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***Forest dynamics, management and ecosystem services: the future of
European mountain forests in an era of climate change***

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Summary

In an era characterized by rapid changes of environmental, particularly climatic, and socio-economic conditions, there is a growing need to better understand the influence of these changes on forests and their capacity to provide key ecosystem services (ES) to human communities. Since climate change is particularly pronounced in mountain regions, mountain forests deserve particular attention to assess the impacts of these changes. Moreover, as forests develop slowly over decades to many centuries, possible adaptation measures must be planned in the long term as well, and they should be based on thorough scientific knowledge.

Dynamic vegetation models (DVMs) are often used to investigate climatic influences on long-term forest dynamics, and more recently also to explore management impacts. Among the many types of DVMs, forest gap models are flexible tools to analyze future forest development, but management regimes have received little attention to date. Although these models include the inter-specific sensitivity to the environment, intra-specific local adaptation and intra-annual variations in the environmental responses are not considered. This is especially important for capturing drought effects on growth and limits the reliability of gap models in drought-prone forests.

The overall objective of this thesis was to evaluate the potentials and limitations of current and alternative forest management strategies on the provision of multiple ES in European mountain forests under climate change. To this end, I improved the gap model ForClim in two respects: (1) the modeling of harvesting, and (2) the growth response to drought. I then applied the improved model in four mountain regions across central and southern Europe.

In *Chapter I*, I firstly analyzed and improved the influence of crown characteristics on diameter growth in the model and implemented new harvesting functions to more accurately predict forest properties (e.g., basal area, stem number and diameter distribution) in intensively managed stands. Model performance was evaluated at ten sites in the European Alps using inventory data, showing that analytical management algorithms (e.g., removals of basal area in relative diameter classes) should generally be preferred over empirical ones (e.g., single stem removals in static diameter classes). I also highlighted the importance of accurately modeling management interventions when predicting long-term forest dynamics. Secondly, future forest development was simulated for 37 representative stands in the Dinaric Mountains under current management and three climate scenarios. Strongly different impacts of climate change were found depending on elevation. Low-elevation stands showed a drought-induced decrease of productivity and higher tree mortality, while stands at higher elevations profited from more favorable growing conditions. Although timber stocks will be maintained, the interacting effects of management and climate change were found to induce a strong shift in species composition, favoring broadleaves (e.g., European beech) at the expense of the currently dominant conifers (silver fir, Norway spruce). This indicates the need for detailed investigations on adaptive management to preserve the conifers, as they are of high ecological and economic importance in the Dinaric Mountains.

Based on these results, in *Chapter II* I explored further management options for the Dinaric mountain forests. Under current climate and two transient climate change scenarios, I simulated future forest dynamics under business-as-usual and three alternative management regimes in the same set of representative stands, including a scenario of non-intervention and an assessment of the impact of large ungulates using different browsing pressures. Alternative management regimes would not be able to maintain current proportion of conifers in the future, although promis-

ing management approaches were identified, such as changes in the harvesting diameters (e.g., retain silver firs with diameter <25 cm) and reduction of the abundance of large ungulates.

To extend the assessment over a broader range of European mountains, including drought-prone areas, the impact of seasonal water scarcity needs to be reflected accurately in the model. In *Chapter III*, I used a forward modeling approach of tree-ring growth to quantify the intra-annual response to drought of Scots pine. Based on tree ring-width data from 16 sites along a moisture gradient covering most of the environmental conditions of this species, I optimized season-specific parameters capturing the level of soil moisture below which growth is not possible and the threshold above which growth is not limited by moisture. I implemented these functions in a new submodel that relates drought to growth. I found that Scots pine adapts locally to cope with drought, and this can be included in the model to improve the local accuracy of the simulations, albeit with a potential loss of generality. Simulations with the previous and new model versions were compared with long-term forest inventory records from six stands in two regions (central Spain and an inner Alpine valley). The higher performance of the new variant suggested that ForClim – and other DVMs – should consider drought at the intra-annual scale for simulating forest dynamics in water-limited environments. Additionally, this chapter showed the power of model-data fusion using tree-ring data for improving or calibrating DVMs.

Chapter IV was dedicated to the application of these two model versions to project the future provision of ES by representative stands in four European mountain regions under different climate and management scenarios. Specifically, I analyzed the trade-offs and synergies between forest ES and evaluated their variability according to changes in climate and management. I selected 25 representative forest stands along elevation gradients in central and southern Europe: Iberian Mountains, Western and Eastern Alps, and Dinaric Mountains. Forest development was simulated under current climatic conditions and five transient climate change scenarios including three management strategies: business-as-usual, non-intervention and an alternative regime. An indicator-based approach was used to quantify the provision of four ES: timber production, carbon storage, biodiversity conservation and protection against natural hazards (rockfall and avalanches). Simulation results indicated that climate change would have very heterogeneous impacts on ES provision, depending on current stand properties and local climate. Strong impacts of climate change were identified in all forests in the Western Alps, while Iberian Scots pine forests showed low sensitivity. In the Eastern Alps and in the Dinaric Mountains negative impacts were observed mainly at low elevations and only under the most severe climate projection. In general, changes in the management had a stronger impact on ES provision than climate change. Alternative management regimes may have the capacity to increase multiple ES provision in some regions, but shifts in management must be assessed carefully, considering the contrasting effects of climate change on forest stands along gradients of elevation and species composition.

Based on these results, I recommend that future studies that aim to assess the impacts of climate change under different management strategies should: i) assess stand vulnerability to disturbance using a set of models that operate on different spatial scales; ii) expand the analysis to more stands and evaluate additional management strategies; iii) quantify ecosystem services using multiple indicators or region-specific trait-based approaches; iv) explore other assessment methodologies that consider non-linear interactions between ES. I demonstrated that DVMs are important and useful tools to assess the impacts of anthropogenic climate change on forest dynamics. As these impacts are likely to vary strongly among and within mountain regions, future studies should consider local and regional differences in environmental conditions and in stand structure. The role of small-scale forest management is especially crucial in these assessments, since its impact is likely to be more pronounced than the impact of climate change *per se*.

Zusammenfassung

Die gegenwärtige Ära ist geprägt durch rasche Umweltveränderungen, insbesondere des Klimas, sowie des sozioökonomischen Umfelds. Ein besseres Verständnis des Einflusses dieser Veränderungen auf Wälder und deren Kapazität, Ökosystemdienstleistungen (ES) für die menschliche Gemeinschaft zu erbringen ist daher unabdingbar. Da in Gebirgsregionen Klimaveränderungen besonders ausgeprägt sind, gebührt diesen spezielle Beachtung, um Auswirkungen der Veränderungen zu erfassen. Zudem entwickeln sich Wälder langsam über Jahrzehnte bis zu vielen Jahrhunderten, weshalb mögliche Anpassungsmassnahmen langfristig geplant werden müssen und auf wissenschaftlich exaktem Wissen fundieren sollten.

Dynamische Vegetationsmodelle (DVMs) werden häufig für Untersuchungen von Klimaeinflüssen auf die langfristige Walddynamik gebraucht und neuerdings ebenfalls angewandt, um Bewirtschaftungseinflüsse zu untersuchen. Unter den vielen Typen von DVMs sind Waldsukzessionsmodelle flexible Werkzeuge, um die zukünftige Waldentwicklung zu analysieren, wobei Bewirtschaftungsformen bisher wenig Beachtung gefunden haben. Obwohl diese Modelle eine interspezifische Umweltsensitivität miteinbeziehen, sind intraspezifische lokale Anpassungen und intraannuelle Variationen der Umweltreaktionen nicht berücksichtigt. Dies wäre jedoch von besonderer Wichtigkeit, um Effekte der Trockenheit auf das Wachstum zu erfassen und schränkt deswegen die Zuverlässigkeit von Gap-Modellen in trockenheitsanfälligen Wäldern ein.

Die Zielsetzung vorliegender Doktorarbeit war die Evaluation des Potentials und der Begrenzungen aktueller und alternativer Waldbewirtschaftungsstrategien zur Erbringung vielfältiger ES europäischer Gebirgswälder unter Einfluss des Klimawandels. Zu diesem Zweck wurde das Gap-Modell For-Clim in zweierlei Hinsicht verbessert: (1) die Modellierung der Holzernte und (2) die Wachstumsreaktion auf Trockenheit. Danach wurde das verbesserte Modell in vier Gebirgsregionen in Zentral- und Südeuropa angewandt.

In *Kapitel 1* wurde zuerst der Einfluss von Kroneneigenschaften auf das Durchmesserwachstum im Modell analysiert und verbessert, sowie neue Erntefunktionen implementiert, um Waldeigenschaften (z.B. Grundfläche, Stammzahl und Durchmesserverteilung) in intensiv bewirtschafteten Beständen besser prognostizieren zu können. Danach wurde das Modellverhalten mittels Inventurdaten von zehn Standorten in den Alpen getestet. Dies zeigte, dass analytische Bewirtschaftungsalgorithmen (z. B. Ernte von Grundfläche in relativen Durchmesserklassen) gegenüber empirischen (z.B. Einzelstammnutzung in statischen Durchmesserklassen) generell bevorzugt werden sollten. Für die Vorhersage der langfristigen Walddynamik ist eine exakte Modellierung von Bewirtschaftungseingriffen von zentraler Bedeutung. In einem zweiten Schritt wurde die zukünftige Waldentwicklung für 37 repräsentative Bestände im Dinarischen Gebirge unter aktueller Bewirtschaftung und drei Klimaszenarien simuliert. Es wurden stark unterschiedliche Auswirkungen des Klimawandels in Abhängigkeit der Höhe festgestellt. Bestände in tiefen Lagen zeigten eine durch Trockenheit induzierte Minderung der Produktivität sowie höhere Baummortalität während Bestände in höheren Lagen von günstigeren Wachstumsbedingungen profitieren konnten. Obwohl die Holzvorräte erhalten blieben, verursachten die interagierenden Effekte der Bewirtschaftung und des Klimawandels einen starken Baumartenwechsel zugunsten der Laubholzarten wie Buche auf Kosten der momentan dominanten Nadelholzarten wie Weisstanne oder Fichte. Dies weist auf die Notwendigkeit detaillierter Untersuchungen einer adapti-

ven Bewirtschaftung zur Erhaltung der Nadelholzarten hin, da diese im Dinarischen Gebirge von grosser ökologischer und ökonomischer Bedeutung sind.

Basierend auf diesen Resultaten wurden in *Kapitel II* weitere Bewirtschaftungsoptionen für die Wälder des Dinarischen Gebirges untersucht. Unter dem gegenwärtigen Klima sowie zwei Klimaveränderungsszenarien wurde die zukünftige Walddynamik unter aktueller Bewirtschaftung und drei alternativer Bewirtschaftungsstrategien für dieselbe Auswahl repräsentativer Bestände, inklusive eines Szenarios ohne Bewirtschaftung und einer Prüfung des Einflusses von Huftieren mittels verschiedener Verbissintensitäten, simuliert. Alternative Bewirtschaftungsformen werden nicht in der Lage sein, den gegenwärtigen Anteil an Koniferen zukünftig zu erhalten. Nichtsdestotrotz wurden vielversprechende Bewirtschaftungsansätze gefunden, wie Änderungen in den Erntedurchmessern (z.B. Erhalt von Weisstannen mit Durchmesser <25 cm) und Reduktion der Anzahl Huftiere.

Um die Untersuchung auf einen grösseren Bereich europäischer Gebirge ausweiten zu können, insbesondere trockenheitsanfällige Gebiete, sollte der Einfluss saisonaler Wasserknappheit im Model exakt wiederspiegelt werden. In *Kapitel III* wurde ein Vorwärtsmodellierungsansatz des Jahrringwachstums gewählt, um die intraannuellen Reaktionen der Waldföhre auf Trockenheit zu quantifizieren. Basierend auf Daten der Jahrringbreiten von 16 Standorten entlang eines Feuchtigkeitsgradienten, welche den grössten Teil der Umweltbedingungen dieser Art abdecken, wurden seasonspezifische Parameter der Bodenfeuchteniveaus, unterhalb derer Wachstum nicht möglich ist sowie der Schwellenwert über dem Wachstum nicht durch Feuchtigkeit limitiert wird, optimiert. Diese Funktionen wurden in einem neuen Submodell implementiert, welches Trockenheit mit Wachstum verknüpft. Demnach kann sich die Waldföhre lokal anpassen, um mit der Trockenheit umgehen zu können. Dies kann im Modell zur Verbesserung der lokalen Genauigkeit miteinbezogen werden, wodurch jedoch ein potentieller Verlust an Allgemeingültigkeit erzeugt wird. Simulationen der vorhergehenden und neuen Modellversion wurden mit Langzeit Inventurdaten von sechs Beständen in zwei Regionen verglichen (Zentralspanien und ein inneralpines Tal). Die höhere Leistungsfähigkeit der neuen Modellversion deutet darauf hin, dass ForClim – und andere DVMs – Trockenheit für die Simulation der Walddynamik in wasserlimitierten Umgebungen auf dem interannuellen Massstab berücksichtigen sollten. Zusätzlich konnte in diesem Kapitel die Stärke des Zusammenschlusses von Modell und Jahrringdaten zur Verbesserung oder Kalibrierung von DVMs gezeigt werden.

Kapitel IV wurde der Anwendung der zwei Modellversionen zur Projektion der zukünftigen Erbringung von ES in repräsentativen Beständen vier europäischer Gebirgsregionen unter verschiedenen Klima- und Bewirtschaftungsszenarien gewidmet. Es wurden besonders die Tradeoffs und Synergien zwischen Waldökosystemdienstleistungen analysiert und ihre Variabilität bezüglich Veränderungen des Klimas und der Bewirtschaftung evaluiert. Entlang von Höhengradienten in Zentral- und Südeuropa wurden 25 repräsentative Bestände im Iberischem Gebirge, den West- und Ostalpen sowie dem Dinarischen Gebirge ausgewählt. Die Waldentwicklung wurde unter gegenwärtigen klimatischen Bedingungen und fünf Klimaveränderungsszenarien sowie drei Bewirtschaftungsstrategien (gegenwärtige Bewirtschaftung, ohne Bewirtschaftung und alternative Bewirtschaftung) simuliert. Eine auf Indikatoren basierte Vorgehensweise wurde herangezogen, um die Bereitstellung von vier ES zu quantifizieren: Holzproduktion, Kohlenstoffspeicherung, Erhalt der Biodiversität, und Schutz gegen Naturgefahren (Steinschlag und Lawinen). Simulationsresultate zeigten, dass Klimaveränderungen, abhängig von gegenwärtigen Bestandeseigenschaften und lokalem Klima, sehr heterogene Auswirkungen auf die Bereitstellung von ES haben werden. Starke Auswirkungen der Klimaveränderung wurden für alle Wälder der Westalpen prognostiziert, während Iberische Waldföhrenwälder kleine Sensitivität zeigten. In den Ost-

alpen und dem Dinarischen Gebirge wurden negative Auswirkungen vorwiegend in tiefen Lagen und unter der stärksten Klimaveränderung beobachtet. Im Allgemeinen hatten Bewirtschaftungsänderungen stärkere Auswirkungen auf die Erbringung von ES als dies die Klimaveränderung hatte. Alternative Bewirtschaftungsstrategien könnten das Potential mit sich bringen, die Erbringung vielfältiger ES in bestimmten Regionen zu erhöhen. Allerdings muss dabei der Wechsel der Bewirtschaftung, vor dem Hintergrund verschiedenartiger Effekte der Klimaveränderung auf Waldbestände entlang von Höhengradienten und der Artenzusammensetzung, umfassend beurteilt werden.

Basierend auf diesen Resultaten wird empfohlen, dass zukünftige Studien über die Auswirkungen der Klimaveränderung unter verschiedenen Bewirtschaftungsstrategien, folgende Punkte berücksichtigen: i) Beurteilung der Bestandesempfindlichkeit gegenüber Störungen mittels einem Set von Modellen, die verschiedene räumliche Massstäbe berücksichtigen; ii) Ausweitung der Analyse auf eine grössere Anzahl an Beständen und zusätzliche Untersuchung der Bewirtschaftungsstrategien; iii) Quantifizierung von Ökosystemdienstleistungen mittels vielfältiger Indikatoren oder regionsspezifischer und merkmalsbasierter Ansätze; iv) Erkundung anderer Bewertungsmethoden mit Berücksichtigung nichtlinearer Interaktionen zwischen ES. Die Doktorarbeit zeigte, dass DVMs sehr wichtige und nützliche Instrumente darstellen, um die Auswirkungen anthropogener Klimaveränderung auf die Walddynamik zu untersuchen. Weil diese Auswirkungen zwischen und innerhalb von Gebirgsregionen normalerweise stark variieren, sollten zukünftige Studien lokale und regionale Unterschiede der Umweltbedingungen und Bestandesstrukturen berücksichtigen. Die Rolle von kleinräumiger Waldbewirtschaftung ist besonders entscheidend in diesen Untersuchungen, da ihr Einfluss höchstwahrscheinlich ausgeprägter ist als die Auswirkungen der Klimaveränderung *per se*.

Riassunto

In quest'epoca caratterizzata da rapidi cambiamenti climatici e socio-economici, c'è una crescente urgenza di analizzare i possibili effetti di questi mutamenti sugli ecosistemi forestali e sulla capacità di questi ultimi di fornire beni e servizi essenziali per la società. Poiché i cambiamenti climatici influenzano in modo particolarmente significativo le regioni montane, le foreste di montagna meritano particolare attenzione soprattutto nella valutazione degli impatti dovuti a questi cambiamenti. Inoltre, poiché le dinamiche forestali si sviluppano nell'arco temporale di decenni, se non secoli, le possibili misure di adattamento devono essere necessariamente pianificate nel lungo periodo e basate sulla più accurata conoscenza scientifica in campo ecologico.

I modelli ecologici a base funzionale (dynamic vegetation models; DVMs) sono ampiamente utilizzati per valutare gli impatti dei cambiamenti climatici sulle dinamiche forestali nel lungo periodo. Tra le diverse tipologie di DVMs, i modelli forestali denominati '*forest gap models*' sono largamente riconosciuti come strumenti scientifici appropriati e utili per analizzare lo sviluppo futuro delle foreste. Nonostante i *forest gap models* permettano di analizzare la sensibilità ai fattori ambientali di singole specie forestali, questi modelli non considerano in dettaglio i regimi di gestione forestale, così come la possibilità di analizzare potenziali adattamenti intraspecifici locali e le risposte alle variazioni climatiche intra-annuali. Quest'ultimo aspetto è particolarmente importante per modellizzare gli impatti della scarsità idrica sulle dinamiche forestali, ma allo stesso tempo limita l'applicabilità di questi modelli in ecosistemi forestali soggetti a carenze idriche di lungo periodo.

L'obiettivo primario di questa tesi è stato quello di valutare le potenzialità e i limiti delle attuali strategie di gestione forestale ed esaminare possibili alternative per mantenere i molteplici beni e servizi offerti dagli ecosistemi forestali (SEF). Per questo scopo ho perfezionato due aspetti del modello ecologico ForClim: (1) la modellizzazione degli interventi di taglio forestale e (2) gli effetti della siccità sulla crescita forestale.

Nel *Capitolo I*, ho dapprima analizzato l'influenza delle caratteristiche della copertura arborea sull'incremento diametrico, affinandone la simulazione all'interno del modello; successivamente ho implementato dei nuovi algoritmi per predire più accuratamente caratteristiche forestali quali area basimetrica, numero di fusti per ettaro e distribuzione diametrica in popolamenti forestali sottoposti a frequenti interventi di gestione forestale. L'adeguatezza del modello è stata valutata con dati di inventari forestali in dieci diversi siti nelle montagne europee. Ho potuto dimostrare che gli algoritmi basati su funzioni analitiche (ad es. rimozione di una certa percentuale di area basimetrica in classi diametriche calcolate dinamicamente in base alla distribuzione dei diametri simulata) sono preferibili all'uso di funzioni empiriche (ad es. la simulazione di rimozione di singoli fusti in classi diametriche statiche). Ho potuto quindi accertare l'importanza di modellizzare accuratamente gli interventi di gestione negli studi di simulazione di dinamica forestale a lungo periodo. In secondo luogo ho simulato il futuro sviluppo di 37 popolamenti forestali, rappresentativi delle coperture forestali delle montagne dinariche della Slovenia, analizzando tre diversi scenari climatici e includendo le presenti pratiche di gestione forestale (BAU, da *Business-as-Usual*). I risultati delle simulazioni mostrano profonde differenze in base all'altitudine del popolamento. A basse altitudini la produttività dei popolamenti forestali in futuro risulterebbe diminuita a causa di severi eventi siccitosi e conseguenti episodi di mortalità, mentre a quote più alte la crescita forestale sarebbe favorita da temperature più miti. Anche se la quantità di produ-

zione di legname sembra potersi mantenere a livelli attuali, le simulazioni predicono profondi cambiamenti nella composizione delle specie arboree in conseguenza alle pratiche di gestione forestale e agli effetti dei cambiamenti climatici. I risultati mostrano un netto incremento in specie decidue (ad es. faggio) a discapito di conifere (tra cui abete bianco ed abete rosso) che correntemente rappresentano le specie dominanti in queste foreste. Questi risultati sottolineano la necessità e l'urgenza di studi dettagliati su possibili adattamenti delle presenti pratiche di gestione forestale atte a preservare la presenza di conifere, aventi alta rilevanza sia ecologica che economica nelle foreste delle montagne dinariche in Slovenia.

Sulla base di questi ultimi risultati, nel *Capitolo II* ho esplorato ulteriori opzioni di gestione forestale che potrebbero essere effettuate in queste foreste, con particolare attenzione alla conservazione delle due specie di conifere. Ho effettuato un ulteriore studio di simulazione di dinamiche forestali con diversi scenari futuri, climatici (serie storica e due scenari di cambiamento climatico), gestionali (BAU, tre regimi di gestione alternativi e uno di non-intervento) e di brucatura da ungulati (no-brucatura, medio e alto carico di ungulati). I risultati di questo studio dimostrano che i regimi di gestione alternativi non sembrano essere in grado di riuscire a mantenere le presenti proporzioni di conifere in questi popolamenti forestali, anche se è stato possibile identificare alcuni approcci promettenti, come per esempio la ritenzione di abeti bianchi con diametro < 25 cm e una rilevante riduzione della presenza di ungulati, avente un impatto notevole sulla rinnovazione naturale.

Per poter estendere l'applicabilità di ForClim ad ulteriori zone biogeografiche del continente Europeo, in particolare a foreste minacciate da sempre più estesi periodi siccitosi, era necessario migliorare il sottomodello che permette di valutare l'influenza della carenza idrica sulla crescita degli alberi simulati. Nel *Capitolo III* ho quindi utilizzato un approccio basato sulla modellizzazione degli anelli legnosi per quantificare la risposta intra-annuale alla siccità in foreste di pino silvestre. Una serie di parametri stagionali rappresentanti le soglie di disponibilità idrica sopra/sotto delle quali la crescita della specie è ottimale/prevenuta, è stata ottimizzata in 16 siti comprendenti un largo gradiente delle condizioni di crescita della specie e in cui cronologie di anelli legnosi erano disponibili da diverse fonti. Questi parametri sono poi stati utilizzati in una nuova versione di ForClim per simulare più accuratamente l'impatto della carenza idrica sulla crescita forestale, potendo dimostrare che popolamenti di pino silvestre si adattano a livello locale per contrastare prolungati periodi siccitosi. Questi adattamenti possono essere implementati in modelli ecologici a base funzionale tramite l'uso di specifici parametri, anche se questo potrebbe compromettere il loro utilizzo ad ampia scala (perdita di *generalità*). I risultati di simulazione con le due diverse versioni di ForClim sono stati comparati a dati inventariali in sei siti forestali in due diverse aree biogeografiche (Spagna centrale e Alpi centrali). La più alta performance della nuova versione del modello suggerisce che modelli come ForClim, e DVMs in generale, dovrebbero considerare l'influenza della scarsità idrica a scala intra-annuale, soprattutto se applicati in ambienti in cui la siccità è un fattore chiave nella crescita e nello sviluppo forestale. Inoltre, questo studio ha permesso di dimostrare che i dati ottenuti da anelli legnosi possono essere molto utili per calibrare e migliorare processi e simulazioni in modelli ecologici a base funzionale.

Il *Capitolo IV* è dedicato all'applicazione delle due versioni di ForClim per simulare future provvigioni dei SEF in popolamenti rappresentativi di quattro regioni montane in Europa. Sinergie e *trade-offs* tra i diversi SEF sono stati analizzati e la loro variabilità è stata valutata in relazione a diversi scenari climatici e di gestione forestale. Un totale di 25 popolamenti forestali sono stati selezionati lungo gradienti vegetazionali e climatici nelle montagne dell'Europa meridionale e centrale (Sistema centrale Iberico, Alpi occidentali e orientali, Montagne Dinariche). La dinamica forestale è stata simulata utilizzando serie climatiche storiche e cinque diversi scenari di

cambiamento climatico, mentre gli scenari di gestione forestale includevano BAU, uno scenario di non-intervento e un regime alternativo. Un approccio basato su diversi indicatori è stato utilizzato per quantificare la provvigione di quattro principali SEF: produzione di legname, stoccaggio di carbonio, conservazione della biodiversità e protezione da caduta massi e valanghe.

