.europa.eu/environment/forests/fprotection.htm>.
- Gret-Regamey, A., Brunner, S.H. & Kienast, F. (2012) Mountain ecosystem services: who cares? *Mountain Research and Development*, **32**, S23–S34.
- Härtl, F.H., Barka, I., Hahn, W.A., Hlásny, T., Irauschek, F., Knoke, T. et al. (2015) Multifunctionality in European mountain forests – an optimization under changing climatic conditions. *Canadian Journal of Forest Research*, **46**, 163–171.
- Hlásny, T., Barcza, Z., Barka, I., Merganicova, K., Sedmak, R., Kern, A. et al. (2014) Future carbon cycle in mountain spruce forests of Central Europe: modelling framework and ecological inferences. *Forest Ecology and Management*, **328**, 55–68.
- Irauschek, F., Rammer, W. & Lexer, M.J. (2015) Can current management maintain forest landscape multifunctionality in the Eastern Alps in Austria under climate change? *Regional Environmental Change*. doi:10.1007/s10113-015-0908-9.
- Klopcic, M., Leitner, T., Pardos, M., Barka, I., Calama, R., Cordonnier, T. et al. (2013) Component of ARANGE Deliverable D1.3 – Current and Historical Forest Management in the Case Study Areas. University of Ljubljana, Slovenia. available via http://www.arange-project.eu/wp-content/uploads/ARANGE-D1.3_FMIntheCSAs.pdf (accessed 4 July 2015).
- Klopcic, M., Boncina, A., Enache, A. & Lexer, M.J. (2015) Component of ARANGE Deliverable D5.2 – Recommendations for Multifunctional Forest Management Strategies. University of Ljubljana, Slovenia. available via http://www.arange-project.eu/wp-content/uploads/ARANGE-D5.2_recommendations.pdf (accessed 4 July 2015).
- Knoke, T., Ammer, C., Stimm, B. & Mosandl, R. (2008) Admixing broad-leaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research*, **127**, 89–101.
- Körner, C. & Ohsawa, M. (2005) Mountain Systems. *Ecosystems and Human Well-Being. Current States and Trends* (ed Millennium Ecosystem Assessment), pp. 681–716. Island Press, Washington, DC, USA.
- Krumm, F., Kulakowski, D., Spiecker, H., Duc, P. & Bebi, P. (2011) Stand development of Norway spruce dominated subalpine forests of the Swiss Alps. *Forest Ecology and Management*, **262**, 620–628.
- Kutnar, L. & Kobler, A. (2011) Prediction of forest vegetation shift due to different climate-change scenarios in Slovenia. *Sumarski List*, **135**, 113–126.
- Lafond, V., Cordonnier, T. & Courbaud, B. (2015) Reconciling biodiversity conservation and timber production in mixed uneven-aged mountain forests: identification of ecological intensification pathways. *Environmental Management*, **56**, 1118–1133.
- Lal, R., Lorenz, K., Hüttl, R.F., Schneider, B.U. & von Braun, J.E. (2013) *Ecosystem Services and Carbon Sequestration in the Biosphere*. Springer, Netherlands.
- Lassaue, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **11**, 1027–1039.
- Lê, S., Josse, J. & Husson, F. (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, **25**, 1–18.
- Lexer, M.J. (2013) Component of ARANGE Deliverable D1.2 – Catalogue of Harmonized Environmental Variables. Institute for Silviculture and Forest Engineering, University of Life Sciences Vienna, Vienna, Austria. available via http://www.arange-project.eu/wp-content/uploads/ARANGE-Deliverable-D12_06092013.pdf 04.10.2015
- van der Linden, P. & Mitchell, J.F.B. (2009) *ENSEMBLES: Climate Change and Its Impacts: Summary of Research and Results from the ENSEMBLES Project*. Met Office Hadley Centre, Exeter, UK. available via http://ensembles-eu.metoffice.com/docs/Ensembles_final_report_Nov09.pdf
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J. et al. (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, **259**, 698–709.
- Lutz, D.A., Burakowski, E.A., Murphy, M.B., Borsuk, M.E., Niemiec, R.M. & Howarth, R.B. (2016) Tradeoffs between three forest ecosystem services across the state of New Hampshire, USA: timber, carbon, and albedo. *Ecological Applications*, **26**, 146–161.
- Maroschek, M., Rammer, W. & Lexer, M.J. (2014) Using a novel assessment framework to evaluate protective functions and timber production in Austrian mountain forests under climate change. *Regional Environmental Change*, **15**, 1543–1555.
- Martínez-Vilalta, J. & Piñol, J. (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management*, **161**, 247–256.
- MEA (2005) *Millennium Ecosystem Assessment: Ecosystems and Human Well-Being – Synthesis*. Island Press, Washington, DC, USA.
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D. et al. (2016) Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Global Change Biology*, **22**, 903–920.
- Millar, C.I. & Stephenson, N.L. (2015) Temperate forest health in an era of emerging megadisturbance. *Science*, **349**, 823–826.
- Mina, M., Bugmann, H., Klopčič, M., Cailleret, M. (2015) Accurate modeling of harvesting is key for projecting future forest dynamics: a case study in the Slovenian mountains. *Regional Environmental Change* (in press).
- Mina, M., Bugmann, H., Cordonnier, T., Irauschek, F., Klopčič, M., Pardos, M. et al. (2016a) Data from: future ecosystem services from European mountain forests under climate change. *Dryad Data Repository*. <http://dx.doi.org/10.5061/dryad.21sj8>
- Mina, M., Martín-Benito, D., Bugmann, H. & Cailleret, M. (2016b) Forward modeling of tree-ring width improves simulation of forest growth responses to drought. *Agricultural and Forest Meteorology*, **221**, 13–33.
- Neuner, S., Albrecht, A., Cullmann, D., Engels, F., Griess, V.C., Hahn, W.A. et al. (2015) Survival of Norway spruce remains higher in mixed stands under a dryer and warmer climate. *Global Change Biology*, **21**, 935–946.
- Nogues-Bravo, D., Araujo, M.B., Errea, M.P. & Martínez-Rica, J.P. (2007) Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change-Human and Policy Dimensions*, **17**, 420–428.
- O'Hara, K.L. & Ramage, B.S. (2013) Silviculture in an uncertain world: utilizing multi-aged management systems to integrate disturbance. *Forestry*, **86**, 401–410.