I risultati delle simulazioni indicano un impatto molto eterogeneo dei cambiamenti climatici sulla provvigione dei diversi SEF, in relazione alle presenti strutture dei popolamenti e al clima a livello locale. I maggiori impatti del cambiamento climatico sono stati identificati in tutti i popolamenti forestali nelle Alpi occidentali, mentre le foreste di pino silvestre nelle montagne del Sistema centrale Iberico sembrano essere caratterizzati da una minore sensibilità. Nelle Alpi orientali e nelle foreste delle montagne Dinariche, invece, impatti negativi sono stati riscontrati solamente nei popolamenti a basse altitudini e in relazione allo scenario di cambiamento climatico di maggior severità. In generale questo studio ha permesso di constatare che cambiamenti dei regimi di gestione avrebbero un maggior impatto sui SEF rispetto agli effetti diretti del cambiamento climatico. Regimi di gestione alternativi potrebbero avere la capacità di incrementare la provvigione di molteplici SEF, ma modifiche alla gestione forestale devono essere valutate attentamente tenendo conto degli effetti contrastanti del cambiamento climatico sulle assai dissimili foreste delle montagne europee.

Sulla base di questi risultati, è dunque possibile raccomandare che studi futuri di valutazione degli impatti del cambiamento climatico sotto diversi sistemi di gestione forestale dovrebbero: i) valutare la vulnerabilità ai diversi disturbi naturali (ad es. schianti da vento, infestazioni di insetti) utilizzando differenti modelli che operano a diverse scale spaziali; ii) ampliare l'analisi ad ulteriori popolamenti forestali e valutare l'impatto di altre tipologie di regime di gestione; iii) quantificare i SEF utilizzando molteplici indicatori e approcci specifici sviluppati a scala regionale; iv) esplorare diverse metodologie di valutazione che considerino interazioni non-lineari tra SEF. Ho potuto inoltre dimostrare che i DVMs sono degli strumenti utili e importanti per valutare gli impatti del cambiamento climatico sulle dinamiche forestali. Siccome è molto probabile che questi impatti siano molto variabili nelle diverse zone montane in Europa, è cruciale che studi futuri considerino le differenze delle condizioni ambientali e forestali a scala locale e regionale. Per effettuare queste valutazioni il ruolo della gestione forestale a piccola scala è fondamentale, dato che i suoi effetti sulle dinamiche forestali possono avere un peso maggiore rispetto agli effetti diretti del cambiamento climatico stesso.

General Introduction

European mountain forests, ecosystem services and climate change

More than 40% of the European continent is covered by mountains (Price et al. 2004), where forests are the dominant land cover (41%; cf. Price et al. 2011). Mountain forests are thus key landscape elements of this continent and providers of a wide array of ecosystem services (EEA 2010; Gret-Regamey et al. 2012). Mountain forests offer natural habitats for a large number of plant and animal species and are hotspots for biodiversity conservation (Estreguil et al. 2012), they sequester carbon from the atmosphere and store it in the long term (Ciais et al. 2008), and they also protect the land surface against erosion and natural hazards (Dorren et al. 2004). Besides providing timber and non-wood products (Price et al. 2000), mountain forests also contribute to climate regulation and have an important recreational and cultural value (Peña et al. 2015). For all these reasons, preserving the long-term supply of ecosystem services from mountain forests is key for assuring the well-being of human communities, not only in Europe but worldwide (MEA 2005).

Since the last ice age, climate has not remained constant. During some particular historic periods, parts of Europe were warmer or colder than now (e.g., medieval climate optimum) and forest composition responded accordingly to these climatic changes (Huntley 1990; Kirby and Watkins 2015a). However, the observed increase in temperature anomaly over the period 1951-2010 is unprecedented compared to changes during other historic periods (e.g., a century ago 1880-1919; cf. Stocker et al. 2013). Since the industrial revolution, the atmospheric concentrations of carbon dioxide and other greenhouse gases (e.g., methane, nitrous oxide) have risen sharply (Raupach et al. 2007) and much faster than over the past 18.000 years (Mannion 2006). Human activities related to emissions of greenhouse gases but also land use changes (e.g., deforestation, which increased land surface albedo) have been identified as major drivers of change in the Earth's energy balance (Stocker et al. 2013). Climate projections for the future indicate that changes in precipitation patterns are subject to strong spatial variation, with large decreases in annual precipitation in the subtropics and Mediterranean regions, and increases at high latitudes (Collins et al. 2013). Mean surface air temperature, however, is predicted to rise more uniformly and quite strongly during the 21st century (mean global increase compared to the period 1986-2005 ranges from 1 to 3.7 °C; cf. Stocker et al. 2013).

The velocity of global climate change during the last century was particularly prominent in mountain regions, where the temperature increase during the last 40 years was found to be twice to three times as large as the global average (Auer et al. 2007; Mountain Research Initiative 2015). Since climate is a powerful driver of changes in forest growth, functions and structure (Fujimori 2001; Penuelas et al. 2004), mountain forests are considered to be particularly exposed to climate change (Price et al. 2011; Trujillo et al. 2012).

A growing number of studies reported impacts of the changing climate on the vitality and growth of European mountain forests (Bigler et al. 2006; Jump et al. 2006; Lenoir et al. 2008; Carnicer et

al. 2011). Temperature rise and changes in precipitation patterns (Kirtman et al. 2013) showed positive effects at higher elevations due to the extended vegetation period (i.e., more favorable conditions for tree growth; cf. Tardif et al. 2003; Jolly et al. 2005; Büntgen et al. 2007), while at lower elevations extreme drought events have induced a growth reduction and increased tree mortality rates, particularly in water-limiting sites such as Mediterranean mountains and dry Alpine valleys (Linares et al. 2011; Rigling et al. 2013; Cailleret et al. 2014; Allen et al. 2015). The rapid changes in climate also altered the regenerative capacity of forests (Delitti et al. 2005; Smith et al. 2009), which may influence the future structure and composition of the forests in the long-term, especially in areas where species are at the edge of their distribution range (Castro et al. 2004; Vilà-Cabrera et al. 2013). In addition, a strong increase in the frequency and intensity of natural disturbances has been observed during the last decades (Schelhaas et al. 2003; Westerling et al. 2006; Gardiner et al. 2010; Weed et al. 2013). Disturbance events such as wildfire, windthrow, pests and pathogens outbreaks are crucial drivers of forest dynamics as they can induce sudden shifts in forest structure and composition (Franklin et al. 2002; Turner 2010). Recent studies have shown that this trend is likely to continue in the future as a result of climate change (Reichstein et al. 2013; Temperli et al. 2013; Seidl et al. 2014).

The effects of climate change on mountain forest dynamics may jeopardize their important role as provider of a wide array of ecosystem services (Lindner et al. 2010). For example, several studies showed that carbon sequestration and timber production would be affected substantially by decreases in productivity due to climate change (Zierl and Bugmann 2007; Elkin et al. 2013). The provision of protection against natural hazards such as avalanches, rockfall and flooding may also be threatened by climate change directly (e.g., changes in species composition, cf. Bugmann 1997; Lexer et al. 2002) or indirectly (e.g., via disturbances such as windthrow or fire, cf. Schumacher et al. 2006), thus posing serious concerns in densely populated mountain areas. However, since European mountains are highly heterogeneous in terms of their micro-environment (i.e., topography; cf. Engler et al. 2011) and soil conditions (Austin and Van Niel 2011), the sensitivity of mountain forests to a changing climate will vary strongly across short distances (Lindner et al. 2010). Moreover, European mountains have been a living place for human populations for thousands of years, and their forests have undoubtedly been modified in their distribution, structure and composition across the continent (Kirby and Watkins 2015b). Thus, we cannot discuss climate change impacts without considering past, current and future management practices, particularly since forest management interventions influence strongly the sensitivity of mountain forests to a changing climate (Spittlehouse and Stewart 2003).

Forest management in an uncertain future

Forest management can play a key role to improve the ability of mountain forests to adapt to a changing climate (i.e., their adaptive capacity) at different spatial and temporal scales (Bravo et al. 2008). The development of forest management strategies usually involves long-term planning, and requires the consideration of many uncertainties, traditionally ranging from the potential variation in timber prices to changes of the economic and societal situation at the regional, continental or even global scale. However, as climate change may have direct and indirect effects on forest growth, disturbance risks and the delivery of ecosystem services, there is a growing need for forest managers to evaluate the utility of current management strategies and possibly develop alternative (or adaptive) strategies to cope with future uncertainties (Fitzgerald et al. 2013). For

example, management actions in stands that are most vulnerable to climate change can proactively facilitate the transition to better-adapted forest states (e.g., by increasing species mixture; cf. Millar and Stephenson 2015) and therefore avoid a sudden decline in the provision of ecosystem services due to unexpected changes in forest properties (e.g., after a massive drought-induced mortality event).

Several research projects, reviews and region-specific guidelines have recently been dedicated to adaptive forest management (Bernier and Schöne 2009; Lindner et al. 2010; Fitzgerald and Lindner 2013; Bussotti et al. 2015; Keenan 2015; Reyer et al. 2015), and a wide range of possibilities has been proposed for adapting silvicultural systems to a rapidly changing climate. The main options include enhancement of forest's stress resistance by fostering stand heterogeneity e.g., by increasing species mixture and facilitating the transition to forest types more adapted to novel conditions (Bolte et al. 2010; Fitzgerald et al. 2013), and promoting resilience to extreme events e.g., by emulating natural disturbances through management interventions (Drever et al. 2006). Other possibilities have been recommended for particular cases, such as assisted migration of seed material from provenances that have already experienced similar climatic conditions than those expected for the future (e.g., more drought tolerant; cf. Gray et al. 2011; Kreyling et al. 2011) or the intensification of thinning interventions to reduce stand water use, thus increasing water availability for the remaining trees (Kerhoulas et al. 2013; Elkin et al. 2015). However, due to the diversity of European forest ecosystems and their different regional sensitivity to climate change, adaptation of management strategies may vary substantially depending on the zone that is considered (Lindner et al. 2010).

Traditional forest management has typically been driven by the maximization of the provision of one single service, i.e., timber production (Bürgi 2015). It was assumed that all other services would be provided equally well, such that timber production could be considered a “keystone” service (e.g., Glück 1987). The existence of trade-offs in ecosystem service provision has been acknowledged only recently (cf. Briner et al. 2013), and the increasing societal demand for a larger array of ecosystem services requires practitioners to change their planning strategies from a single-good objective towards multifunction-oriented management (Quine et al. 2013; Klopčič et al. 2015; Messier et al. 2015). Therefore, it must be carefully assessed whether current management practices and potential adaptation measures actually fit the objective of preserving multifunctionality, i.e. providing an ample portfolio of ecosystem services under novel climatic conditions. This evaluation strongly depends on current stand properties such as species composition or tree size distribution (Lindner 2000; Seidl et al. 2011; Temperli et al. 2012; Bircher et al. 2015). In addition, since forest dynamics is a process that takes place over multiple decades and even centuries, possible adaptations of forest management must be planned and evaluated in the long term, and they need to be based on thorough knowledge of the underlying population and ecosystem processes.

Observational or (rarely) experimental studies that aim at better understanding the functioning of forest ecosystems are of great value in this regard, but for two reasons they are not sufficient: First, they normally disregard management aspects and thus fall short when it comes to providing recommendations for future management actions to decision makers in policy and forestry. Second, their findings cannot readily be extrapolated to the novel environmental conditions that will prevail in many regions within a few decades from now. Instead, our knowledge and understanding need to be extrapolated into the future with quantitative, evidence-based models of forest dy-

namics (Kimmins et al. 2010). Yet, integrating ecological processes and management options to obtain reliable long-term projections of forest dynamics in decision-support tools (e.g., computer-based models) has proved to be complex and challenging (Bugmann 2014).

Models for simulating forest dynamics and management

Traditionally, predictions of future forest growth and the choice of a particular management option in forestry were based on past ‘experience’ (Kimmins et al. 2010). The first tools used for studying stand growth were developed more than two centuries ago. They consisted of maps and yield tables (Pretzsch et al. 2008), which were the first form of quantitative model. Yield tables were available for pure even-aged forest stands and allowed forest managers to estimate site-specific fertility, volume growth, and potential short-term future yields. However, these tables cannot be generalized in space or time (Pretzsch 2009) and cannot be used in more complex ecological systems such as uneven-aged mixed stands with heterogeneous site conditions, and temporally changing management actions. Thus, multiple and complex forest processes that act at different temporal and spatial levels needed to be integrated in a mathematical form with the first models.

In the 1960s, researchers developed the first stand-scale growth models. They were based on differential equation systems (Buckman 1961; Moser 1972) and were aiming to generate stem number frequencies in different size classes. They were useful to estimate assortment yield and financial return. With increasing computer power, different types of models started to be developed, aiming to simulate not only short-term growth and yield but also longer-term forest dynamics (e.g., Newnham 1964) and species succession (e.g., Siccama et al. 1969). Meanwhile, many authors have proposed different categorizations for these models on the base of the approach used to incorporate ecosystem processes, but also on their applicability under different spatio-temporal scales (Porté and Bartelink 2002; Canham et al. 2003; Messier et al. 2003; Pretzsch et al. 2008; Fontes et al. 2010). Following Kimmins et al. (2010), a simple approach is to classify them in three main categories: ‘historical bioassay’ or – perhaps more easily understandable – empirical models (Pretzsch et al. 2006a; Liang and Picard 2013), ecophysiological process-based models (Mäkelä et al. 2000; Keenan et al. 2008), and hybrid simulation models (Valentine and Mäkelä 2005; Mäkelä 2009).

Empirical models (EMs) are typically built on past observations (i.e., forest inventory data) and use statistical relationships to predict future growth and yield (Pretzsch et al. 2006a). They were initially developed to forecast forest growth for practical forest management and to improve planning in commercial forests (for this reason also called forest growth simulators; cf. Pretzsch et al. 2002). Among the most widely used tree-level simulators for European forests are MOSES (Hasenauer et al. 2006), SILVA 2.2 (Pretzsch et al. 2006b), PROGNAUS (Monserud and Sterba 1996), and MASSIMO (Thürig et al. 2005). Due to the fact that they forecast forest growth based on empirical data alone, EMs are generally unsuitable for projections beyond the historical range of climate variability (Kimmins et al. 2005).

More complex models that simulate ecological processes at a detailed temporal and spatial scale such as ecophysiological process-based models (PBMs; e.g., GOTILWA in Gracia et al. 1999; and CASTANEA in Dufrêne et al. 2005) are able to capture responses to changing environments,

but they often require extensive parameter calibration, which limits their range of applicability without major parameterization efforts to local conditions (Mäkelä et al. 2000; Fontes et al. 2010).

An approach to ‘bridge’ between the impossibility of EMs to portray the effects of climate change and the calibration issues of PBMs was the development of so-called ‘hybrid’ models (HMs). They take advantage of the process-based approach, necessary for modeling changes in environmental conditions, but use empirical elements as their structural foundation, thus bypassing the need for large parameterization efforts (Kimmins et al. 2010). The turning point in the development of HMs lies in the design of JABOWA (Botkin et al. 1972), the first model introducing the concept of simulating establishment, growth and mortality of individual trees on small patches of land as a function of environmental and biotic factors. This pioneer model stimulated the development of a wide ensemble of models during the next decades that were successfully employed in different ecosystems worldwide. These were labeled “gap models” based on the process in which the mortality of a large tree creates a gap, which induces a regeneration wave that thus fosters successional dynamics (Watt 1947; Bugmann 2001).

The basic assumption of most gap models is their abstraction of the forest as a composite of many homogeneous small patches of land (0.01 to 0.1 hectare), each composed by individual trees in different successional stages (Bugmann 2001). Some gap models do not simulate individual trees but tree cohorts, which are assumed to be composed by trees of identical size, species and age (Bugmann 1996). New saplings (typically, trees with a diameter at breast height >1 cm) establish at a given time step in the patch if environmental conditions expressed as a series of filters (i.e., light availability, winter temperature, growing degree days and browsing pressure) are met (Price et al. 2001). The diameter growth of every tree (or cohort) is typically 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 such as available light, growing degree days, soil moisture and nitrogen availability are at suboptimal levels (Moore 1989; Bugmann 2001). Tree properties such as height and leaf area are calculated using species-specific allometric functions based on diameter at breast height (dbh) of the trees (Didion et al. 2009), although in some cases site conditions are used to determine maximum tree height (Rasche et al. 2012). Tree mortality is simulated as a combination of a stress-induced (e.g., response to drought conditions or competition for light) and a ‘background’ component (Keane et al. 2001; Bircher et al. 2015).

Forest gap models account for the inter-specific sensitivity to environmental variables (e.g., growing degree days, drought, light availability) through species-specific parameters that vary in number and type depending on model complexity (e.g., see Morin et al. 2011 for the model ForClim). However, intra-specific adaptation to local conditions and intra-annual changes in species responses to environment are not normally considered. In addition, the models are prone to considerable uncertainties regarding the species-specific parameters describing environmental tolerances (Weber et al. 2008; Gutiérrez et al. 2016). This is particularly true for simulating limitations due to drought, since most gap models consider that all droughts have the same influence on growth irrespective of their timing within the growing season (Bugmann and Cramer 1998). This assumption is not realistic as tree species usually adjust their hydraulic system (e.g., isohydric species) and phenology to the specific moisture conditions to avoid drought or at least reduce their vulnerability (Berninger 1997; Martinez-Vilalta et al. 2009). This feature limits strongly the

reliability of forest gap models in areas where drought is the main constraint to tree growth, such as in the Mediterranean area but also in the dry valleys in the European Alps. Thus, an important topic of this thesis is how to better capture the influence of seasonally varying environmental variables on modeled tree growth, using drought as an example.

Most gap models were developed and used to simulate ‘potential natural vegetation’ in the absence of management (e.g., Lindner et al. 1996 using FORSKA; Bugmann and Solomon 2000 using ForClim) or to study vegetation patterns across landscapes (e.g., Urban et al. 2000 using ZELIG). Recent research aimed at better representing ecological processes such as tree establishment (Wehrli et al. 2007), growth (Rasche et al. 2012), mortality (Bircher et al. 2015), or natural disturbances (Seidl et al. 2008), by implementing equations that are biologically more accurate or using re-calibration methods (e.g., inverse modeling approach; Hartig et al. 2012). Thinning and management algorithms were often considered only more recently (Garman et al. 1992; Lasch et al. 2005; Pabst et al. 2008; Ranatunga et al. 2008) and particularly for exploring alternative management regimes to cope with climate change (Lindner et al. 2000; Rasche et al. 2013). However, the application of different harvesting functions on simulated forest dynamics have been evaluated only rarely (Rasche et al. 2011). For relying on forest gap models as decision-support tools in forestry under climate change, their capability to accurately simulate management interventions is an essential precondition. Another important topic of this thesis is thus to evaluate the importance of accurately simulating forest management interventions in models of long-term forest dynamics.

In my thesis, I focus on the development, evaluation and use of the forest gap model ForClim (Bugmann 1996) for central and southern European mountain forests. The dissertation is part of the European-scale research project ARANGE (“Advanced multifunctional forest management in European mountain RANGES”) whose main goal was to evaluate the consequences of changing climatic and socio-economic conditions on the provision of ecosystem services by mountain forests in Europe. The project builds on seven case study regions in the major mountain ranges of Europe, among which four have been selected for this dissertation, covering a wide range of forest types, governance settings and cultural contexts. ARANGE aimed to analyze four main ecosystem services: timber production, protection against gravitational natural hazards, carbon storage/sequestration, and biodiversity conservation (MEA 2005). State-of-the-art (“advanced”) forest models and indicator-based approaches were applied in ARANGE to quantify and understand the provision of ecosystem services. In this framework, my thesis attempts to evaluate potential and combined impacts of climate change and forest management regimes on stand-scale forest dynamics with a modeling approach.

Aims and structure of the thesis

The central objective of this PhD thesis is to contribute to the assessment of the potentials and limitations of current and alternative management strategies in a range of European mountain forests for providing ecosystem services under climate change.

I first focused on a regional case study, the Dinaric Mountains, where I further developed and evaluated a stand-scale model of forest dynamics (ForClim), especially regarding its ability to reproduce forest dynamics under specific harvesting interventions, which is a precondition to

analyze future management regimes under climate change. Thus, the main aims of *Chapter I* and *Chapter II* of this thesis were:

1. To improve and evaluate the performance of a model of forest dynamics with a focus on correctly simulating forest properties and harvesting interventions in intensively managed stands
2. To assess the impact of climate change on future forest dynamics under current and alternative forest management strategies in the Dinaric mountain forests.

For obtaining reliable projections with ForClim beyond temperate forests and for subsequently applying the model in Sub-Mediterranean forests (e.g., southern Europe), *Chapter III* focused on the ecological factor that was found to impose limitations on ForClim's applicability and one of the key factors that represents a challenge for many models of forest dynamics: drought. Thus, I evaluated model behavior in drought-prone forest stands with the following objective:

3. To investigate the importance of considering intra-annual and site-specific growth responses to drought in dynamic models, and propose a novel methodology to incorporate this key feature of drought-prone forests.

Lastly, in *Chapter IV* I employed the knowledge gained in the previous parts and performed a comprehensive simulation study in four European mountain forest stands to evaluate potential changes in future provision of ecosystem services in four cases study regions. To this end, I will use the ForClim versions developed in Chapters I and III to:

4. To project the impacts of climate change on the future provision of multiple ecosystem services in European mountain forests under current and alternative management practices.

To address these aims, the thesis is structured as follows:

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

Evaluating the potential effects of climate and management measures on future forest dynamics is challenging but also necessary for assessments of ecosystem goods and services. The specific objectives of this first chapter were threefold: (i) to improve the forest gap model ForClim for better depicting tree growth in managed stands and enhance the flexibility of its management module; (ii) to evaluate model performance against inventory data, with a focus on its sensitivity to specific harvesting functions; and (iii) to study the impact of climate change on future forest dynamics under current management practices in this case study region. I described model enhancements and tested the new model version in differently managed stands using analytical and empirical harvesting algorithms to verify whether different approaches to simulate stem removals would lead to different results. I then applied the model in a range of forest stands in the Dinaric Mountains (Slovenia) under a business-as-usual management regime and two climate change scenarios in addition to baseline climate, and I recommended further investigations on potential adaptive management measures in Slovenian mountain forests.

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

Based on the results from previous chapter, in a study led by Matija Klopčič (University of Ljubljana, Slovenia) we evaluated alternative options to business-as-usual management (BAU) in the Dinaric mountain forests and their impacts on forest dynamics, with a particular focus on the combined impacts of climate change and ungulates, focusing on the fate of the two main autochthonous conifer species in the region (Norway spruce and silver fir). I ran simulations for 31 mixed forest stands including five management strategies, two levels of browsing pressure and three climate scenarios. Outcomes from this simulation study were used for discussing potential conservation measures that can be applied to counteract the observed and projected decline of autochthonous conifers in the Dinaric mountain forests.

Chapter III: Forward modeling of tree-ring width improves simulation of forest growth responses to drought

The intra-annual variability of growth response to drought is rarely considered in dynamic vegetation models that aim to simulate shifts in species composition and growth rate variations due to changing environmental conditions. The main objective of this chapter was to improve the simulation of the impact of drought on tree growth in ForClim while maintaining its parsimony regarding structural complexity and the number of parameters. For this, I used a forward modeling approach of tree-ring growth using the VS-Lite model (Tolwinski-Ward et al. 2011). Based on the principle of growth limiting factors, this model derives intra-annual growth responses to drought from tree ring-width data. I quantified the seasonal growth responses to drought of Scots pine at sixteen sites along a gradient that covers most of the environmental conditions of the species in central and southern Europe and implemented these responses in ForClim. Finally, I evaluated the new model formulation with forest inventory data from managed Scots pine stands in Central Spain and Switzerland, suggesting a satisfactory performance that was much improved compared to the original ForClim version.

Chapter IV: Future ecosystem services from European mountain forests under climate change

In this chapter, I applied ForClim in four European mountain regions and evaluated the future provision of four main ecosystem services: timber production, carbon sequestration, biodiversity conservation, and protection against natural hazards. Forest dynamics were simulated under three management scenarios (no management, business-as-usual, and one alternative management regime) and five climate change projections, focusing on selected “representative stand types” (RST) of these mountain regions that cover different forest types and governance settings of central and southern Europe. Indicators of ecosystem services were calculated using “linker functions”, and they allowed for the quantification and comparison of ecosystem services from simulated stand attributes. I also analyzed the trade-offs and synergies between ES, and evaluated their variability according to changes in climate and management regimes.

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Chapter I

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 of 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.

Keywords: mountain forests, climate change, gap model, ForClim, Business-As-Usual management, forest inventory data

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 (Spathelf et al. 2014; Elkin et al. 2015). 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 are forest gap models (also called forest succession models; cf. Shugart 1984; Bugmann 2001). 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 (Garman et al. 1992; Ditzer et al. 2000), 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 (i) to evaluate the performance of a forest gap model with a focus on its sensitivity to specific harvesting functions; and (ii) 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 (Moore 1989; Bugmann 2001). 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 mono-specific 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:

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

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:

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

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:

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

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:

$$gLA1 = kA_{1MAX} - kA_{1diff} * gLAI \quad (4)$$

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:

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

Management

We complemented the management submodel by two harvesting functions that enhance model flexibility. The first function, labelled 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 growth-and-yield plots in Switzerland and five forest compartments in the Snežnik area in southern in Slovenia (Table 1; Appendix 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 are 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 Appendix 1.

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 (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).

Region	Site	Coordin. (°N ; E)	Elevation (m a.s.l.)	Temp (°C)	Precip (mm)	Site area (ha)	BS (mm)	Nitrogen (kg/ha *yr)	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

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 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*):

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

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

We further compared the simulated vs. 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; Rebetz 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 (Diaci et al. 2010; Boncina 2011; 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. Secondly, forest structure data – tree species composition and DBH structure – were derived from a series of inventories for the period 1963-2003. Twenty-six RTSs were identified as even-aged stands with different development stages (i.e., pole, mature, and regenerated stands) while the remaining 11 RTSs featured uneven-aged stand structures. Characteristics for each RST are reported in Table S4, Appendix 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 section 2.3. 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 Appendix 2), assuming a constant climate after 2100. The establishment submodel was slightly modified for the model application, as explained in Appendix 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 Appendix 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 towards the end of the simulation, resulting in a good match with the observed DBH distribution (cf. Fig. 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 cm 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 suggests (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 Appendix 1).

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 Appendix 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).

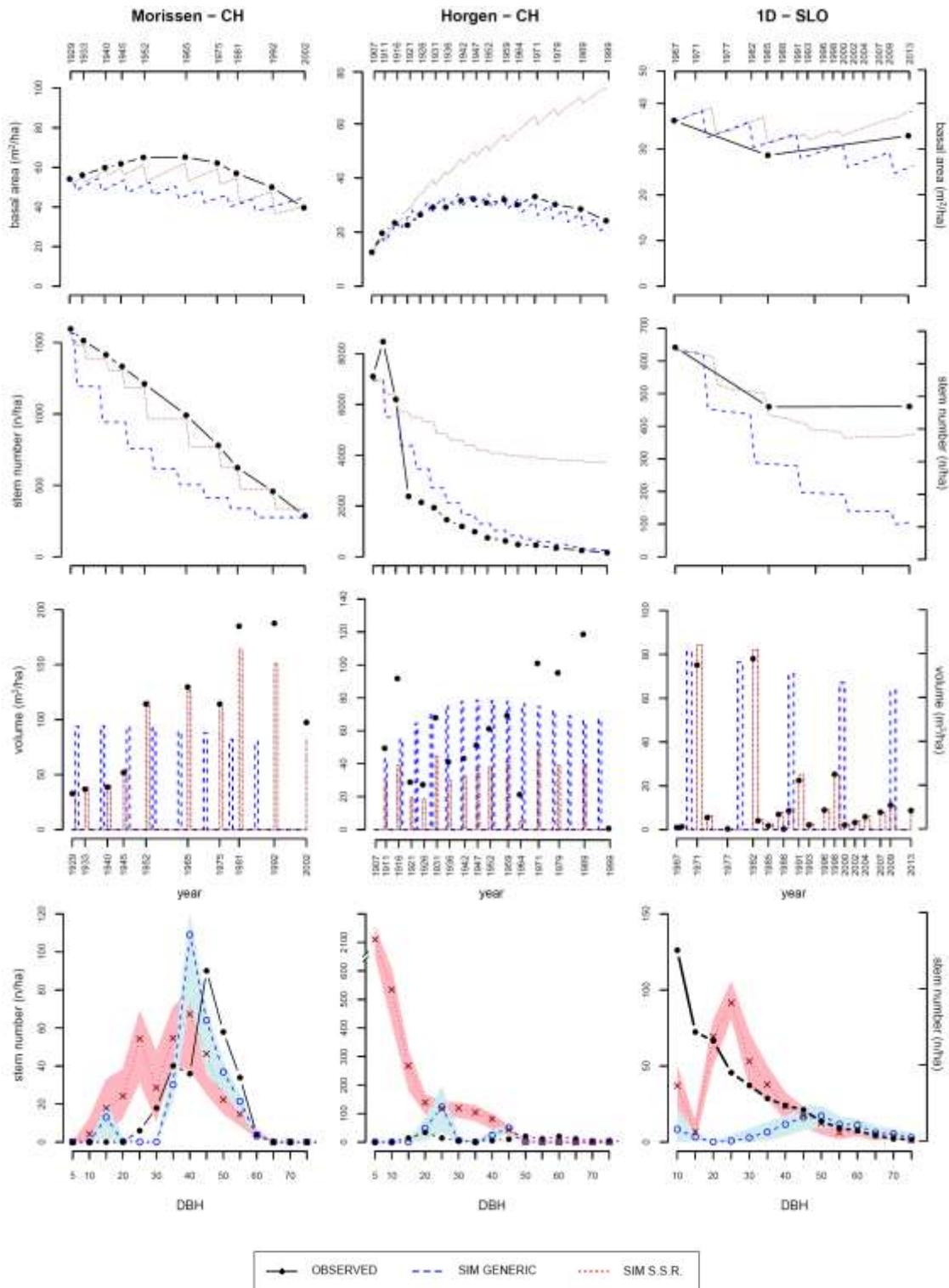


Fig. 1 Change over time of stand basal area (m²/ha), stem numbers (per ha), and volume harvested (m³/ha/yr) based on inventory data (black) and simulated by ForClim using the GEN (blue) and SSR (red) functions. Diameter distributions (5-cm bins) at the last inventory and at the end of the simulations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

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. 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 indicating that distributions significantly differ with a p-value < 0.05.

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	stat
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

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 $75.8 \pm 17.1\%$) 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 $41.4 \pm 23.8\%$ and reached >60% in medium-elevation stands, but its share did not exceed 15% for most RSTs in 2150 ($10.2 \pm 8.9\%$, 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 of 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 of 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 of 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.

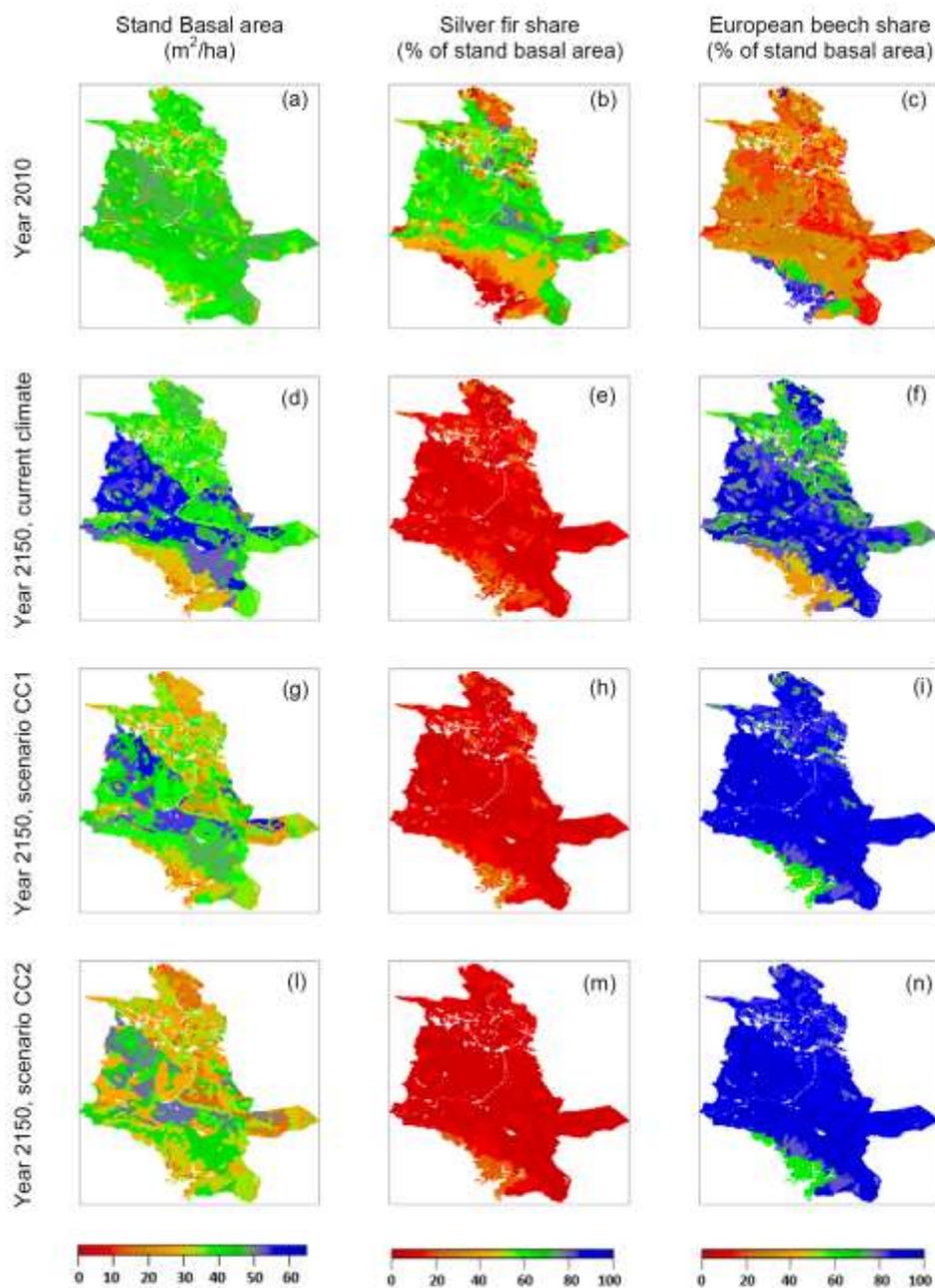


Fig. 2 Current (in 2010) and projected (in 2150) stand basal area and share of Silver fir and beech (in percentage of basal area) extrapolated to the entire Snežnik area. Simulations into the future were run using three climate scenarios: current climate, CC1 and CC2. The maps were generated by plotting 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 Appendix 3).

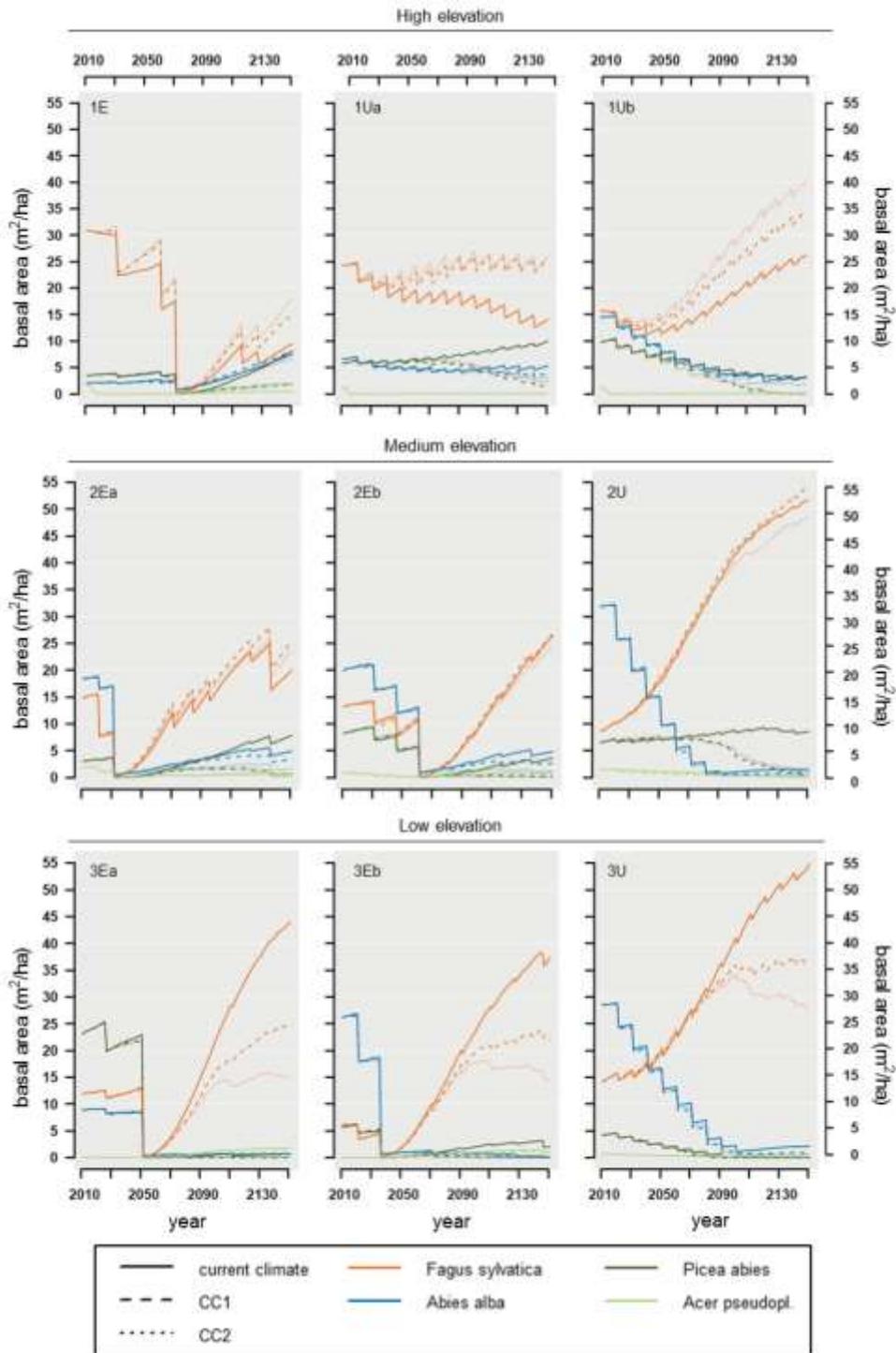


Fig. 3 Simulated change in Basal Area of *Fagus sylvatica*, *Abies alba*, *Picea abies* and *Acer pseudoplatanus* under current climate and two climate change scenarios for nine RSTs of the Snežnik area. These RSTs were selected at three elevations to represent the diversity in stand structure, species 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 Appendix 3.

Effect of climate change

Changing climate conditions – i.e., warmer and drier climate especially during summer (Table S3, Appendix 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 m²/ha 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 ($5.2 \pm 6.1\%$ under the CC2 scenario; Fig. 2m). In contrast, climate change further promoted beech dominance over the whole area (mean share $89.6 \pm 9.3\%$ 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 towards the end of the management cycle (Fig. 3, lower panels). Interestingly, a reduction of 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. Fig. 3).

Discussion

General model performance

For model evaluation, we used relatively long inventory periods (50-104 years) and multi-species stands, in 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 Appendix 1). We suggest that the reduction in diameter growth due to short 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. section 0). 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 growth-and-yield plots, and consequently their growing stock (Bircher et al. 2015) as mortality rates (and deadwood pools) are 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 Appendix 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) vs. 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 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 pre-selected 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 on 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 of 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 require-

ments 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 20th century in these forests (Klopcic 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; Poljanec et al. 2010; Klopcic and Boncina 2011). 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 (Klopcic et al. 2010; Cailleret et al. 2014), 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 (Elkin et al. 2013; Cailleret et al. 2014).

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 of 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; Oliva and Colinas 2007; Klopčič and Boncina 2011), recent paleo-ecological 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. Klopčič et al. 2010; Diaci et al. 2011) 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 (i) maintain current growing stocks except at low elevations, and (ii) 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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Appendix 1

Model evaluation: description of historical data and simulation settings

Switzerland (CH)

Five forest growth and yield plots that had been set up and are monitored by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) were chosen from the eight plots used by Rasche et al. (2011) for evaluating a former version of ForClim. We omitted stands with low harvesting rates that are uninteresting to compare model behavior under different management scenarios, and oak-dominated stands, as this species is not present in the five Slovenian sites used for model evaluation (see below).

The five plots (Fig. S1) are located in the submontane to the upper subalpine vegetation belt, have different stand structure and include species such as Norway spruce, European beech, Silver fir and European larch. Inventory data comprise the species and DBH of living, dead and harvested stems, collected at intervals that ranged between 1 and 13 years for a long time (70-100 years). For each site, baseline climate (1960-2006) was obtained from the WSL database and spatially interpolated with DAYMET (Thornton et al. 1997) to a grid cell size of 1 ha. From daily climate data, averages of monthly temperature and precipitation, as well as their standard deviations and cross-correlations were calculated as inputs for ForClim. Bucket size (i.e., water holding capacity), available nitrogen, slope and aspect parameters were estimated from the site descriptions (Rasche et al. 2011). Since the inventory data did not differentiate the causes of tree death (i.e., individual-tree mortality due to natural causes; disturbances affecting many trees simultaneously; harvesting damages; etc.), we switched off the mortality function of ForClim and included the number of trees labeled as “dead” in the pool of harvested trees. Inventory data indicated that almost no regeneration took place in the plots, with the exception of Aarburg (beech-dominated). Therefore, we allowed natural establishment only at this latter site.

Slovenia (SLO)

Five compartments whose area ranges between 5.2 and 9.0 ha were selected in the Snežnik area in southern Slovenia (Fig. S1). The Dinaric Mountains are located in the western part of the Balkans and extend from southern Slovenia to Albania along the Adriatic Sea. The Snežnik area is a karst limestone plateau covering about 5000 ha with a mean elevation of around 1000 m a.s.l. (range 600-1796 m). At 1000 m a.s.l., annual temperature averages 6.2 °C, with mean monthly temperatures around -3 °C in January and 15 °C in July. Annual precipitation is rather high (>1500 mm year⁻¹) and evenly distributed over the year (see Appendix 2, Fig. S5). Snow cover duration is relatively long, often >120 days per year (average ≈90 days) at mean elevations. Forests in Snežnik have a long tradition of planned forest management, although in the 18th and 19th century they were subjected to uncontrolled harvesting and serious forest degradation (Klopčič and Boncina 2011). With the development of plenter forest management in the early 20th century, this region is now mostly managed using uneven-aged silvicultural practices (Boncina 2011).

The forest stands in the compartments are located at an elevation of 800 to 1220 m a.s.l., and they are characterized by an uneven-aged structure. In each compartment, data from three inventories between 1963 and 2013 were used for the model evaluation. In each inventory, the number of trees with DBH ≥10 cm for each 5 cm diameter class and each species was recorded (SFS 2013).

The model was initialized with the data from the first inventory. It is noteworthy that an unspecified number of small trees (i.e., those below the callipering limit) were present at this time, but they could not be taken into account in the model. Since in ForClim new trees are established as saplings with 1.27 cm DBH, new cohorts require several years or even decades until they reach the callipering limit of 10 cm. This produced an artificial underestimation of stem numbers in the low diameter classes that must be considered when comparing empirical and simulated diameter distributions over time.

Monthly climate data were derived from daily climate data of the closest E-OBS 0.25 deg. grid points for the period 1951-2011 (van den Besselaar et al. 2011). Weather files for different altitudinal zones, slopes and aspects were generated with the mountain microclimate model MTCLIM (Thornton et al. 2000). Due to the lack of records from weather stations, lapse rates for maximum, minimum temperature and precipitation required by MTCLIM were determined from the E-OBS dataset surrounding the area (Appendix 2, Table S1). Bucket size values for the five forest compartments were derived from the RSTs in the Snežnik area (see section 2.4 in the main paper for the definition of RST) based on expert knowledge (unpublished data).

Removals were obtained from harvesting registers between 1963 and 2012 for which conifers and broadleaves had been aggregated in 5 cm diameter classes. Since harvested trees were not available at the level of individual species, we calculated the removals of each conifer (spruce and Silver fir only) proportionally to their initial share with respect to stand basal area in the compartments. For broadleaves we assumed that the removals were entirely composed of beech. In contrast to the sites in Switzerland, we allowed natural mortality in the model since the number of trees removed due to natural mortality or disturbances were not recorded in the harvesting registers. In addition, we allowed natural regeneration in all compartments to compensate for the lack of trees <10 cm DBH at the time of model initialization.

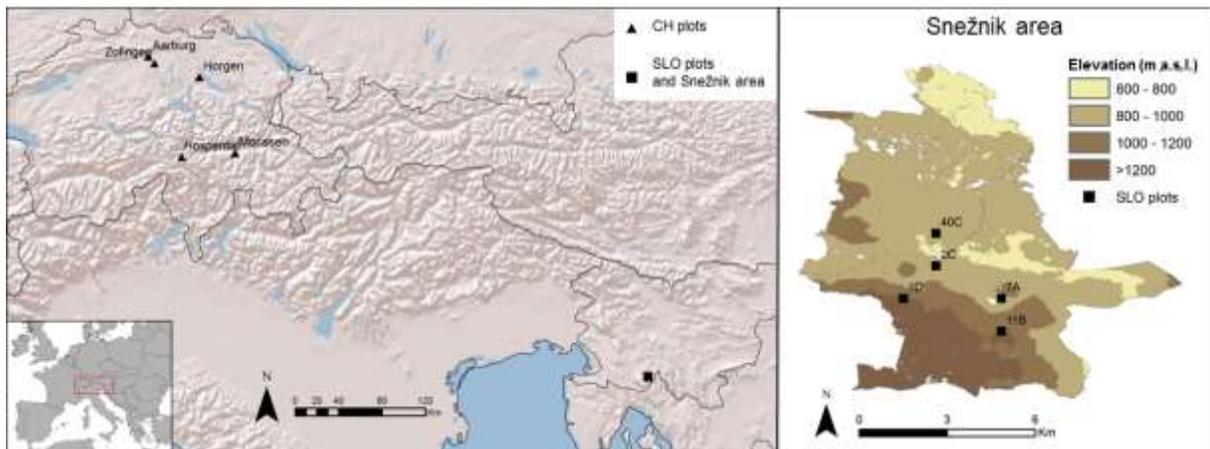


Fig. S1 Location of the sites used to evaluate the model across the Alpine region (left panel) and within the Snežnik area (right panel). CH = Switzerland, SLO = Slovenia.

Model evaluation: additional simulation results

Visual comparison of basal area and stem numbers over time, diameter distribution at the last measured year and volume harvested against inventory data for the remaining seven sites (not shown in Fig. 1) is presented in Fig.S2. As for the site Zofingen the SSR function strongly underestimated harvested stems for the first two interventions (not noticeable when only harvested volume is shown), we displayed this in Fig.S3.

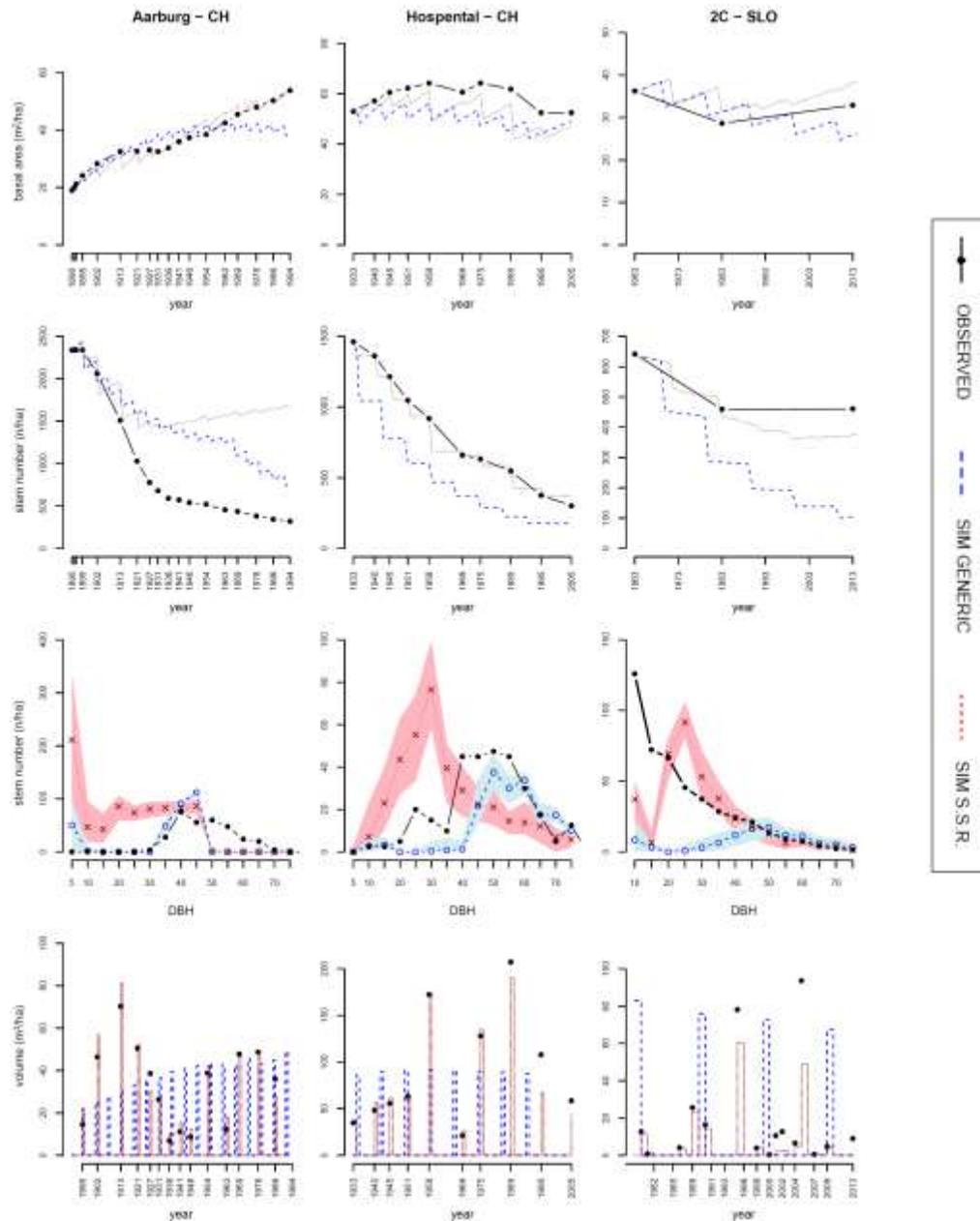


Fig.S2 Change over time of stand basal area (m²/ha), stem numbers (per ha), and volume harvested (m³/ha/yr) calculated using inventory data (observed; in black) and simulated by ForClim using the GEN (blue) and SSR (red) functions. Diameter distributions (5-cm bins) at the last inventory and at the end of the simulations were also represented. The colored areas revealed the 2.5th and 97.5th percentile of the simulations.