- Pardos, M., Pérez, S., Calama, R., Alonso, R. & Lexer, M.J. (2016) Ecosystem service provision, management systems and climate change in Valsain forest, central Spain. *Regional Environmental Change*, doi: 10.1007/s10113-016-0985-4.
- Peña, L., Casado-Arzuaga, I. & Onaindia, M. (2015) Mapping recreation supply and demand using an ecological and a social evaluation approach. *Ecosystem Services*, **13**, 108–118.
- Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N. *et al.* (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, **5**, 424–430.
- Powers, M.D., Kolka, R.K., Bradford, J.B., Palik, B.J., Fraver, S. & Jurgensen, M.F. (2012) Carbon stocks across a chronosequence of thinned and unmanaged red pine (*Pinus resinosa*) stands. *Ecological Applications*, **22**, 1297–1307.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E. & Rötzer, T. (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications*, **5**, art. 4967.
- Price, M.F. & Butt, N. (2000) *Forests in Sustainable Mountain Development: A State of Knowledge Report for 2000*. CABI Pub. in association with the International Union of Forestry Research Organizations, Wallingford, Oxon, UK.
- Price, M., Lysenko, I. & Gloersen, E. (2004) Delineating Europe's mountains. *Revue de géographie alpine*, **92**, 75–86.
- Price, M.F., Gratzler, G., Duguma, L.A., Kohler, T., Maselli, D. & Romeo, R. (2011) *Mountain Forests in a Changing World – Realizing Values, Addressing Challenges*. FAO/MPS and SDC, Rome, Italy.
- Puettmann, K.J., Coates, K.D. & Messier, C.C. (2009) *A Critique of Silviculture: Managing for Complexity*. Island Press, Washington, DC, USA.
- Rasche, L., Fahse, L., Zingg, A. & Bugmann, H. (2011) Getting a virtual forester fit for the challenge of climatic change. *Journal of Applied Ecology*, **48**, 1174–1186.
- Ray, D., Bathgate, S., Moseley, D., Taylor, P., Nicoll, B., Pizzirani, S. *et al.* (2014) Comparing the provision of ecosystem services in plantation forests under alternative climate change adaptation management options in Wales. *Regional Environmental Change*, **000**, 1–13.
- Rebetez, M. & Dobbertin, M. (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, **79**, 1–9.
- Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A. & Pilz, T. (2014) Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Annals of Forest Science*, **71**, 211–225.
- Reyer, C., Bugmann, H., Nabuurs, G.-J. & Hanewinkel, M. (2015) Models for adaptive forest management. *Regional Environmental Change*, **15**, 1483–1487.
- Richardson, D., Hui, C., Nuñez, M. & Pauchard, A. (2014) Tree invasions: patterns, processes, challenges and opportunities. *Biological Invasions*, **16**, 473–481.
- Rodriguez, J.P., Beard, T.D., Bennett, E.M., Cumming, G.S., Cork, S.J., Agard, J. *et al.* (2006) Trade-offs across space, time, and ecosystem services. *Ecology and Society*, **11**, 28.
- Sánchez-Salguero, R., Camarero, J.J., Hevia, A., Madrigal-González, J., Linares, J.C., Ballesteros-Canovas, J.A. *et al.* (2015) What drives growth of Scots pine in continental Mediterranean climates: drought, low temperatures or both? *Agricultural and Forest Meteorology*, **206**, 151–162.
- Schwenk, W.S., Donovan, T.M., Keeton, W.S. & Nunery, J.S. (2012) Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. *Ecological Applications*, **22**, 1612–1627.