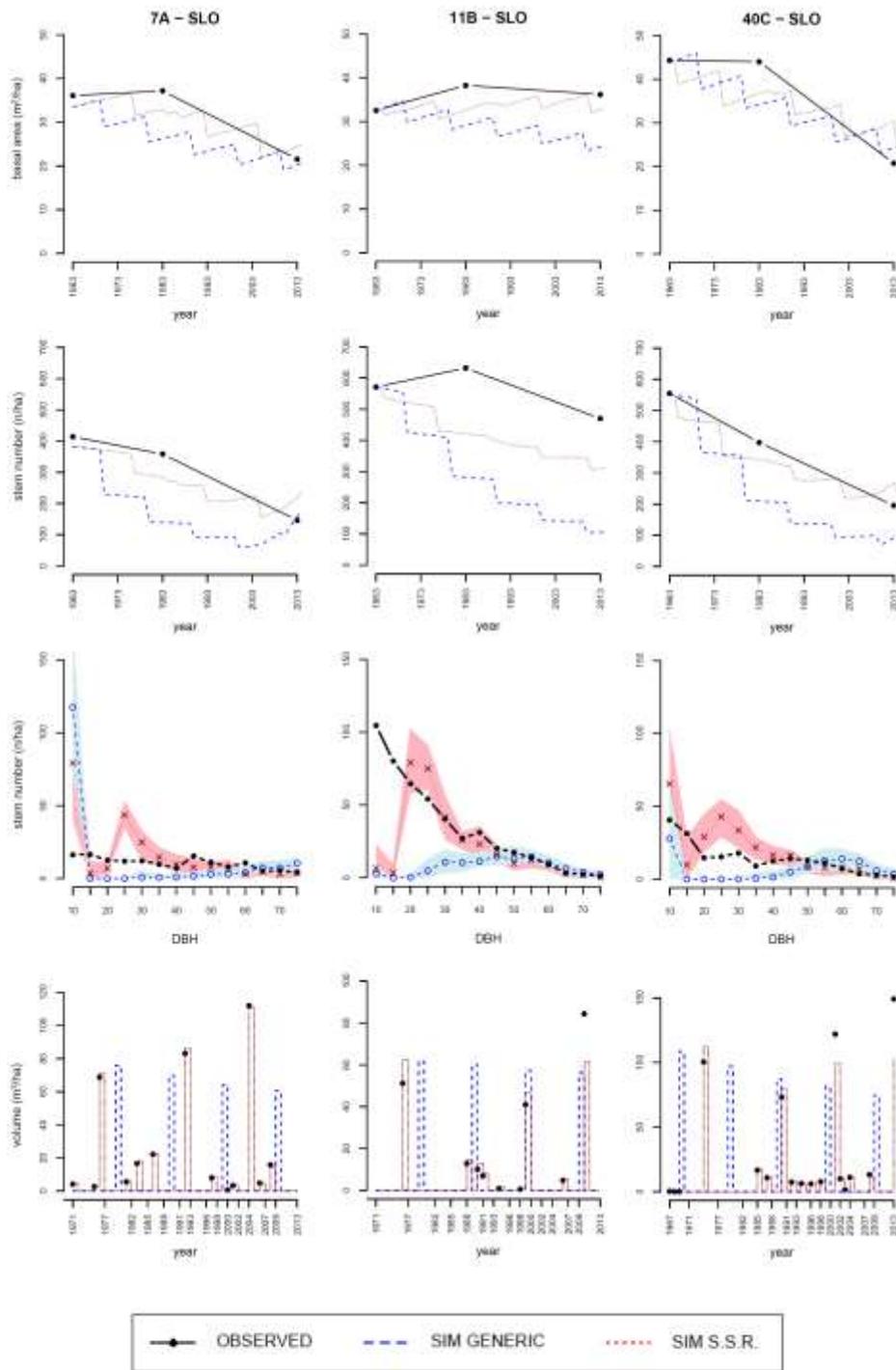


Fig.S2 (Continued)

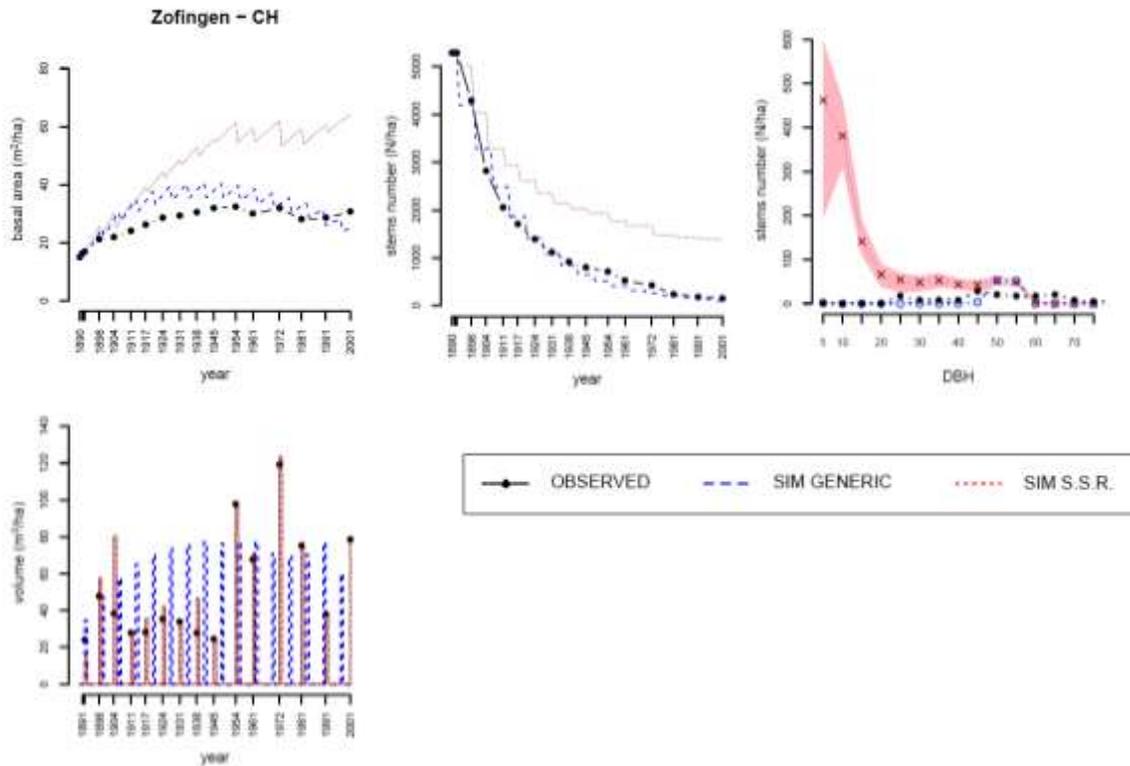


Fig.S2 (Continued)

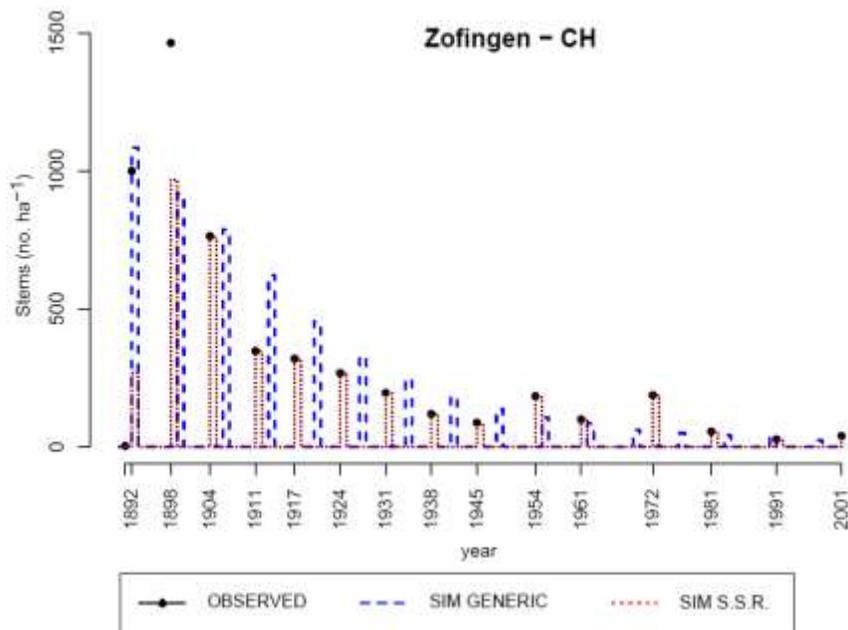


Fig.S3 Number of stems harvested (stems/ha) for the plot Zofingen calculated using inventory data (observed; in black) and simulated by ForClim using the GEN (blue) and SSR (red) functions.

Model evaluation: comparison between ForClim v3.0 and v3.3

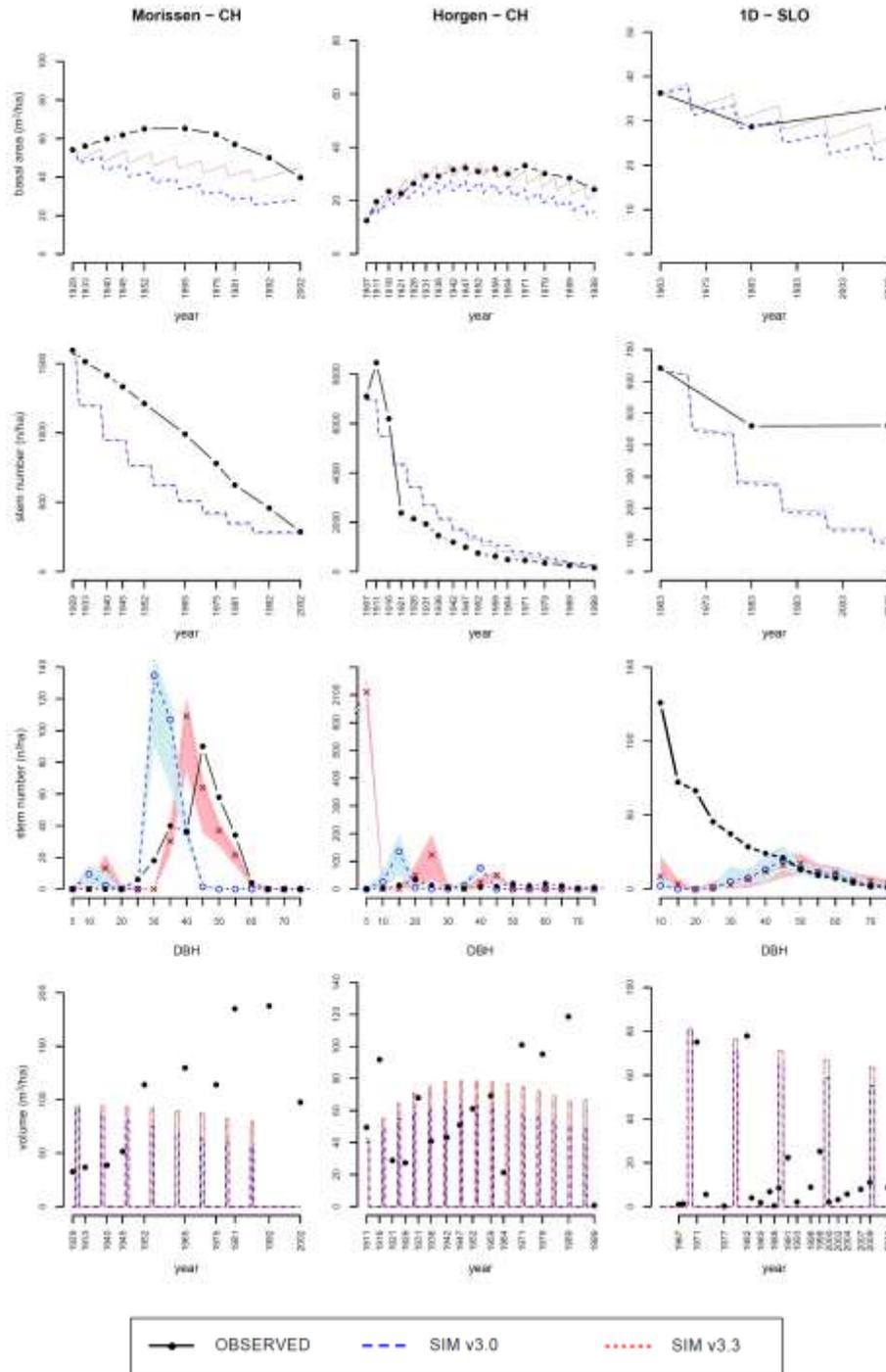


Fig.S4 Change over time of stand basal area (m^2/ha), stem numbers (per ha), and volume harvested ($\text{m}^3/\text{ha}/\text{yr}$) for three sites calculated using inventory data (observed; in black) and simulated by ForClim using the former version 3.0 (blue) and the new version 3.3 (red). In both versions the GEN harvesting function was applied (version 3.0 did not include the SSR function in the model code). Diameter distributions (5-cm bins) at the last inventory and at the end of the simulations are also presented. The colored areas show the 2.5th and 97.5th percentile of the simulations.

Table S1 Relative root mean square error (rmse; in %) and percentage bias (pbias; in %) of basal area and stem numbers simulated by ForClim v3.0 and the latest v3.3 with regard to observed values for all the evaluation sites. In both versions the GEN harvesting function was applied (version 3.0 did not included the SSR function in the model code). 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 indicating that distributions significantly differ with a p-value < 0.05.

Region	Site	Basal area				Stem Numbers				Volume Harvested		DBH Distribution	
		FC v3.0		FC v3.3		FC v3.0		FC v3.3		v3.0	v3.3	v3.0	v3.3
		rmse	pbias	rmse	pbias	rmse	pbias	rmse	pbias	diff	diff	stat	stat
CH	Aarburg	17	-16.2	4	-3.4	49	46.4	48	45.0	-49.0	-40.0	0.25	0.25
CH	Hospental	35	-31.1	17	-14.9	36	-32.2	37	-32.9	-35.4	-20.2	0.37	0.31
CH	Horgen	21	-19.9	2	-1.6	19	17.5	16	15.3	-3.4	20.4	0.62	0.63
CH	Morissen	36	-32.9	19	-17.3	32	-28.7	33	-29.4	-41.4	-28.0	0.25	0.13
CH	Zofingen	1	-0.62	16	15.3	1	0.6	0	0.5	19.8	41.7	0.56	0.63
SLO	1D	17	-11.5	7	-4.6	54	-35.7	51	-34.3	17.3	28.0	0.57	0.57
SLO	2C	24	-15.8	15	-10.1	52	-34.4	47	-31.4	-11.8	-2.9	0.57	0.57
SLO	7A	30	-19.8	23	-15.5	49	-32.7	39	-26.1	-4.8	1.0	0.64	0.71
SLO	11B	37	-24.5	30	-20	65	-43.6	64	-42.7	15.7	26.9	0.64	0.64
SLO	40C	17	-11.6	9	-6.1	39	-26.3	39	-25.8	-31.8	-25.8	0.43	0.43

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Appendix 2

Current and future climate scenarios

Daily temperature and precipitation data were obtained from the nearest E-OBS 0.25° grid point (45° 37' 30" N, 14° 22' 30" E, elevation 877 m a.s.l.) for the period 1951-2011. Climate data were processed in two successive steps. First, a 100-year time series with constant characteristics was produced using the stochastic weather generator LARS-WG (Semenov and Barrow 1997). In a second step, the program MTCLIM was used to derive climatic conditions for each stand according to its elevation, slope and aspect (Thornton et al. 2000).

For assessing the effect of climate change on stand dynamics, we used outputs from two Regional climate models (RCM) that projected future climate in the Slovenian region based on the A1B greenhouse gas emission scenario (IPCC 2007), i.e. the DMI-HIRHAM5_ARPEGE and HadRM3_HadCM3Q16 simulation runs, respectively, hereafter named scenario *CC1* and *CC2*. Season-specific delta values for future climate (2070-2100) were calculated taking baseline climate as a reference (Table S2).

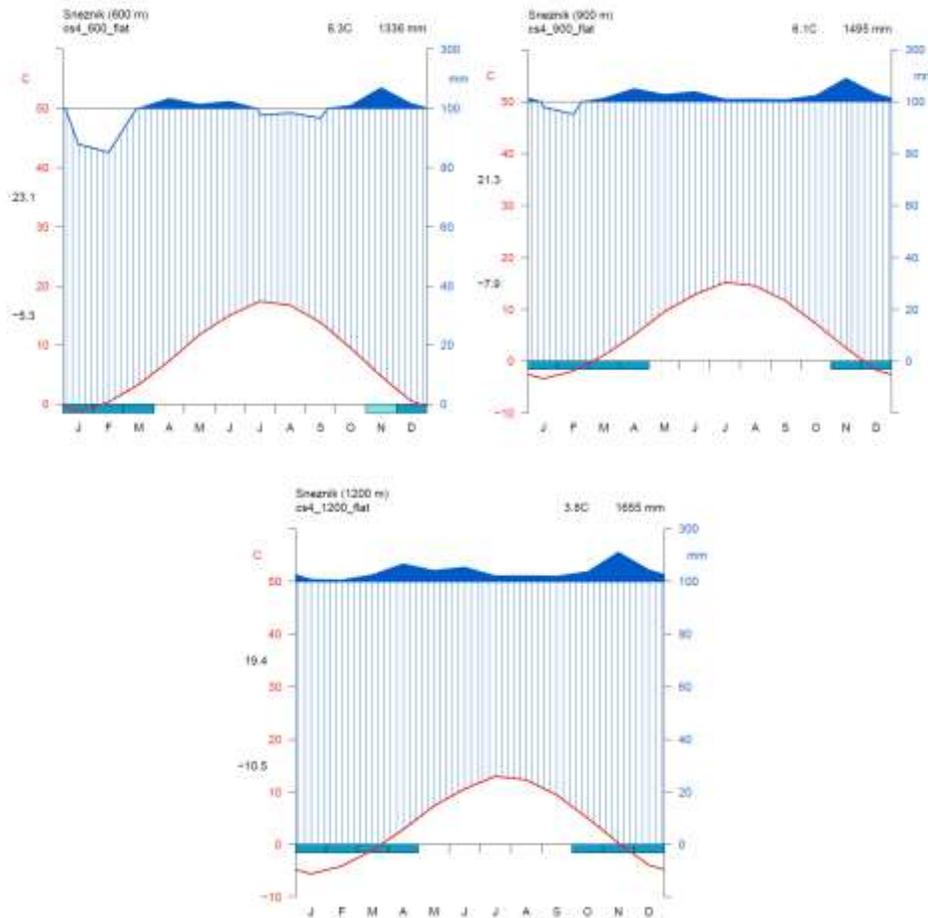


Fig S5. Climate diagrams for the Snežnik area (cf. Walter and Lieth (1960)) at low (600 m), medium (900 m) and high elevations (1200 m). Temperature and rainfall data are representative for the baseline period 1951-2011.

Table S2. Temperature and precipitation lapse rates per 1000 meters for the Snežnik area. The rates were calculated from the E-OBS dataset surrounding the area.

Maximum temperature (°C)	Minimum temperature (°C)	Precipitation (mm)
-6.15	-8.61	631.3

Table S3. Seasonal mean temperature (Mean T) and precipitation (Mean P) anomalies, together with standard deviation of the seasonal mean (sd T, sd P) for future climate (2070-2100) compared with reference scenario (1951-2011) along the elevation gradient in Snežnik (600, 900 and 1200 m a.s.l.). We assumed monthly cross-correlations (rTP) to stay constant during climate change.

elevation	variable	unit	Scenario CC1				Scenario CC2			
			Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
600	Mean T	°C	+2.3	+3.7	+1.9	+1.9	+4.4	+5.0	+4.8	+5.4
	sd T	°C	-0.1	+1.6	+0.9	+1.1	+0.0	+1.7	+0.5	+1.4
	Mean P	%	-8.7	-31.8	-8.9	+1.0	-5.9	-30.5	-13.6	+8.0
	sd P	%	+30.7	+77.7	+39.8	+13.0	+29.4	+64.4	+43.0	-12.6
	rTP	-	-0.5	-0.3	0.1	0.1	-0.6	-0.4	-0.3	-0.3
900	Mean T	°C	+2.3	+3.7	+1.9	+2.0	+4.4	+5.0	+4.8	+5.4
	sd T	°C	-0.1	+1.6	+0.9	+1.1	+0.0	+1.7	+0.5	+1.4
	Mean P	%	-8.5	-31.3	-8.8	+1.0	-5.7	-30.0	-13.4	+7.9
	sd P	%	+31.3	+80.5	+40.9	+12.3	+29.9	+66.4	+44.3	-13.9
	rTP	-	-0.5	-0.3	0.1	0.1	-0.6	-0.4	-0.3	-0.3
1200	Mean T	°C	+2.2	+3.7	+1.9	+1.9	+4.4	+5.0	+4.8	+5.4
	sd T	°C	-0.1	+1.6	+0.9	+1.1	+0.0	+1.7	+0.5	+1.4
	Mean P	%	-8.3	-30.9	-8.7	+0.9	-5.6	-29.4	-13.2	+7.8
	sd P	%	+31.8	+83.2	+42.0	+11.7	+30.2	+68.3	+45.5	-15.1
	rTP	-	-0.5	-0.3	0.1	0.1	-0.6	-0.4	-0.3	-0.3

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Appendix 3

Model application: establishment settings, RSTs list and additional simulation results

Modifications to the establishment submodel

In contrast to the model evaluation part (short-term simulation), we modified the establishment submodel of ForClim for the model application. Typically, gap models feature unrestricted seed availability (Price et al. 2001). To account for differences in regeneration strategies among tree species, the maximum number of trees to be established in ForClim ($kEstMax$) depends on a maximum establishment density ($kEstDens$, $0.006 \text{ m}^{-2} \text{ yr}^{-1}$) and the species-specific shade tolerance class ($kLas$; Risch et al. 2005; Cailleret et al. 2014). It is calculated as

$$kEstMax = (int) (0.5 + kEstDens * patchsize * kLa) \quad (8)$$

This induces a higher maximum regeneration rate for spruce ($kLa = 5$) than for beech and Silver fir ($kLa = 1$). However, regeneration data from Snežnik clearly showed a general dominance of beech over the other tree species in the regeneration layer. Saplings (DBH <10 cm) of beech were predominant although seedlings (height < 150 cm) were distributed fairly equally among the four main species. We therefore decided to change kLa in Eq. 1 to an ‘establishment potential factor’ based on the proportions of saplings in the data. We assigned a factor 7 to beech (mean share: 71-91%), a factor 2 to Silver fir (4-21%) and a factor of 1 to spruce and maple, as their shares were <8%.

The establishment potential of each species was reduced by browsing, whose general intensity was set to 10%. Although this intensity was constant among stands, its effect on regeneration rates was species-specific as each species is parameterized with different sensitivity to browsing (parameter $kBrow$; see details in Didion et al. 2011). With the exception of the minimum winter temperature for beech ($kWiT$), which was modified to -7 °C to allow for its regeneration at high elevations, as observed in the region, we did not modify other species-specific parameters related to the establishment factors regulating the effect of climate and competition in ForClim (see the parameter list for all species in Morin et al. 2011, Appendix S1).

Table S4 List of the Representative Stand Types (RST) with specification of: ID used in the simulations, stand development stage (or age), type of forest management (EA-FM = even-aged; UEA-FM = uneven-aged), elevation range, slope, aspect, water holding capacity (BS=Bucket Size). The last column associates the RST with the stands plotted in Fig.3.

RST ID	Stand dev. stage	Management	Elevation range	Slope (°), Aspect	BS (mm)	Ref. Fig.3
1.2	pole	EA-FM	700-1100	0°	120	-
1.3	mature	EA-FM	700-1100	0°	120	-
1.4	rejuvenation	EA-FM	700-1100	0°	120	2Ea
2.2	pole	EA-FM	1100-1400	25°, N	100	-
2.3	mature	EA-FM	1100-1400	25°, N	100	1E
2.4	rejuvenation	EA-FM	1100-1400	25°, N	100	-
4.3	mature	EA-FM	600-900	0°	120	-
4.4	rejuvenation	EA-FM	600-900	0°	120	3Eb
5.3	mature	EA-FM	710-1100	0°	120	-
5.4	rejuvenation	EA-FM	710-1100	0°	120	-
6.2	pole	EA-FM	710-1070	0°	120	-
6.3	mature	EA-FM	710-1070	0°	120	-
6.4	rejuvenation	EA-FM	710-1070	0°	120	-
7.3	mature	EA-FM	730-1150	25°, N	120	-
7.4	rejuvenation	EA-FM	730-1150	25°, N	120	-
8.3	mature	EA-FM	760-940	25°, S	120	-
8.4	rejuvenation	EA-FM	760-940	25°, S	120	-
9.2	pole	EA-FM	600-820	0°	120	-
9.3	mature	EA-FM	600-820	0°	120	3Ea
9.4	rejuvenation	EA-FM	600-820	0°	120	-
10.2	pole	EA-FM	700-1070	0°	120	-
10.3	mature	EA-FM	700-1070	0°	120	-
10.4	rejuvenation	EA-FM	700-1070	0°	120	-
11.2	pole	EA-FM	700-1090	0°	120	-
11.3	mature	EA-FM	700-1090	0°	120	2Eb
11.4	rejuvenation	EA-FM	700-1090	0°	120	-
12.0	uneven-aged	UEA-FM	1060-1350	25°, N	100	1Ua
14.0	uneven-aged	UEA-FM	750-980	0°	120	2U
15.0	uneven-aged	UEA-FM	750-980	0°	120	-
16.0	uneven-aged	UEA-FM	750-1050	0°	120	-
17.0	uneven-aged	UEA-FM	790-1100	25°, N	120	-
18.0	uneven-aged	UEA-FM	760-1100	25°, N	120	-
19.0	uneven-aged	UEA-FM	760-1050	25°, S	120	3U
20.0	uneven-aged	UEA-FM	820-1220	25°, N	100	-
21.0	uneven-aged	UEA-FM	780-1140	25°, N	120	-
22.0	uneven-aged	UEA-FM	820-1200	25°, N	100	-
23.0	uneven-aged	UEA-FM	1050-1360	25°, N	100	1Ub

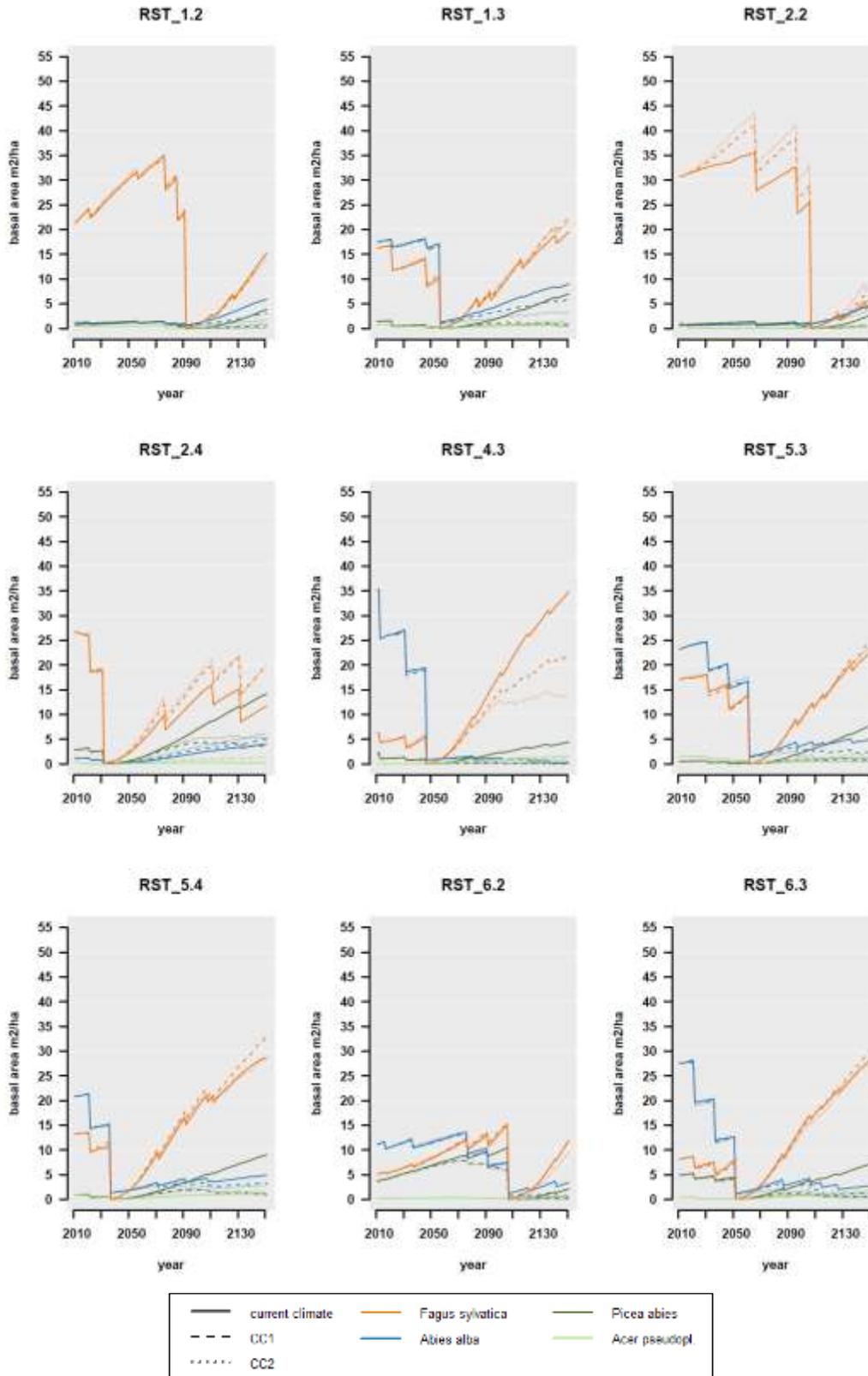


Fig S6 Simulated forest development for the remaining RST (not shown in Fig.3). The lines represent species-specific basal area, averaged from 200 simulation patches.

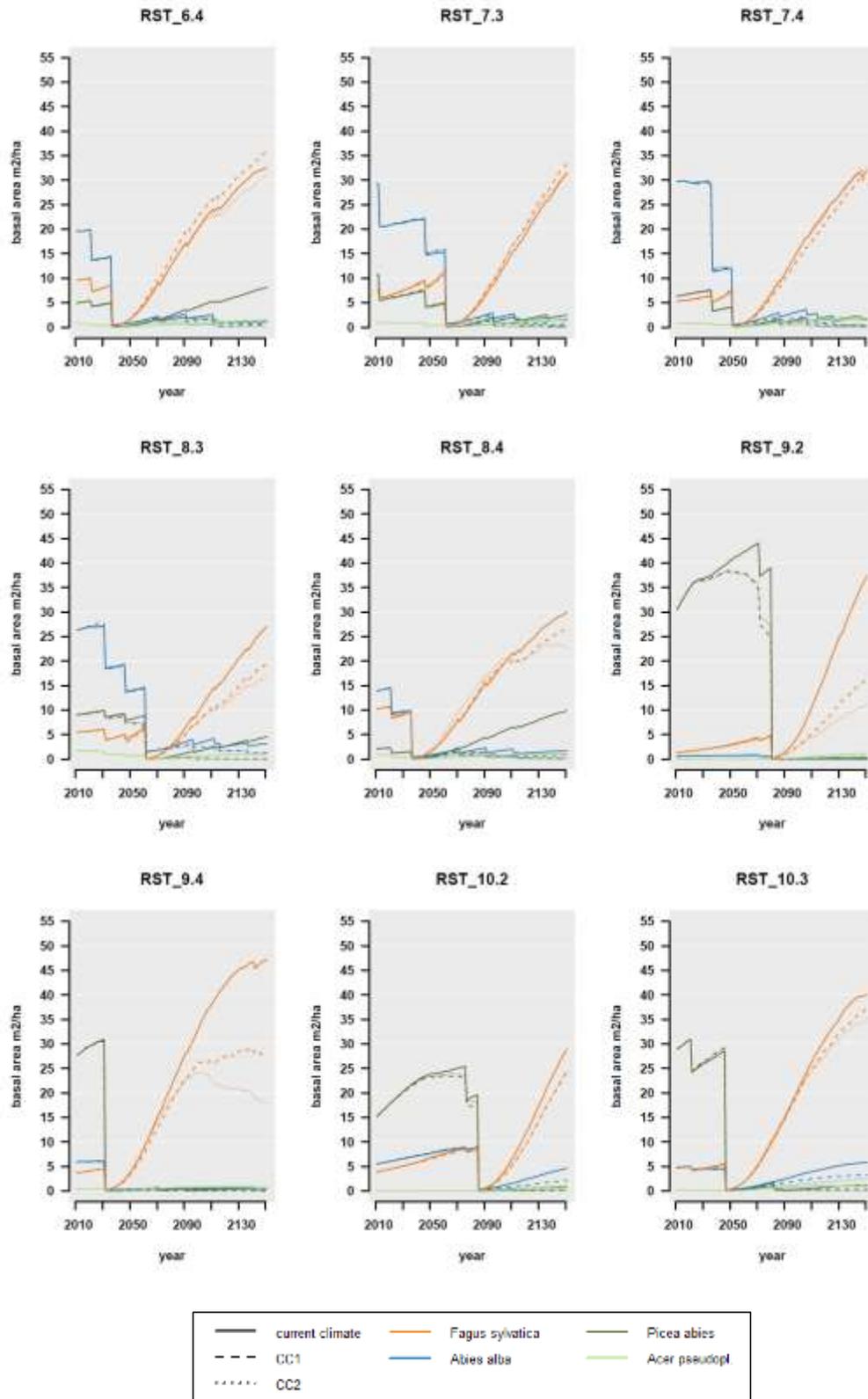


Fig S6 (Continued)

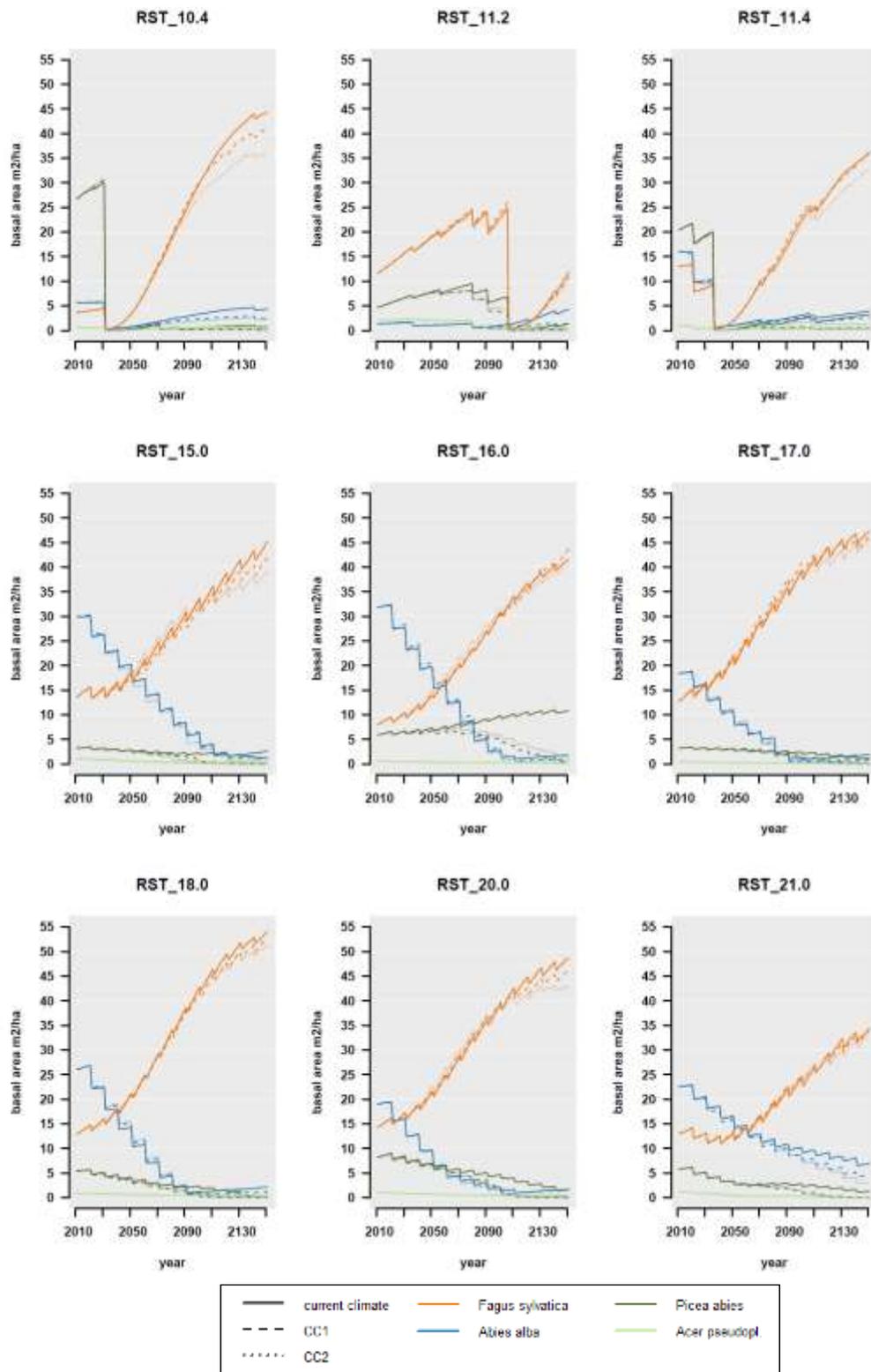


Fig S6 (Continued)

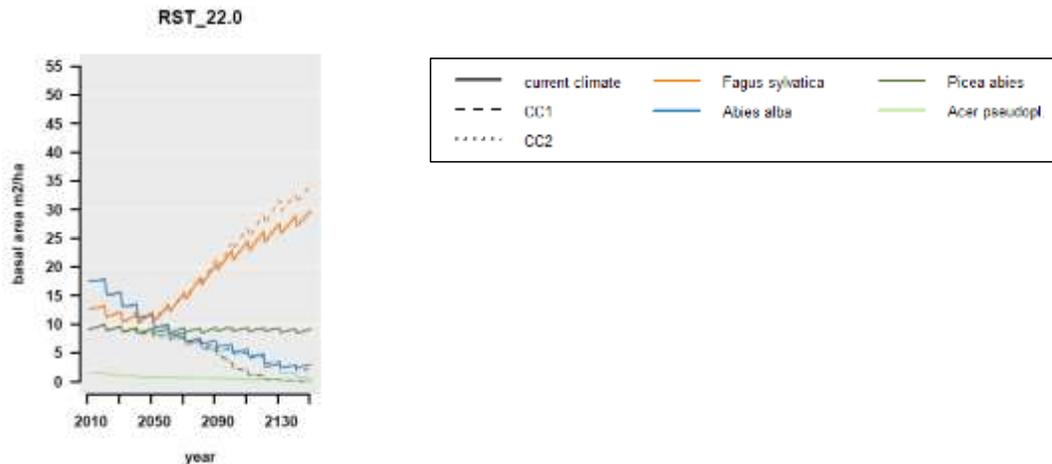


Fig S6 (Continued)

Methodology used for mapping simulation results displayed in Figure 3

Similarly as presented by Busing et al. (2007), for providing an overview of the simulation outputs for all stands at the final year we generated the maps shown in Fig. 2 by plotting RST-level simulation results into raster polygons (Fig. 5 and Fig. S7). Note that a single RST could be associated to multiple polygons, as displayed in Fig.S8. Maps were produced with the following methodology: (1) we extracted the ASCII Grid file for the different RSTs from available GIS data for the Snežnik study area; (2) we assigned simulation values (e.g., 40 m²/ha of total basal area) to each polygon of the ASCII Grid file allocated to each RST; (3) we plotted raster files with different colors depending on the value assigned to each RST. The procedure was accomplished using the `raster` package of the open-source software R (R Core Team 2014).

In contrast to landscape-scale, spatially-explicit models (e.g., LandClim; cf. Schumacher et al. 2004) horizontally non-explicit forest gap models such as ForClim do not consider seed dispersal, species migration and large-scale external disturbance events such as wind-throws. Therefore these maps should not be considered as landscape-maps, but as aggregation of individual stands, for which model simulations have been performed separately (in our case for a total of 37 stands).

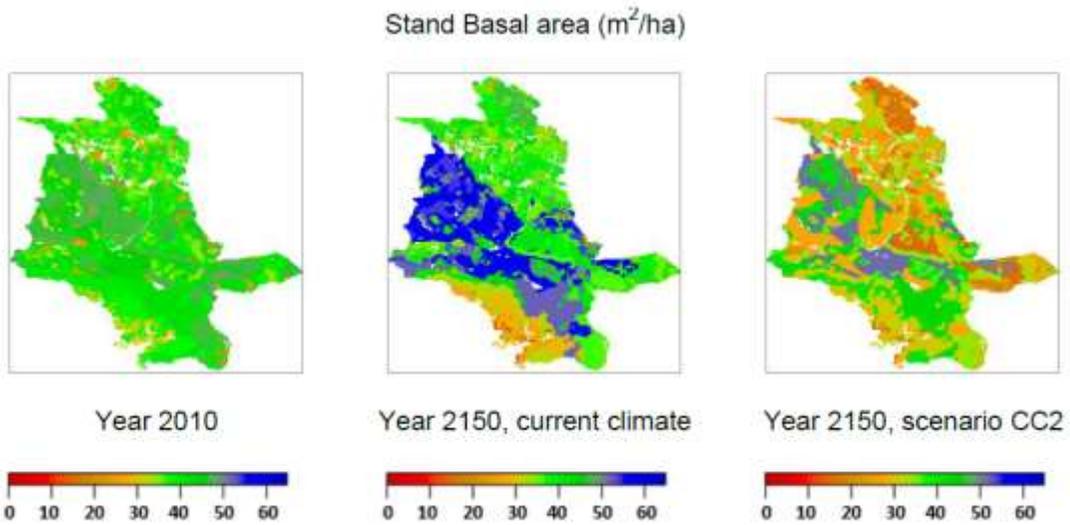


Fig S7 Example of map that display aggregated simulated stand basal area.

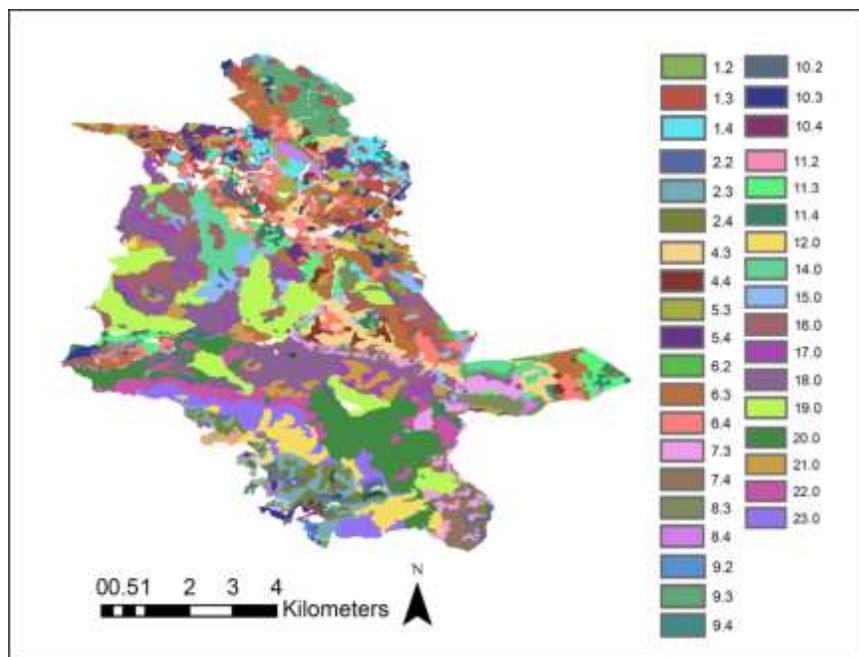


Fig S8 Map showing the distribution of the 37 simulated RSTs (see Table S4) in the Snežnik study area.

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Chapter II

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

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Abstract

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

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

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

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

Introduction

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

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

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

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

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

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

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

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

Study area

The study was conducted in the Snežnik region of the Dinaric Mountains in Slovenia (45° 36'N; 14° 28'E), where mixed silver fir-European beech-Norway spruce mountain forests prevail. The forests are characterized by high stand volume (>400 m³ ha⁻¹), and stands are mainly of an uneven-aged structure (i.e. 'plenter' and irregular shelterwood stands; Mathews 1999). The main tree species are silver fir (hereinafter fir), European beech (hereinafter beech), Norway spruce (hereinafter spruce) and sycamore maple (*Acer pseudoplatanus*), but many other species, such as wych elm (*Ulmus glabra*), rowan (*Sorbus aucuparia*), small-leaved lime (*Tilia cordata*), yew (*Taxus baccata*) and others, are sporadically present (SFS 2012). Extensive information on the analyzed forests and their past dynamics can be found in Klopčič and Bončina (2011).

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

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

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

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

Methods

Data acquisition

Forest stand data

Data on the current state of forest stands were obtained from the databases of the Slovenia Forest Service (SFS 2012), comprising diameter distribution (i.e. number of trees per tree species by 5-cm diameter classes, the measurement threshold being 10 cm in dbh) and regeneration. For each stand type, the diameter distribution per tree species was obtained from a set of permanent sampling plots (grid 200×250 m, 500 m² each, measurement threshold dbh=10 cm) located in stands identified as an individual stand type and surveyed in 2004 (for details see Appendix 1); in total 823 permanent sampling plots were included in the calculation. Regeneration per tree species was surveyed on 42 temporary sampling plots located in different stand types. Due to the lack of plots in some stand types, regeneration data was additionally obtained from neighboring stands similar in stand and site characteristics. Regeneration data considered in AM3 were obtained from the fenced areas within the case study area. The regeneration was surveyed on 33 plots 4 m×4 m in size, placed in two fenced areas at 4-m intervals along transects located approximately 50 m from the fence (Klopčič et al. 2010).

Forest management data

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

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

Simulation of forest development

Model description

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

Simulation experiments

For each stand type we initialized 100 forest patches (default patch size 800 m²) with the diameter distribution per tree species from the last forest inventory (SFS 2012). Data on site conditions such as slope, aspect, nitrogen availability and water holding capacity were used as inputs in the model (see Appendix 1). Subsequently, we simulated forest development for a century, i.e. until 2110. For simulations between 2100 and 2110, we assumed that climate would remain constant as simulated in 2100. Establishment settings (i.e. calibration of the establishment potential by species based on regeneration data) and harvesting interventions were adopted from Mina et al. (2017).

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

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

Strategy	Simulated area (ha)	Silvicultural system	Rotation period	Thinning		Regeneration	regeneration period length	Regeneration harvests		Other guidelines	Browsing
				frequency	intensity ^c			frequency & intensity ^d	species composition		
BAU	4206	small-scale irregular shelterwood	130-140y	4 operations (only first 2 in high-elevation stratum) in stands of DBH _{lim} =15-50 cm	1: 2.2%, 2: 1.5%, 3 & 4: 1.0%	natural	20-35 y	1: 33%, 2: 40-70%, 3: 100%	proportional to stand mixture	-	on
NOM	4206	-	-	-	-	-	-	-	-	-	on
AM1 ^a	3459	single tree selection	-	comprised in selection harvests	-	natural	-	15%	proportional to stand mixture lower	-	on
AM2	4206	small-scale irregular shelterwood	130-140y	same as BAU	-	natural + planting	20-35 y	1: 33%, 2: 40-70%, 3: ~97%	proportion of fir & higher of beech and spruce than in stand mixture lower	fir conservation ^d	on
AM3 ^b	881	small-scale irregular shelterwood	130-140y	same as BAU	-	natural (fenced)	20-35 y	1: 33%, 2: 40-70%, 3: ~97%	proportion of fir & higher of beech and spruce than in stand mixture lower	fir conservation ^d	off

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

^b AM3 was simulated only in selected stand types since regeneration in the fenced areas corresponded only to these stand types.

^c Thinning and regeneration harvest intensity is given per operations (1-4 or 1-3, respectively), expressed in % of stand volume.

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

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

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

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

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

Simulation outputs

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

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

Results

Simulations under the current climate and BAU

Under the current climate and BAU, the proportion of fir in the study area was simulated to drop substantially (Figure 1), from $52.7 \pm 17.3\%$ (weighted mean \pm SD) in 2010 to $44.1 \pm 21.4\%$ in 2060 ($p < 0.01$), until reaching only $24.6 \pm 13.2\%$ in 2110 ($p < 0.01$). In contrast, the decrease in spruce proportion between 2010 and 2110 was projected to be only minor (from $13.1 \pm 6.4\%$ to $12.9 \pm 4.8\%$).