- Seidl, R., Rammer, W. & Lexer, M.J. (2011) Climate change vulnerability of sustainable forest management in the Eastern Alps. *Climatic Change*, **106**, 225–254.
- Seidl, R., Rammer, W., Jäger, D., Currie, W.S. & Lexer, M.J. (2007) Assessing trade-offs between carbon sequestration and timber production within a framework of multi-purpose forestry in Austria. *Forest Ecology and Management*, **248**, 64–79.
- Seidl, R., Rammer, W., Jäger, D. & Lexer, M.J. (2008) Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *Forest Ecology and Management*, **256**, 209–220.
- Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, **4**, 806–810.
- Smith, W., Germino, M., Johnson, D. & Reinhardt, K. (2009) The altitude of alpine treeline: a bellwether of climate change effects. *The Botanical Review*, **75**, 163–190.
- Stokland, J., Tomter, S. & Söderberg, U. (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. Monitoring and Indicators of Forest Biodiversity in Europe—From Ideas to Operationality, (ed. M. Marchetti). *EFI Proceedings*, **51**, 207–226.
- Taeger, S., Fussi, B., Konnert, M. & Menzel, A. (2013) Large-scale genetic structure and drought-induced effects on European Scots pine (*Pinus sylvestris* L.) seedlings. *European Journal of Forest Research*, **132**, 481–496.
- Temperli, C., Bugmann, H. & Elkin, C. (2012) Adaptive management for competing forest goods and services under climate change. *Ecological Applications*, **22**, 2065–2077.
- Thompson, J.R., Foster, D.R., Scheller, R. & Kittredge, D. (2011) The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications*, **21**, 2425–2444.
- Vayreda, J., Martínez-Vilalta, J., Gracia, M. & Retana, J. (2012) Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. *Global Change Biology*, **18**, 1028–1041.
- Vazquez, A., Climent, J.M., Casais, L. & Quintana, J.R. (2015) Current and future estimates for the fire frequency and the fire rotation period in the main woodland types of peninsular Spain: a case-study approach. *Forest Systems*, **24**, e031.
- Wehrli, A., Dorren, L.K.A., Berger, F., Zingg, A., Schonenberger, W. & Brang, P. (2006) Modelling long-term effects of forest dynamics on the protective effect against rockfall. *Forest Snow and Landscape Research*, **80**, 57–76.

Received 12 April 2016; accepted 11 August 2016

Handling Editor: Paulo Brando

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary methods and data.

Table S1.1. Description of the silvicultural interventions under BAU and AM in the four case study areas.

Fig. S1.1. Baseline climate in the four case study areas.

Table S1.2. Ranking of the climate change scenarios for each case study area based on the increase of mean annual temperature.

Fig. S1.2. Changes of temperature and precipitation for the four case study areas in the five climate change scenarios.

Appendix S2. Description of ecosystem service indicators.

Table S2.1. Multiple factor analysis.

Fig. S2.1. First two dimensions from the Multiple Factor Analysis performed with the initial 22 indicators characterizing the four ES.

Appendix S3. Additional simulation outputs.

Fig. S3.1. Simulated volume by species for each RST in the four CSAs.

Fig. S3.2. Additional radar plots of the projected future provision of ES.

Appendix S4. Supplementary discussion on methodological aspects.