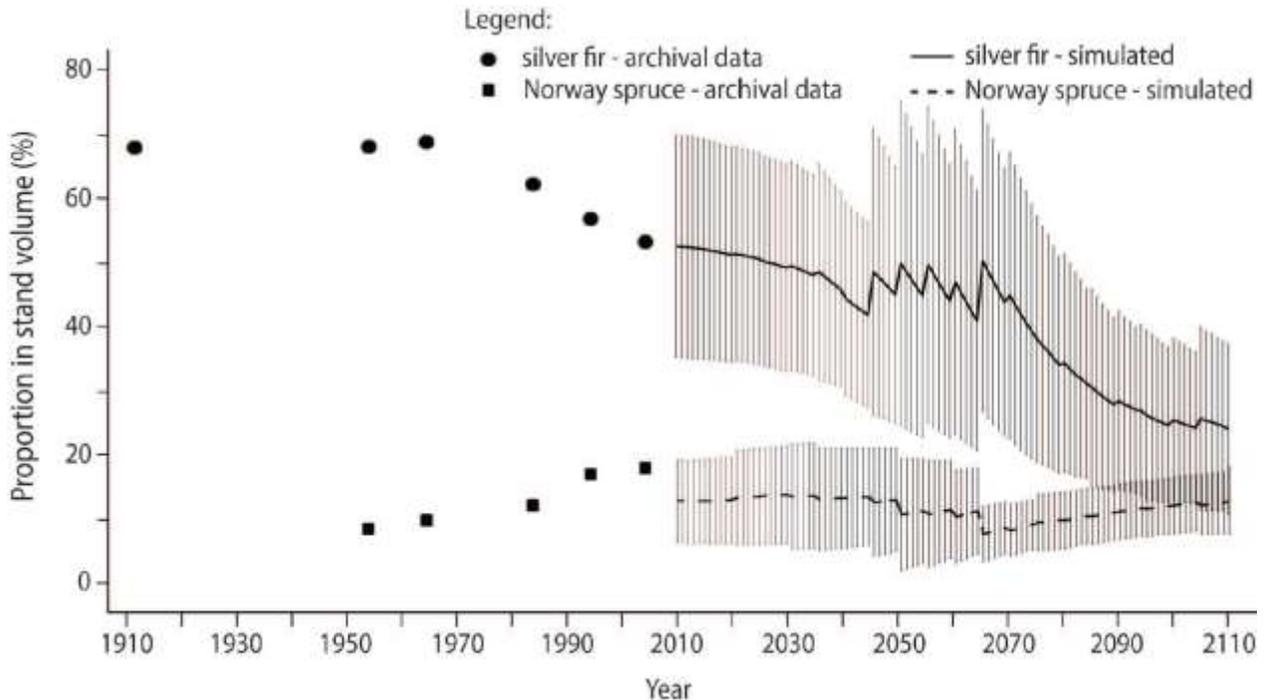


Fig. 1 Changes in fir and spruce proportions in the study area in the period 1912-2110. For the period 1912-2004, archival data are shown (adopted after Klopčič and Bončina (2011)); for 1912, data for fir represents all conifers), while simulation results under the baseline climate scenario cover the period 2010-2110 (data displayed as weighted means with standard deviations).

However, strong differences were forecasted along the elevation gradient (Figure 2, rows b-d and Figure 3, rows b-d). The largest relative changes were projected in stands at low-elevation, where the proportion of fir was projected to decline from $78.3 \pm 4.5\%$ to $30.2 \pm 7.7\%$ by 2060 and to $3.5 \pm 0.5\%$ by 2110. In the mid-elevation stands, the decrease in fir proportion was simulated to be substantial as well, but its proportion was projected to remain at $24.1 \pm 10.7\%$ in 2110. In the high-elevation stands, BAU simulations showed a strong rise in fir (from $17.4 \pm 13.0\%$ in 2010 to $34.1 \pm 27.9\%$ in 2060 and to $37.2 \pm 17.1\%$ in 2110) together with a noticeable increase in spruce (from $14.9 \pm 6.7\%$ in 2010 to $22.0 \pm 7.8\%$ in 2110).

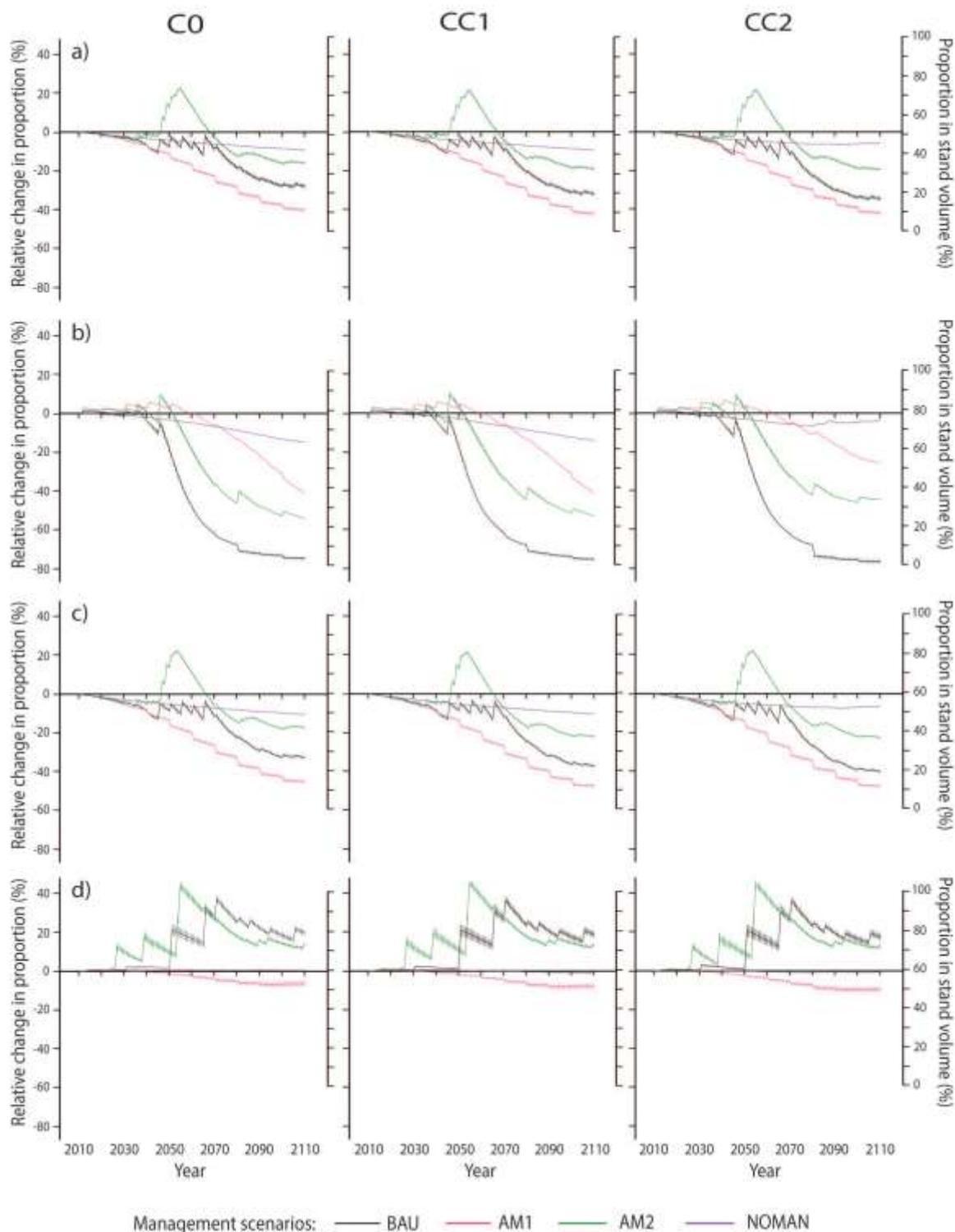


Fig. 2 Changes in fir proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in fir proportion in the stand volume (right axis in each chart) under different management strategies and climate scenarios: columns represent different climate scenarios (C0, CC1 and CC2) and rows different elevation strata: a) the entire study area; b) low-elevation stands; c) mid-elevation stands; d) high-elevation stands. Data are displayed as weighted means $\pm 1.96 \times SE$

Simulations under “no management”

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

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

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

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

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

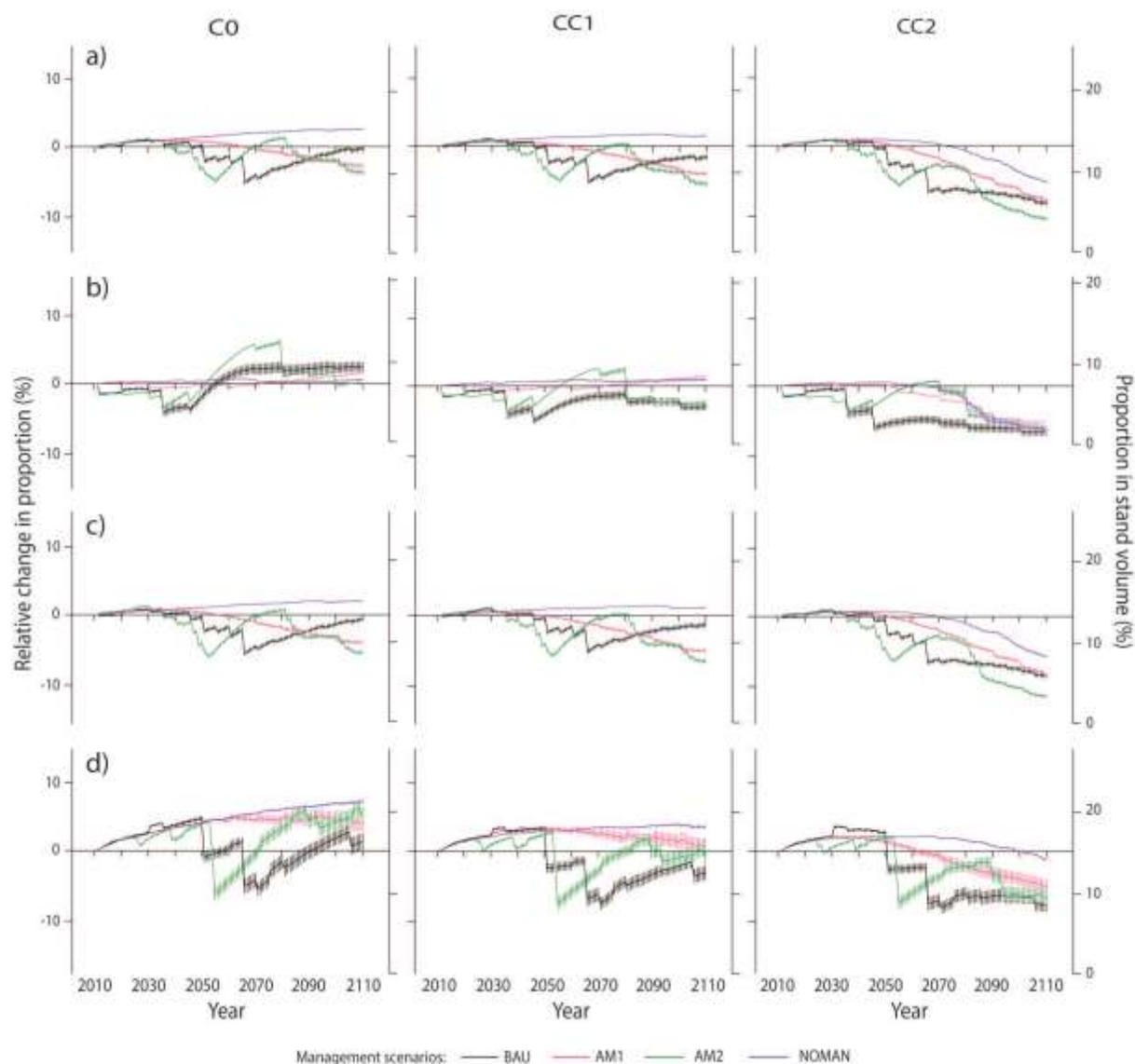


Fig. 3 Changes in spruce proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in spruce proportion in the stand volume (right axis in each chart) under different management strategies and climate scenarios: columns represent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

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

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

The number of small-sized fir (10-15 cm in dbh) was projected to increase in the middle of the simulation period, but drop afterwards (Figure 5). This indicated that after 2080 fir recruitment was hindered by climate-related factors, although differences between stands at different elevations were detected. In the low-elevation stands, fir recruitment was projected to be almost absent, resulting in a declining number of small-sized fir. On the other hand, in the high-elevation stands, fir recruitment was projected to be quite abundant, resulting in a substantially higher number of small-sized fir in the second half of the simulation period than at its beginning.

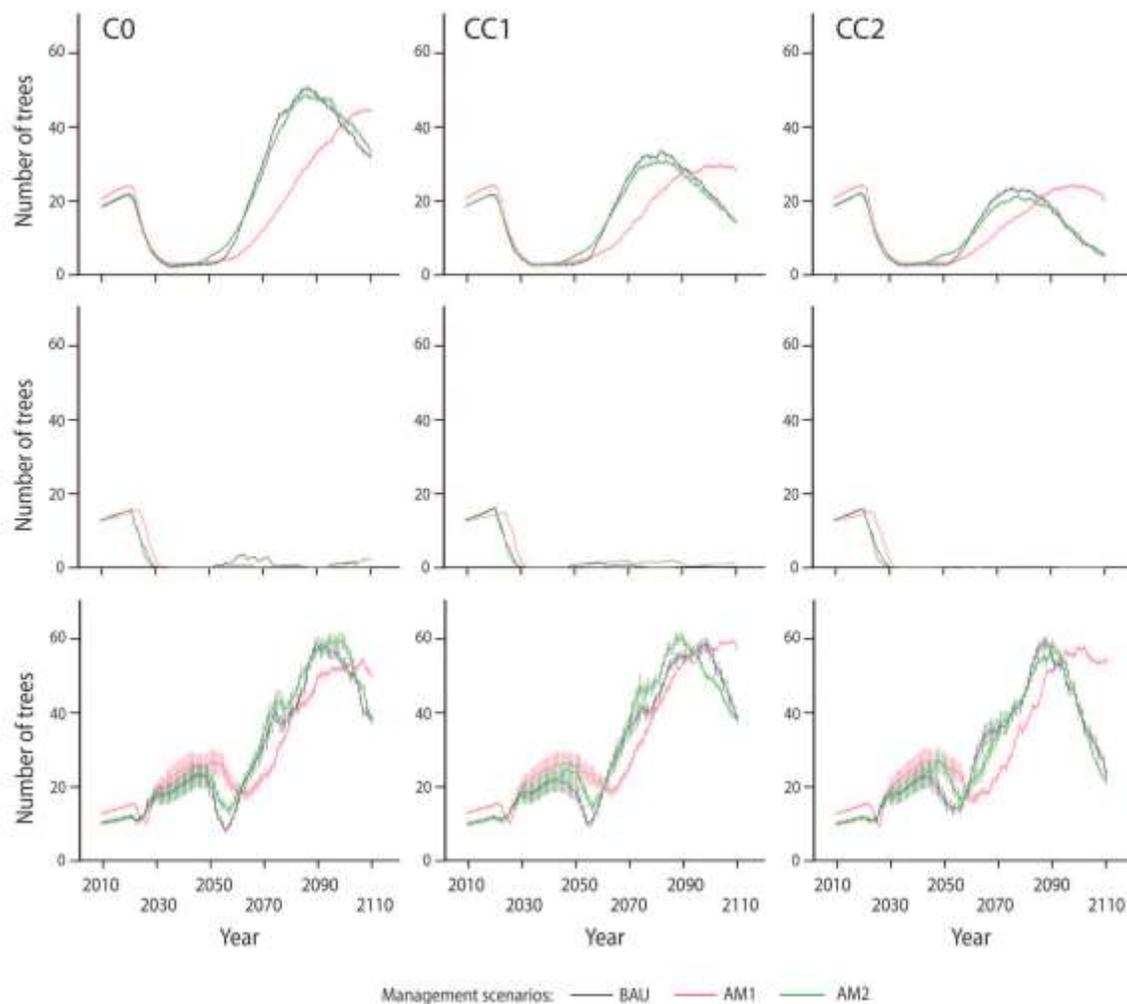


Fig. 4 Number of small-sized fir (10-15 cm in dbh) indicating its recruitment in the simulation period 2010-2110 in the study area (upper row), low-elevation stands (middle row), and high-elevation stands (bottom row). Data displayed are weighted mean values $\pm 1.96 \times SE$

Impact of large ungulates

Compared to BAU and AM2, simulations of AM3 showed higher proportions of fir under all climate scenarios (Figure 5). This was expected since the regeneration potential of fir in fenced areas was much higher. When omitting the past and future impact of large ungulates, the simulation under C0 showed a significantly higher proportion of fir in the second half of the simulation period than under BAU or AM2 (both $p < 0.01$). In contrast, AM3 did not result in a higher proportion of spruce compared to BAU and AM2 (6.1 % vs. 13.1 % and 4.6 % in 2110, respectively). The AM3 simulation also resulted in a significantly higher number of small-sized trees below 15 cm in dbh compared to BAU or AM2 (Figure 6). However, during the first decades of simulation, the absence of saplings 5-10 cm in dbh can be observed, followed by a drop in the number of trees 10-15 cm in dbh. This happened because, when initializing the model, seedlings and saplings below the measurement threshold of 10 cm in dbh were not considered although they were present in stands. Nevertheless, the proportion of fir in the total number of trees 10-15 cm in dbh was projected to increase from 24.3% in 2010 to 26.5% in 2110, while the final proportion under BAU and AM2 would be only 13.0% and 14.2%, respectively. Furthermore, between 2010 and 2110, the fir proportion on the observed area would decrease by only 4.0% instead of 18.0% or 30.7% as in AM2 and BAU, respectively.

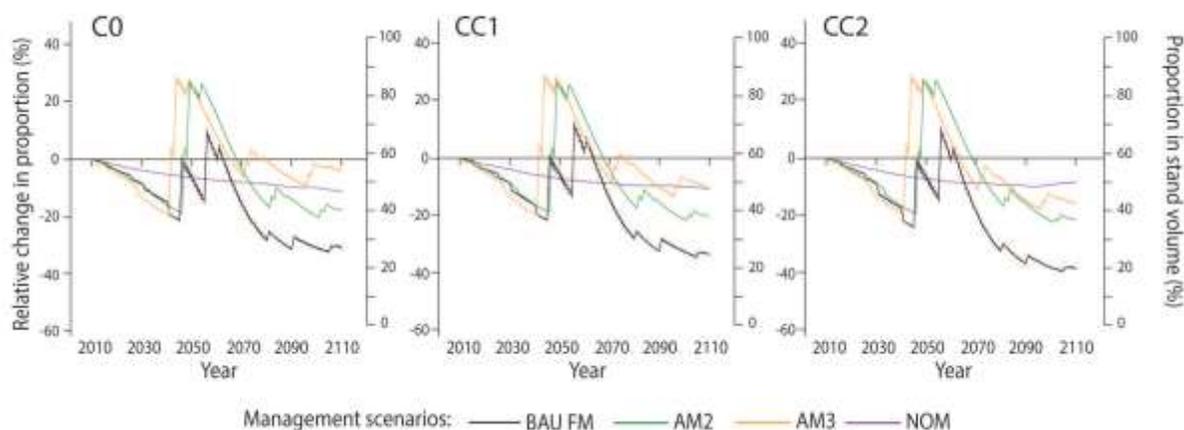


Fig. 5 Changes in fir proportion in relation to its base proportion in the stand volume in 2010 (relative change; left axis in each chart) and absolute changes in fir proportion in the stand volume (right axis in each chart) under different management strategies and different climate scenarios in selected mid-elevation stand types. Data displayed are weighted mean values $\pm 1.96 \times SE$

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

ungulates under extreme climate change. The lower number of small-sized fir confirmed the significant influence of climate change and large ungulates on the fir population.

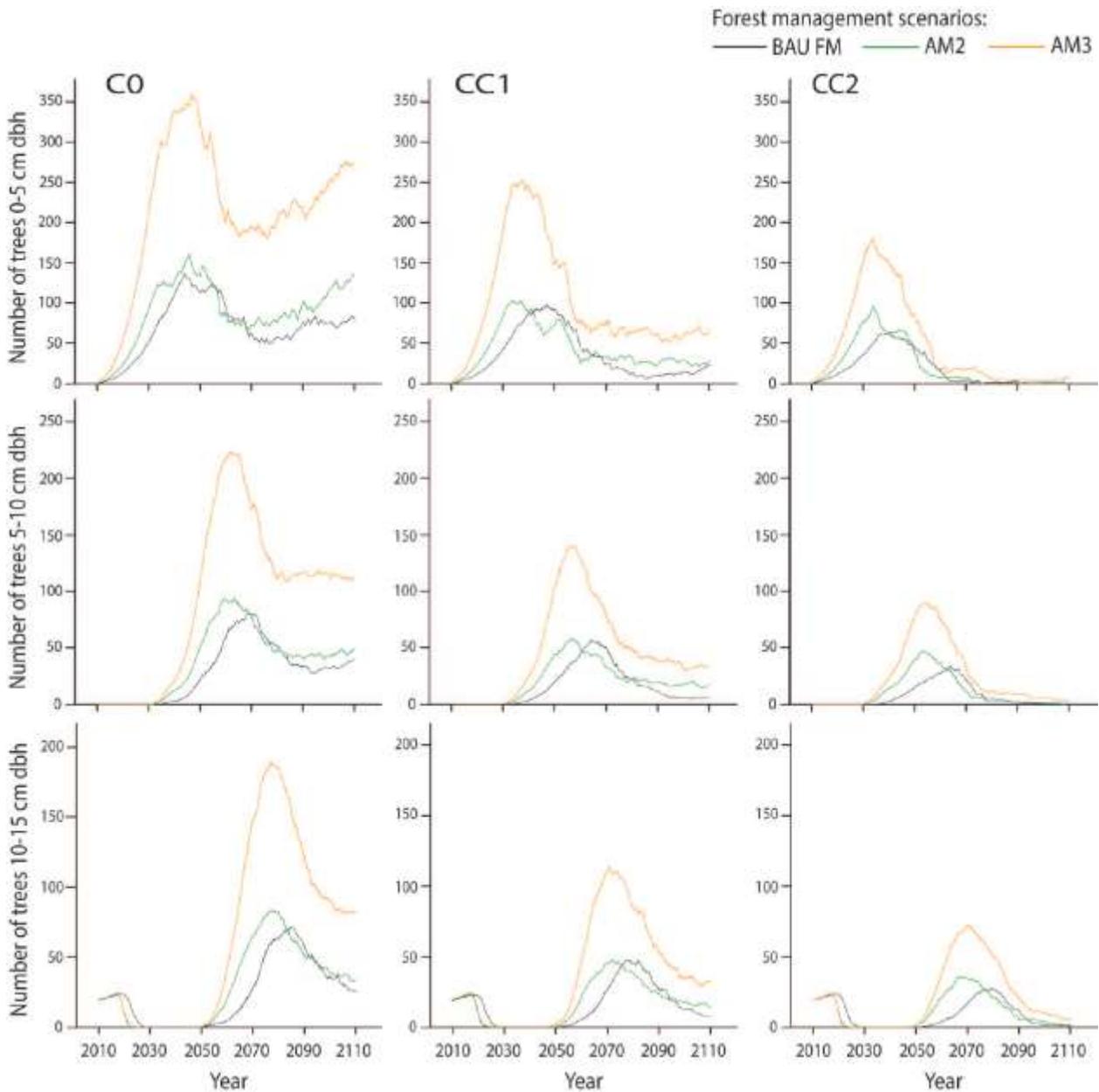


Fig. 6 Number of fir saplings (0-5 cm dbh; upper row) and small-sized trees (5-10 cm dbh; middle row; 10-15 cm dbh; bottom row) simulated under BAU, AM2 and AM3 and climate scenarios C0, CC1 and CC2 (columns). Data displayed are weighted mean values $\pm 1.96 \times SE$

Discussion

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

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

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

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

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

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

The prospects of silver fir and Norway spruce

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

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

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

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

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

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

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

Conclusions and implications for forest management

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

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

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

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

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

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Appendix 1

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

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

Two basic datasources to determine the initial diameter distribution of each stand types were used (SFS 2012): 1) permanent sampling plots (PSP) on a fixed grid (200×250 m, $n=823$, 500 m² each), comprising data on individual trees with registered location within the plot (i.e. azimuth and distance to the plot centre), tree species, 5-cm diameter class, social and health status, quality, and some other individual tree characteristics, and 2) forest stand map and database, comprising polygons delineating individual stands and data on main stand characteristics (i.e. area, stand volume, volume of each tree species, volume increment, allowable cut) for each polygon/stand. The procedure to acquire the initial diameter distribution was conducted in two steps. First, when stand type was defined for all stands, we overlapped the GIS layers of i) forest stands and ii) PSP in order to identify PSP located in particular stand type. Second, we extracted PSP per stand type and calculated the average diameter distribution in 5-cm diameter classes, starting at the measurement threshold of 10 cm in dbh. The number of PSP per stand type varied between 4 and 109, but only in 7 stand types out of 31 the number of plots were less than 10. The calculated average diameter distribution was a direct input for initializing the ForClim model.

Another input for the ForClim model were the regeneration data. The detailed data on the density of seedlings and saplings per height classes (i.e. 0-15 cm, 15-30 cm, 30-60 cm, 60-130 cm, 0-10 cm in dbh) per each tree species were acquired from 33 regeneration inventory plots located in the study area. For initializing AM3, the data acquired in the regeneration survey in the fenced areas were used (for details see Klopčič et al. 2010).

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

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

* water holding capacity (in mm of water column which can be stored in a soil profile)

** soil nitrogen availability (in kg/ha/y)

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Chapter III

Forward modeling of tree-ring width improves simulation of forest growth responses to drought

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Abstract

Drought is a key factor affecting forest ecosystem processes at different spatio-temporal scales. For accurately modeling tree functioning – and thus for producing reliable simulations of forest dynamics – the consideration of the variability in the timing and extent of drought effects on tree growth is essential, particularly in strongly seasonal climates such as in the Mediterranean area. Yet, most dynamic vegetation models (DVMs) do not include this intra-annual variability of drought effects on tree growth. We present a novel approach for linking tree-ring data to drought simulations in DVMs.

A modified forward model of tree-ring width (VS-Lite) was used to estimate seasonal- and site-specific growth responses to drought of Scots pine (*Pinus sylvestris* L.), which were subsequently implemented in the DVM ForClim. Ring-width data from sixteen sites along a moisture gradient from Central Spain to the Swiss Alps, including the dry inner Alpine valleys, were used to calibrate the forward ring-width model, and inventory data from managed Scots pine stands were used to evaluate ForClim performance.

The modified VS-Lite accurately estimated the year-to-year variability in ring-width indices and produced realistic intra-annual growth responses to soil drought, showing a stronger relationship between growth and drought in spring than in the other seasons and thus capturing the strategy of Scots pine to cope with drought.

The ForClim version including seasonal variability in growth responses to drought showed improved predictions of stand basal area and stem number, indicating the need to consider intra-annual differences in climate-growth relationships in DVMs when simulating forest dynamics. Forward modeling of ring-width growth may be a powerful tool to calibrate growth functions in DVMs that aim to simulate forest properties in across multiple environments at large spatial scales.

Keywords: Drought; Tree growth; Scots pine; Forward modeling; Tree-ring width; Dynamic vegetation model

Introduction

Drought is one of the main drivers of forest dynamics. It impacts a variety of plant physiological processes (Ryan 2011) and modifies the structure, functioning and vitality of individual trees at both the short and the long term (Breda et al. 2006). The carbon budget of trees is highly sensitive to drought via stomatal closure which impacts photosynthesis, but also via limitations on secondary growth (i.e., wood formation; McDowell et al. 2010; Muller et al. 2011; Palacio et al. 2014). Intense drought may also induce xylem embolism, changes in carbon allocation, and an increased risk from abiotic and biotic disturbance agents (e.g., fungal pathogens, insects, frost events; cf. Camarero et al. 2015; Sangüesa-Barreda et al. 2015). Moreover, drought can induce changes in tree regeneration rates, and mortality of individual trees in case of extreme and/or recurring events (McDowell et al. 2008). Although the global drought has shown little change during the last decades (Sheffield et al. 2012), many regions have experienced increases in drought intensity and frequency with negative consequences on forest ecosystems (Bigler et al. 2006; Allen et al. 2010; Anderegg et al. 2013). Frequency and intensity of drought events are expected to continue intensifying in the future (Dai 2013; Cook et al. 2014), and hence there is a strong need for better understanding tree responses to drought (Allen et al. 2015).

Xylem growth is among the main and first processes impacted by drought (see Palacio et al. 2014) and it can be reduced for several years after a severe drought event (i.e., legacy effects; cf. Anderegg et al. 2015). First, xylogenesis requires certain ranges of temperatures and soil moisture to allow for cell division (Mooney and Dunn 1970), and it stops when water potential is too low. As a consequence, a bimodal growth pattern is observed for several species growing under continental Mediterranean climates (Camarero et al. 2010; Gutierrez et al. 2011; Primicia et al. 2013), experiencing double winter-summer stress (Mitrakos 1980). Second, xylem growth is indirectly affected by drought through the reduction in photosynthetic rates caused by stomatal closure, reducing the amount of carbohydrates available for building new cells (Zweifel et al. 2006; Palacio et al. 2014). The intra-annual variation of cambial and photosynthetic activity depends strongly on the species, which have evolved to use different strategies for facing drought (Zweifel et al. 2009; Lévesque et al. 2014). For example, isohydric species are able to maintain high mid-day leaf water potential by reducing their crown-level stomatal conductance with the decrease in soil water availability (McDowell et al. 2008). Contrarily, anisohydric species tend to keep their stomata open during drought to maximize carbon assimilation which leads to more negative leaf water potentials (Tardieu and Simonneau 1998). Moreover, the intra-specific differences in growth responses to dry conditions observed between provenances and populations (Martín et al. 2010; Herrero et al. 2013; Sánchez-Salguero et al. 2015) demonstrate the importance of site-specific adaptations to drought.

This intra-annual variability in growth response to drought is partially considered in some process-based Dynamic Vegetation Models (DVMs) that simulate physiological mechanisms on an hourly or daily basis (Fontes et al. 2010). In most ‘mechanistic’ DVMs, however, the impact of

drought on plant growth is not captured accurately because growth is assumed to be exclusively source-driven (i.e., simulated growth is limited only by carbon assimilation; cf. Fatichi et al., 2014; but see Davi et al., 2009; Schiestl-Aalto et al., 2015). In another class of DVMs, such as forest succession models (also called 'patch' or 'gap' models, cf. Bugmann 2001), sink limitation is assumed to be the main process driving growth (Leuzinger et al. 2013), and water stress limitation is captured through an annual drought index calculated as an average over the growing season that reduces growth rates (Bugmann and Cramer 1998; Pausas 1999). In contrast to global DVMs, which typically are based on plant functional types rather than species (De Kauwe et al. 2015), forest succession models account for the inter-specific sensitivity to drought using species-specific parameters as a threshold of maximum drought tolerance. Nevertheless, they do not consider local adaptation to drought (i.e., intra-specific and intra-annual variability) and still are prone to considerable uncertainties regarding the drought tolerance parameters (e.g., Weber et al. 2008; Gutiérrez et al. 2016). In addition, the intra-annual growth pattern related to drought is not taken into account because in most models every month within the growing season has the same influence on the calculation of the annual drought index (Bugmann and Cramer 1998).

In the studies that focused on improving and applying succession models in Mediterranean-type ecosystems, drought effects were modeled by increasing the temporal resolution of the water balance submodel to a daily time step (Pausas 1998; Fyllas and Troumbis 2009). This modification imposed limitations to the general applicability of the models, particularly due to constraints on deriving accurate local daily time series data of weather variables (in contrast to widely available monthly time-series). Thus, there is scope for improving the modeling of drought impacts on tree growth in forest succession models without a strong increase in model complexity. In addition, reliable forest models incorporating data related to species- and site-specific growth responses are essential for forecasting the effect of climate change on species composition, and for improving management and conservation practices (Fontes et al. 2010; Sánchez-Salguero et al. 2015).

Simulating the effects of drought more mechanistically remains a challenge, regardless of the type of model considered (e.g., Gustafson et al. 2015). In the case of forest succession models, it requires the determination of robust growth functions by means of high temporal and spatial (i.e., on different individuals/populations) resolution measurements of growth and climate for a long time period, followed by skillful model simplification to make the approach tractable in long-term simulations.

Tree-rings are a potentially powerful source of data, as they allow for the investigation of a large amount of samples with an individual and annual resolution. While ring-width data are often used to evaluate the performance of forest models (Li et al. 2014), they have been rather neglected in the calibration phase or for deriving new functions (but see Guiot et al. 2014; Gea-Izquierdo et al. 2015). Tree-rings have been used to derive empirical growth-mortality functions and to calibrate growth response to temperature in DVMs (Rickebusch et al. 2007; Bircher et al. 2015). However, ring-width data have never been employed for improving processes at the intra-annual scale in forest models.

In the present study, we explore a novel approach to improve the simulation of drought effects on tree radial growth in a forest succession model while maintaining its structural simplicity. We define drought as insufficient soil water availability for tree growth, soil moisture being dependent on soil properties, precipitation and actual evapotranspiration. Specifically, we incorporate a forward modeling approach of tree-ring width, the Vaganov-Shashkin Lite model (VS-Lite, cf. Tolwinski-Ward et al. 2011) in the forest succession model ForClim (Bugmann 1996) to determine seasonal growth responses to drought for Scots pine (*Pinus sylvestris* L.) in sixteen sites that cover most of the environmental conditions of the species in Europe. Scots pine is a keystone species in many forest ecosystems and has a high importance in terms of forest economics, habitat conservation and biodiversity (Matias and Jump 2012). Being the most widespread conifer globally (Nikolov and Helmisaari 1992), its geographical distribution extends from the northern boreal regions, where growth is limited by growing-season low temperatures, to the southern continental Mediterranean forests, where a combination of summer drought and high temperature is the main limiting factor (Matias and Jump 2012). We (1) describe a methodology to consider the intra-annual variation in growth response to drought in forest succession models, and (2) investigate if intra-annual and site-specific growth strategies should be included in models that aim to forecast forest dynamics at large spatial scales.

Materials and methods

Calibration of the growth responses to drought

Study sites

We re-analyzed published tree-ring width datasets from 16 sites in different European biogeographical regions: the Iberian Central System, the Iberian Mountains, the northern, central and southern Alps, the Swiss Plateau, and the Jura Mountains (Fig.1). Distributed across Switzerland, Spain, and northern Italy, these sites covered a wide climatic gradient in terms of temperature and precipitation (Table 1). The three Iberian sites were characterized by relatively high annual precipitation but dryer summer periods compared to the sites in the inner Alpine valleys (Fig.1).

Ring-width datasets

For nine sites, ring-width data were obtained from Lévesque et al. (2014) and Martin-Benito et al. (2013) (see these two publications for details of the sampling methods) while data for the remaining seven sites were downloaded from the International Tree-Ring Data Bank (ITRDB, <http://www.ncdc.noaa.gov/paleo/treering.html>; last accessed on 11/08/2015; Table 1). Each dataset included between 15 and 48 trees. For each site we built a ring-width index chronology from individual raw ring-width series. First, individual series were detrended to remove non-climatic low-frequency variability (most likely due to tree aging and stand dynamics) using a spline function with a 50% variance cut-off equal to two-thirds of the series length, using the package *dplR*

(Bunn 2008) in R (R Core Team 2014). Second, site chronologies were derived by combining all the individual residual series using a robust biweight estimation of the mean. Finally, we restricted the data to the time period for which instrumental meteorological data were available (see description below; Table 1).

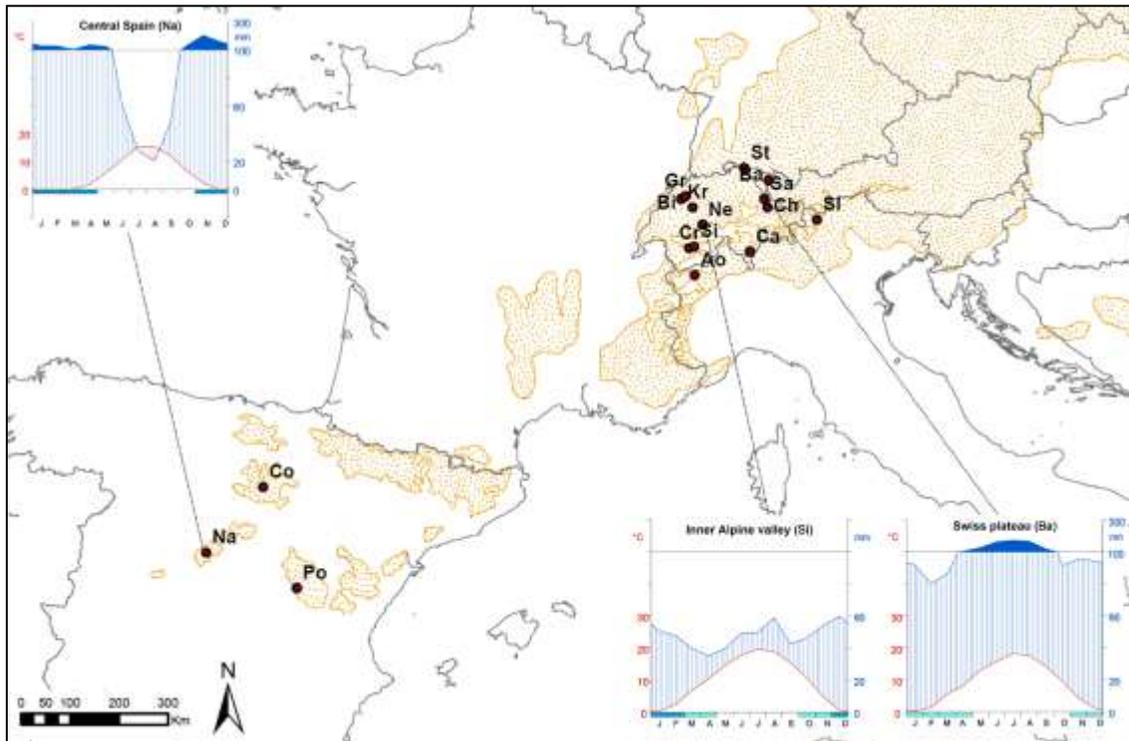


Fig. 1: Location of the study sites distributed across Switzerland, northern Italy and Spain. The brown stippled area shows the current distribution range of Scots pine (<http://www.euforgen.org/distribution-maps/>). Climate diagrams are given for three sites that are representative of the different biogeographical regions; red and blue areas indicate dry and wet conditions respectively. Note the change in the scale of precipitations above 100mm.

Forward tree-ring based modeling using the VS-Lite model

The VS-Lite forward model of tree-ring growth is a simplified version of the full Vaganov-Shashkin model (Vaganov et al. 2006), which operates with daily input climatic variables and >30 parameters for simulating secondary growth of xylem and anatomical features of annual rings (Vaganov et al. 2011). In VS-Lite, the division of cells and the kinetics of xylem formation is not simulated explicitly, but the representation of the principle of limiting climatic factors remains (see Tolwinski-Ward et al. 2011 for development and a detailed description). Using site latitude, monthly mean temperature and monthly accumulated precipitation as inputs, VS-Lite estimates tree-ring width through a scaled proxy for climatological insolation (gE) and nonlinear

responses to temperature (gT) and soil moisture (gM). Both gM and gT are controlled by four adjustable parameters ($T1$, $T2$, $M1$ and $M2$). Two of them ($T1$ and $M1$) represent the temperature and moisture lower limits below which growth is not possible. The other two ($T2$ and $M2$) are thresholds above which growth is not limited anymore. Partial values of growth rates are calculated with a ramp function between these parameters (Tolwinski-Ward et al. 2011, their Eq.1). Based on the principle of the most limiting factor, an overall monthly growth rate (Gr) is calculated as the minimum between gT and gM , modulated by gE . Finally, after aggregating monthly Gr over a time window controlled by two parameters (I_0 and I_f , integer values indicating the months since January) into an annual Gr , the annual time-series of Gr is standardized to obtain a simulated tree-ring width chronology with mean 1.

We modified the VS-Lite model as follows. First, the linear growth response to temperature used in VS-Lite (see Tolwinski-Ward et al. 2011) was changed to an S-shaped Gompertz function. This equation was found to be highly appropriate to fit growth data due to its flexibility and asymmetrical shape (Rossi et al. 2003). Furthermore, the position of the inflection point is controlled by only one parameter (see description below and further details in Zeide 1993), which contributes to maintain the model's structural simplicity. Thus, gT was calculated as:

$$gT = A * \exp \left[- \exp \left[\frac{T2^* * \exp(1)}{A} * (T1 - T_m) + 1 \right] \right] \quad (1)$$

where A represents the asymptote of the curve (in our case $A=1$, indicating no limitation by high temperature; cf. Tolwinski-Ward et al., 2011), and T_m the mean temperature over the month of interest. $T1$ denotes the temperature limit below which growth is not possible, as in the original VS-Lite, and $T2^*$ is a parameter reflecting the shape of the Gompertz curve (see Fig. A1). Second, to better fit with ForClim, we replaced the original 'leaky bucket' model in VS-Lite (Huang et al. 1996) by the water balance model included in ForClim (see description below) to calculate soil moisture at monthly time step (SM_m). A modified version of the Thornthwaite and Mather (1957) model was used for estimating monthly potential and actual evapotranspiration and thus for deriving monthly soil moisture (details in Bugmann and Cramer 1998; but see van der Schrier et al. 2011 for possible over-estimates of extremely warm temperatures on PET with the Thornthwaite and Mather model). In contrast to the 'leaky bucket' model, this model considers for site-specific differences in soil water holding capacity ('bucket size' input variable of ForClim; kBS in mm; see Table 1). For each site, instead of deriving only one pair of $M1$ and $M2$ parameters, we optimized independent sets for each climatic season to account for the intra-annual variability in growth responses to drought: in winter (December, January, and February – parameters $M1_{WI}$ and $M2_{WI}$), spring (March, April, and May – $M1_{SP}$ and $M2_{SP}$), summer (June, July, and August – $M1_{SU}$ and $M2_{SU}$), and fall (September, October, and November – $M1_{FA}$ and $M2_{FA}$). These parameters were expressed as percentages of the site-specific bucket size.

Table 1

Scots pine sites used for the study, sorted from the driest to the wettest according to the water balance values. The period indicates the time series that overlap between available meteorological and tree-ring data. Mean annual temperature and precipitation sum are calculated over the specified period. The last column indicates the source of the tree-ring width series (ITRDB code; a=from Lévesque et al. 2014; b=from Martin-Benito et al. 2013).

Site	Country	Site code	Biogeographical Region	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	Period	Mean annual temperature (°C)	Mean annual precipitation sum (mm)	Water balance ¹ (mm)	Bucket size ² (mm)	Tree-ring data or ITRDB code
Sion	CH	Si	Central Alps	46°18'07"	7°34'12"	540	1905-2007	9.2	574	-265	120	Swit188
Silandro	IT	Sl	Central Alps	46°38'02"	10°47'52"	1145	1941-2011	7.1	500	-167	128	SC ^a
Poyatos	SPA	Po	Iberian Mountains	40°17'00"	1°59'00"	1150	1960-2006	10.3	924	-155	120	PO ^b
Covaleda	SPA	Co	Iberian Mountains	41°58'54"	2°52'09"	1750	1943-1983	5.9	886	-108	100	Spa047
Aosta	IT	Ao	Central Alps	46°38'02"	10°47'52"	1150	1931-2006	7.8	701	-107	82	AO ^a
Cransmontana	CH	Cr	Central Alps	46°16'10"	7°26'12"	1400	1931-1997	5.7	947	-30	186	Swit284
Chur	CH	Ch	Central Alps	46°55'58"	9°31'36"	600	1900-2009	9.0	851	-7	100	Swit276
Navacerrada	SPA	Na	Iberian Central System	40°46'59"	4°01'59"	1890	1946-2008	6.4	1324	27	120	Spa071
Kranichal	CH	Kr	Swiss Plateau	46°59'59"	7°34'12"	615	1910-1976	8.5	990	80	100	Swit178
Steckborn	CH	St	Swiss Plateau	47°39'36"	8°59'46"	535	1959-2011	8.8	1108	116	82	ST ^a
Grenchen	CH	Gr	Jura Mountains	47°12'17"	7°23'59"	590	1959-2011	8.8	1302	127	72	GR ^a
Sargans	CH	Sa	North Swiss Alps	47°04'52"	9°28'09"	700	1900-1960	8.4	1240	200	159	SA ^a
Neuhaus	CH	Ne	North Swiss Alps	46°40'58"	7°48'32"	620	1931-2011	8.6	1207	205	59	NE ^a
Biel	CH	Bi	Jura Mountains	47°09'57"	7°16'06"	750	1959-2009	7.9	1449	224	119	BF ^a
Balgach	CH	Ba	Swiss Plateau	47°24'45"	9°36'25"	600	1900-1996	7.7	1398	360	148	BA ^a
Camorino	CH	Ca	Southern Alps	46°09'15"	9°00'24"	580	1963-2000	11.1	1923	685	100	Swit228

¹ Water balance was calculated as the average over the available time series of the precipitation sums minus potential evapotranspiration (PET) from April to September (Table 1). PET was computed according to Thornthwaite and Mather (1957). A negative water balance indicates that PET exceeded precipitation, denoting moisture deficit.

² The values of the bucket size are derived from Lévesque et al. (2014), Martin-Benito et al. (2013), and from the digital map of soil capacity of Switzerland available from the Swiss Federal Office of Agriculture (<http://www.blw.admin.ch/dienstleistungen/000334/000337/index.html>)

The MATLAB[®] source code of the original VS-Lite model (v2.3, Tolwinski-Ward et al. 2013) is freely available online at the National Oceanic and Atmospheric Administration's Paleoclimatology World Data Center (<ftp://ftp.ncdc.noaa.gov/pub/data/paleo/softlib/vs-lite/>, accessed on 12/02/2015). The modified VS-Lite version was re-coded and tested in R; it can be found in the electronic archive available at <https://doi.org/10.1594/PANGAEA.857289>.

Optimization of the VS-Lite parameters

We calibrated the modified VS-Lite model for each site by optimizing the set of 10 parameters ($T1$, $T2^*$ and the four seasonal pairs of $M1$ and $M2$) to maximize the correlation coefficient between the simulated and observed residual ring-width chronologies using differential evolution algorithms (R-package DEoptim; cf. Mullen et al. 2011). These algorithms use a stochastic and parallel direct method, which is particularly suitable for finding a global optimum for functions of real-valued parameters (Storn and Price 1997). The parameter $T1$ was constrained between 3 °C and 8 °C based on the analyses of Scots pine ring width series by Breitenmoser et al. (2014). The range of $T2^*$ was fixed between 0.1 and 0.4 (unitless; see Fig. A1). The four seasonal pairs of $M1$ and $M2$ were optimized between 0 and 100 % of the site-specific value of soil water holding capacity (kBS). Since several dendroecological studies demonstrated that the annual radial growth of Scots pine is influenced by previous year's climatic conditions (Oberhuber et al. 1998; Gruber et al. 2010), especially in fall (Sánchez-Salguero et al. 2015), and that xylogenesis of Scots pine is still possible after September, we selected a growth season integration window starting from September of the previous year ($I_0=-4$) to December of the current year ($I_f=12$). Following Tolwinski-Ward et al. (2011), Gr was then calculated to obtain the simulated annual tree-ring width index.

Meteorological data

We obtained monthly temperature and precipitation data from meteorological stations near each Scots pine sampling site. Climate data for Switzerland were obtained from the Swiss Federal Office for Meteorology and Climatology (MeteoSwiss) and were available for periods between 40 and 110 years (Table 1). When the difference in elevation between the sampling site and the meteorological station was higher than 100 m, we adjusted the climatic series using site-specific elevational lapse rates. For northern Italy, data were derived from meteorological stations nearby the two sampling sites (see details in Lévesque et al. 2014). For the three sites in Spain, data were acquired from meteorological stations monitored by the Spanish National Meteorological Agency (AEMET). Data were missing only in Covaleda (station Covaleda Castejon); gaps were consequently filled by linear regression using data from three stations located nearby (Vinuesa-El Quintanar at ca. 7 km, Vinuesa at ca. 11 km, Palacios de la Sierra at ca. 20 km) and adjusted with altitudinal lapse rates (Crespo and Gutierrez 2011).

The ForClim model

ForClim is a forest succession model that simulates stand-scale dynamics on small independent forest patches (Bugmann 1996). The model was initially developed for central European conditions, but it can be applied in most temperate forests (Bugmann and Solomon 2000). ForClim has been used in many studies for different purposes, such as investigating natural forest composition across climatic gradients (Bugmann and Solomon 2000) or for projecting future forest dynamics under changing climate and different management scenarios (Rasche et al. 2013; Mina et al. 2017). Three modular submodels – WEATHER, WATER, and PLANT – are run in combination to capture the influence of climate and ecological processes on establishment, growth and mortality of cohorts (i.e., trees of the same species and age) while a fourth submodel – MANAGEMENT – allows for the application of a wide range of silvicultural treatments such as clear-cutting, thinning or planting (Rasche et al. 2011). In the WEATHER and WATER submodels, bioclimatic indices are calculated based on a stochastic weather generator using long-term monthly temperature, precipitation and bucket size. The calculated indices serve as internal input variables for the PLANT submodel, where establishment, growth, and mortality are simulated. Tree growth is based on the principle of growth-limiting factors where species-specific maximum growth rates are reduced depending on the extent to which environmental factors (e.g., degree-day sum, light, nitrogen and soil moisture) are at suboptimal levels (Moore 1989; Bugmann 2001).

The species-specific influence of drought on tree growth is expressed by a soil moisture growth-reducing factor (*SMGF*). This scalar is linearly related to the drought experienced by the species; for evergreen species it is based on an annual soil drought index (*uDrAnn*) and a species-specific drought tolerance parameter (*kDrTol*; cf. Bugmann, 1994).

$$SMGF' = \sqrt{\max(0, 1 - uDrAnn/kDrTol)} \quad (2)$$

The annual soil drought index is obtained by averaging the corresponding monthly indices (Bugmann and Cramer 1998) over the growing season, which is expressed as those months with mean temperature above a development threshold (kDTT equal 5.5°C, cf. Bugmann and Solomon 2000). The annual drought index further serves to reduce the maximum height of each species at a given site due to unfavorable climatic conditions (in addition to low temperatures that are expressed as the annual sum of degree days; Rasche et al. 2012).

Modifications of ForClim

A new annual *SMGF* based on the optimized sets of seasonal *M1-M2* parameters was implemented:

$$SMGF = \frac{1}{N_{kDTT}} * \sum_{\substack{Dec \\ (T_m \geq kDTT) \\ m=Jan}} \max \left\{ \min \left[\frac{SM_m - (kBS * M1_{seas})}{(kBS * M2_{seas}) - (kBS * M1_{seas})} ; 1 \right] ; 0 \right\} \quad (3)$$

where SM_m is monthly soil moisture, $M1_{seas}$ and $M2_{seas}$ are the values of the optimized parameters for the corresponding season, kBS the site-specific soil water holding capacity ('bucket size', in mm), T_m is mean monthly temperature, and N_{kDTT} is the number of months where mean temperature is above $kDTT$. $SMGF$ ranges between 0, when growth is fully inhibited by drought, and 1, when there are no growth limitations due to drought. For consistency with the modified version of VS-Lite, the parameters $M1_{seas}$ and $M2_{seas}$ were expressed in percentage of bucket size (kBS).

We also modified the relationship between drought and simulated maximum tree height (see details and equations in Appendix B). As the $M1$ and $M2$ parameters were derived from tree-ring data, which are typically obtained from sampling adult trees, we did not modify the currently modeled effect of drought on regeneration (i.e., drought establishment filter, cf. Didion et al. 2009).

Sites and data used for model evaluation

We selected six pure Scots pine stands - three in Pfywald (Switzerland) and three in Valsaín (Spain) - for evaluating the performance of the modified model against long-term inventory data (Fig. 1 and Table 1). The Pfywald stands are located in the central part of the Valais valley (elevation 620 m a.s.l.) at approximately 20 km from the weather station Sion. This valley experiences a strong rain shadow by the surrounding mountains, and thus it can be drier than mountain areas in the Mediterranean region (Rebetez and Dobbertin 2004). The Valsaín forest is located in the Iberian Central System and is among the most productive Scots pine areas in Spain (Montes et al. 2005). Here, three stands (elevation ranging between 1500 and 1700 m a.s.l.) were selected at a distance between 4 and 8 km from the weather station Navacerrada.

Monthly climate data from Sion and Navacerrada were used for deriving long-term means of temperature and precipitation. As the stands in Valsaín were located at a lower elevation than the weather station Navacerrada, we adjusted the temperature and precipitation values using annual temperature and precipitation lapse rates calculated from the closest E-OBS 0.25° grid point (van den Besselaar et al. 2011).

In Pfywald, we obtained inventory records from an experiment established in 1965 that included thinning treatments with three different intensities – light, medium and heavy. The dataset included nine subsequent inventories where stem numbers and DBH of trees were recorded before and after thinning. The three treatments had an initial basal area between 38 and 40 m²/ha and were characterized by a high stem density and DBH distribution skewed towards low diameters (mean diameter between 8 and 9 cm). A complete description of the site, the experimental design

of the plots, and the thinning regimes is available in Giuggiola et al. (2013) and Elkin et al. (2015).

The Valsaín forests has been managed – mainly for timber production – since at least 1889, and quantitative inventory data are available since 1941 (Montes et al. 2005). Inventories carried out in 1941, 1948, 1958, 1965, 1989 and 1998 recorded the number of trees by 10-cm diameters classes for different management blocks. The three stands used here – no. 134, 143 and 243 – had an initial basal area of 41.5, 56.6 and 27.7 m²/ha, respectively. They differed strongly in terms of stem density and DBH distribution. Data of the silvicultural treatments were derived from the management plans and their revisions (see Montes et al. 2005 for a comprehensive description). Additional information on the inventory methods and data structure for the stands used in this study is provided in Appendix B.

Simulation setup and assessment of the prediction accuracy of ForClim

At each of the six stands, ForClim was initialized with data from the first inventory, and simulations were run until the year of the last inventory (simulation period of 45 years in Pfywald and 55 years in Valsaín; see Tables B1 and B2). As in all the stands the only species present was Scots pine, we did not allow for establishment or growth of other species in the simulations. Detailed descriptions of the methodology used for model initialization, additional model inputs, and implementation of management interventions are reported in Appendix B. We performed simulations with three different model versions: (1) ForClim v3.3, using the original approach for simulating drought impact on growth; (2) ForClim v3.3-LOC, the modified version using site-specific (i.e., local) optimized sets of *M1* and *M2* parameters for the calculation of *SMGF* (parameters from Sion for the site Pfywald and from Navacerrada for the site Valsaín); and (3) ForClim v3.3-AVG, which used seasonal *M1* and *M2* parameters averaged over all calibration sites. The comparison of simulation results using the latter two versions allowed us to assess the consequence of considering local adaptation to site-specific drought conditions.

For evaluating the goodness-of-fit of the simulation results, we compared simulated and measured basal area and stem numbers per hectare for each stand at each inventory, and calculated the relative root mean square error (RMSE) and the percent bias over the number of inventory observations (see equations in Mina et al. 2017). As the inventory data had a calliper limit of 4 cm in Pfywald and 10 cm in Valsaín, we only considered trees above these thresholds for calculating the indices.

Results

Simulated seasonal tree-ring responses to drought

Using optimized site-specific, seasonal parameter sets, the modified version of VS-Lite accurately estimated the year-to-year variability in ring-width indices (Fig. 2) at all 16 sites (correlation coefficients between observed and simulated ring-width indices ranged between 0.35 and 0.65; $p < 0.01$; Table A1, Fig. A3). The modeled mean growth response of Scots pine to both temperature (gT) and soil moisture (gM), however, differed among sites (Fig. A4). For instance, at the site Navacerrada (Fig. 2a), Scots pine growth was limited by low temperatures ($gT < gM$) except between July and September, when drought was the main limiting factor ($gT > gM$), particularly in August ($gM = 0$). In contrast, at Sion, which is located at low elevation, radial growth was limited by temperature only between November and April (Fig. 2b). The inter-site variability of the $M1$ and $M2$ parameters was considerable for all seasons ($M1$: 83, 93, 92, and 62 % for spring, summer, fall and winter respectively; $M2$: 81, 92, 89 and 75%; Fig. 3, Table A1). For 15 out of 16 sites in spring and summer and for all sites in fall, $M2$ values were quite close to $M1$ values of the same season (see Table A1), revealing a quasi-binary growth response to drought (i.e., $gM = 0$ or 1; Fig. 3).

Based on the optimized parameters, seasonal growth responses to drought were calculated as a function of available water, expressed as a percentage of bucket size (Fig. 3). The responses calculated using $M1$ and $M2$ values that were averaged over all sites (Fig. 3, Table A2) indicated distinct differences between the four seasons. During the spring months, soil moisture above 70% of bucket size was not limiting Scots pine growth, whereas during summer and fall this percentage had to be >58 and $>55\%$, respectively. In spring, summer and fall, the curves exhibited a steep peak of the growth response, similarly to the site-specific curves, while winter showed a gradual increase between 27 and 52% of bucket size (Fig. 3).

For most sites, the difference in growth responses between the seasons was larger than the difference between seasons when the mean curves were considered (Table A1 and A2). For example, if during spring simulated soil moisture fell below 66 and 71% of bucket size for Navacerrada and Sion, respectively, growth was fully limited by drought ($gM=0$). In contrast, in Sion drought was not limiting at soil moisture values above 27% of bucket size during the summer, while in Navacerrada soil moisture below 82% of bucket size caused growth limitations. In winter, the values of $M1$ and $M2$ were lower than for the other seasons, but this did not noticeably impact simulated growth, as the main limitation in winter was low temperature at all sites.

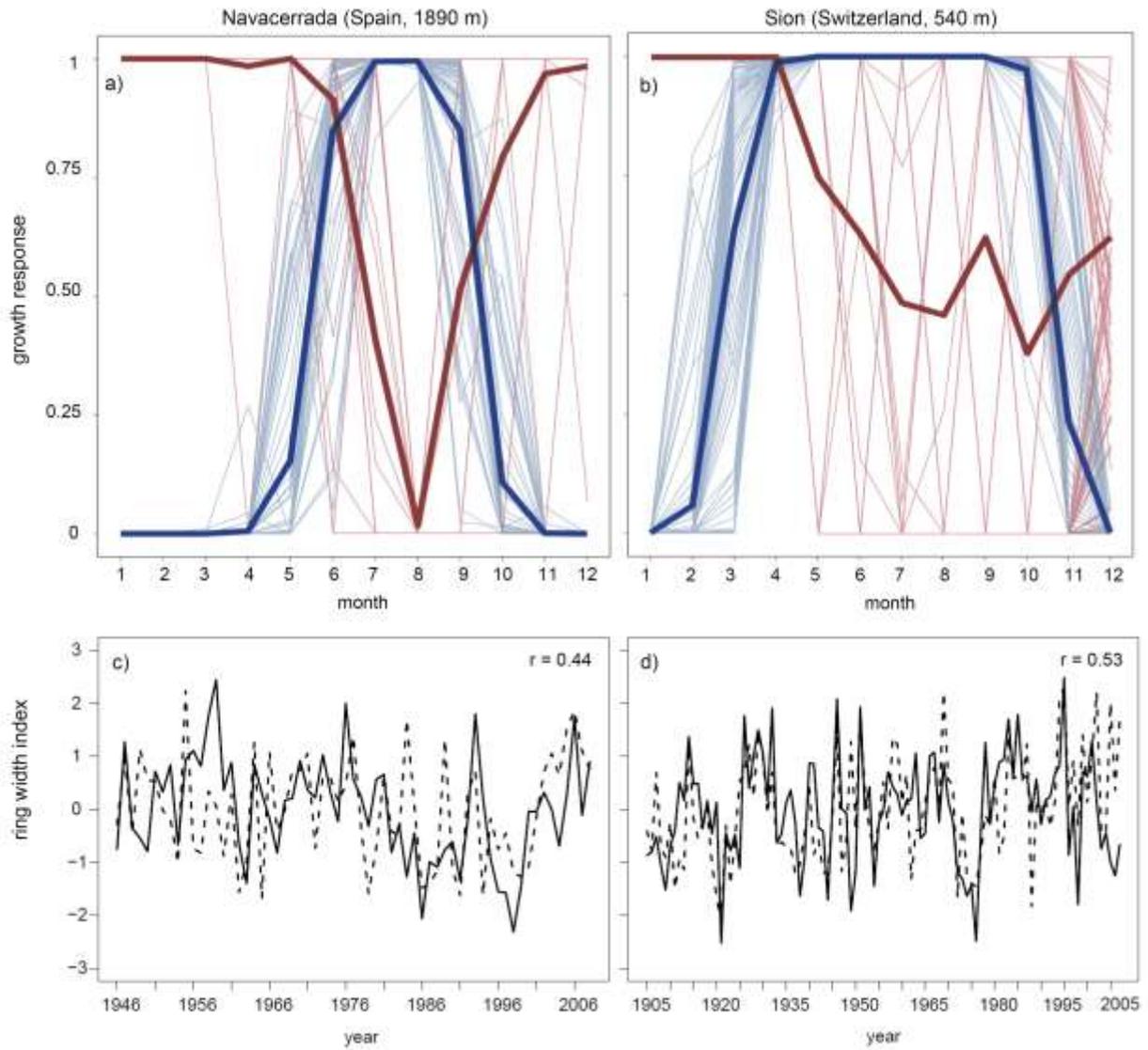


Fig. 2: Upper panels: monthly growth response curves for temperature (blue lines) and soil moisture (red lines) simulated with the modified version of VS-Lite in Navacerrada and Sion. The thin lines represent the curves obtained for each year included in the time series (Table 1) while the thick lines show the long-term means. Lower panels: observed (solid) and simulated (dashed) ring-width indices for Navacerrada ($r = 0.44$, $p < 0.01$) and Sion ($r = 0.53$, $p < 0.01$).

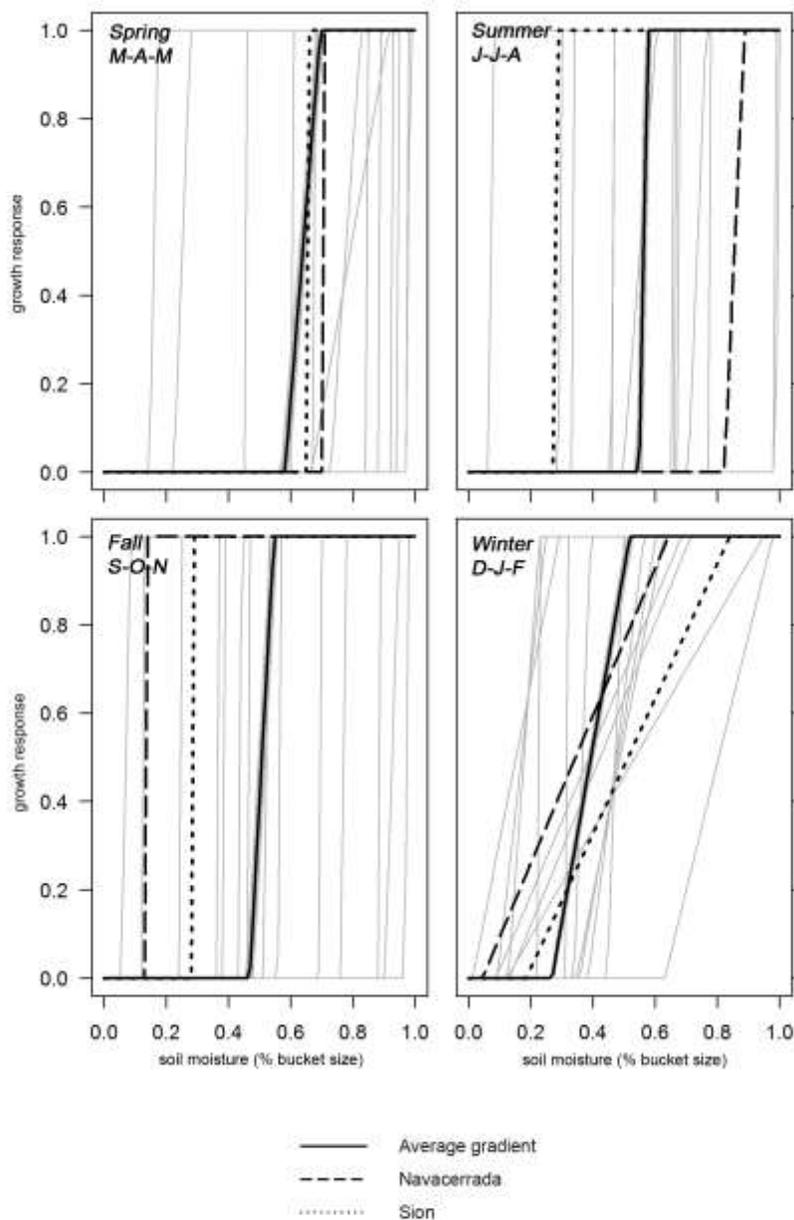


Fig. 3: Growth response to simulated soil moisture for the four seasons. The black solid lines show the growth response functions computed using the average of M1 and M2 parameters over all sites and the grey areas their 95% confidence interval calculated using bootstrap functions (999 resamplings). The black dashed and dotted lines represent the growth response to drought derived from site-specific moisture parameters for Navacerrada and Sion, respectively. Thin grey lines represent the growth response for the remaining 14 sites. Site-specific and averaged values of seasonal M1 and M2 are detailed in Tables A2 and A3.

Evaluation of forest succession model performance

A comparison of the basal area and stem numbers observed and simulated by the three model versions revealed that the new implementation of drought limitation markedly improved the short-term prediction accuracy of ForClim for managed Scots pine stands (Figs. 4 and A5).

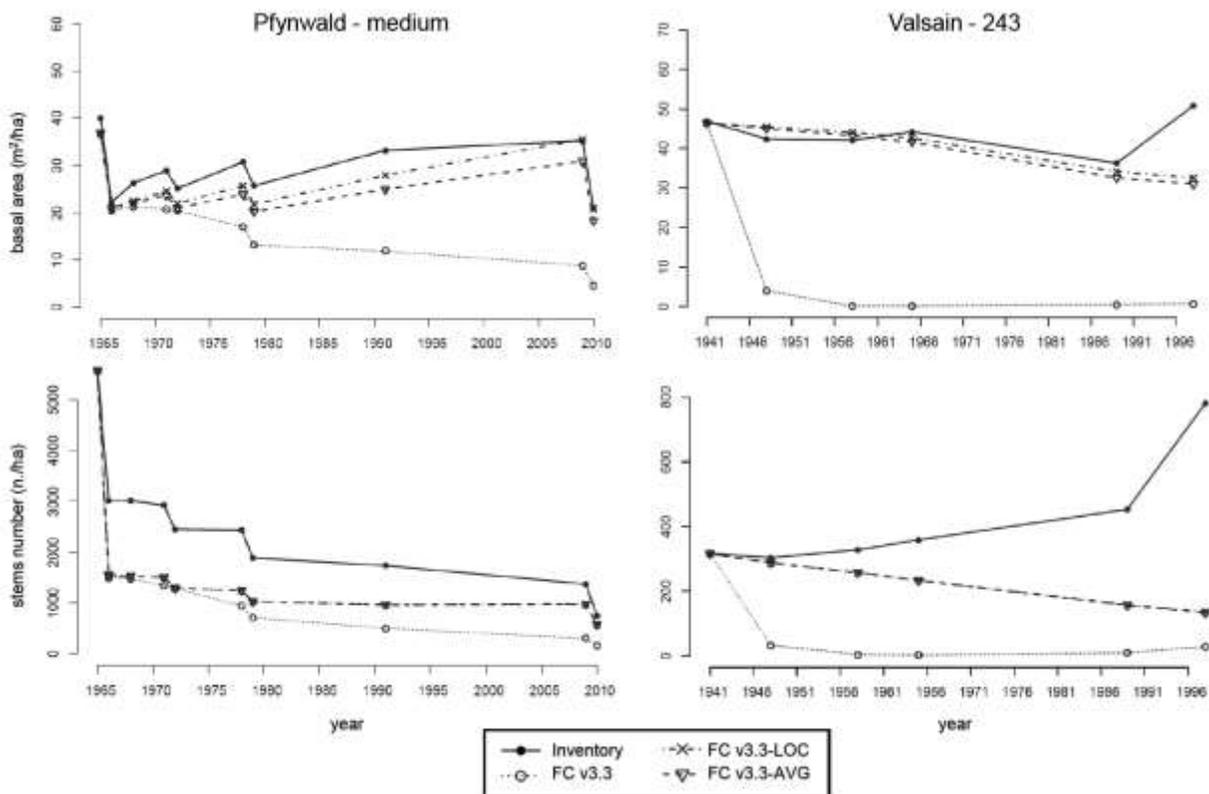


Fig. 4: Stand basal area (m²/ha) and stem numbers (per ha) measured (solid lines) and simulated by three ForClim versions (dashed lines) in the medium thinning experiment of Pfywald (Left) and in the stand 243 from Valsain (Right). Results for the remaining four evaluation stands are displayed in Fig. A5.

In Pfywald, simulations with both new model versions showed lower bias and RMSE than v3.3. The percentage bias of v3.3-LOC and v3.3-AVG was lower for basal area, with simulations by v3.3-LOC being even closer to observed data for the medium and heavy thinning experiment (respectively -10.4% and -11.4% with v3.3-LOC; -15.8% and -18.3% with v3.3-AVG). Better results were also obtained for the light thinning (+5.8% with v3.3-LOC; -0.4% with v3.3-AVG; cf. Table 2 and Figs. 4 and A5). The percentage bias for stem numbers was almost identical between the two new ForClim versions, although v3.3-AVG showed lower bias than v3.3-LOC in all three stands (maximum difference between v3.3-LOC and v3.3-AVG was 0.5% in the heavy treatment; Table 2).

For instance, for the medium thinning experiment that was initialized with 5578 trees/ha with a mean DBH of ca. 9 cm and a reduction of stem number by ca. 50% in the first thinning (Fig. 4, left panels), basal area and stem numbers simulated by ForClim v3.3 decreased strongly over time, yielding to an underestimation of both variables at the end of the simulation (-39% and -45%, respectively). In contrast, basal area simulated with v3.3-LOC agreed well with empirical data towards the end of the period (2009 and 2010) and exhibited a higher increment than v3.3-AVG. Both versions (v3.3-LOC and v3.3-AVG) produced satisfactory results for basal area. In comparison with ForClim v3.3, the bias between simulated and measured basal area was reduced by 73% and 60% with v3.3-LOC and v3.3-AVG, respectively.

The annual *SMGF* (Eq. 3) calculated with v3.3-LOC for Pfywald was higher than the one estimated with v3.3-AVG (average and standard deviation over the simulation period: 0.67 ± 0.02 vs. 0.40 ± 0.01), while with v3.3 it was much lower (0.35 ± 0.01). Nonetheless, the two new model formulations still underestimated stem numbers to some extent (bias for v3.3-LOC and v3.3-AVG decreased to -35% instead of -45% with v3.3; see Table 2).

The higher prediction accuracy of the two new ForClim versions in terms of basal area and stem numbers was more evident in Valsaín, especially for stand 243 (Fig. 4 and A5). Early in the simulation, ForClim v3.3 yielded a steep decline of basal area and stem numbers that was not observed in the inventory data (bias = -80% and -84%, respectively). This anomalous behavior was due to the fact that initial tree height given as model input exceeded the site- and species-specific maximum height (*Hmax*) calculated by the model, which was exceedingly low due to an underestimated *SMGF*. As a consequence, stress-induced mortality was simulated for the trees belonging to these cohorts. In contrast, simulations with the two new model versions did not predict such die-off and simulated a highly accurate development of basal area (bias = -7% and -9% with v3.3-LOC and v3.3-AVG, respectively) except for the last inventory point. Although simulations with both versions showed a decrease in stem numbers over time while the inventory data revealed the opposite trend, this underestimation was much lower than with ForClim v3.3 (bias in stem numbers was reduced by 46%; Table 2). For all the three Valsaín stands, we did not observe differences between ForClim v3.3-LOC and v3.3-AVG regarding stem numbers, although v3.3-LOC performed slightly better for basal area (Table 2).

Similarly as for Pfywald, the annual *SMGF* calculated with v3.3-LOC in all Valsaín stands was higher than with v3.3-AVG (average 1941-1999 with standard deviation: 0.63 ± 0.02 vs. 0.54 ± 0.01 respectively), while with the previous model version the calculated values was considerably lower (0.43 ± 0.01).

In general, in all six stands with the exception of the light thinning treatment in Pfywald, bias between simulated and observed basal area was lower with v3.3-LOC than with v3.3-AVG. Regarding stem numbers, there were almost no differences between simulations with v3.3-LOC and v3.3-AVG (differences in bias between 0.5 and 0.1%), although v3.3-AVG performed slightly better in five out of six stands (Table 2).

Table 2 Percentage bias (Bias; in %) and relative root mean square error (RMSE; in %) of basal area and stem numbers simulated with the standard ForClim version (FC v3.3), the ForClim version using local and averaged M1 and M2 parameters (FC v3.3-LOC and FC v3.3-AVG, respectively) compared with measured values from forest inventories. The column Stand indicates the thinning treatment in Pfywald (e.g., “light” means stand with light thinning treatment, etc.) or the management block in Valsain.

Location	Stand	Basal area						Stem Numbers					
		FC v3.3		FC v3.3-LOC		FC v3.3-AVG		FC v3.3		FC v3.3-LOC		FC v3.3-AVG	
		Bias	RMSE	Bias	RMSE	Bias	RMSE	Bias	RMSE	Bias	RMSE	Bias	RMSE
Pfywald	light	-25.9	28.8	5.8	6.5	-0.4	0.5	-21.2	23.5	-8.6	9.5	-8.4	9.3
Pfywald	medium	-39.3	43.6	-10.4	11.5	-15.8	17.6	-45.1	50.1	-35.4	39.3	-35.3	39.3
Pfywald	heavy	-45.8	50.9	-11.4	12.7	-18.3	20.3	-11.4	12.6	14.1	15.6	13.6	15.1
Valsain	134	-88.1	105.7	-44.4	53.3	-46	55.2	-83.4	100.1	-43	51.6	-42.9	51.4
Valsain	143	-42.3	50.8	-21.5	25.7	-23.1	27.7	-33.6	40.3	-23	27.6	-22.7	27.3
Valsain	243	-80.2	96.3	-6.6	8	-8.7	10.4	-84.5	101.4	-45.4	54.5	-45.5	54.6

Discussion

Based on a modified forward model of ring-width growth (VS-Lite) calibrated with dendrochronological data, we implemented intra-annual growth responses to drought of Scots pine in a forest succession model without increasing its structural complexity. An evaluation of model performance against inventory data revealed decreased bias and RMSE when intra-annual responses were considered in the calculation of the growth reduction due to drought.

Potential and limits of using a tree-ring based forward modeling approach to assess intra-annual growth responses to drought

The main advantage of the forward model of ring-width was its ability to transform the climate signal into a tree-ring chronology, thus allowing model parameterization and validation using measured ring-width series. We used a modified version of the VS-Lite model, which had already shown high potential for exploring intra-annual growth responses to climate for several species and hundreds of sites (Tolwinski-Ward et al. 2011; Evans et al. 2013; Breitenmoser et al. 2014). As highlighted by the high correlation values between simulated and measured ring-width chronologies – comparable to those obtained with physiologically based models (Rathgeber et al. 2005; Li et al. 2014) – VS-Lite produced realistic inter-annual variability in ring-widths at the local scale (i.e., associating observed tree-ring chronologies with meteorological data obtained for a specific site; cf. Tolwinski-Ward et al., 2013).

For Scots pine, the modified version of VS-Lite was able to reproduce realistic intra-annual growth responses to climate. At some sites, e.g., in Navacerrada, the overall growth response followed a bimodal pattern with a strong dependency of ring-width to climate in spring and fall but not in summer, which is characterized by intense drought and a near-complete cessation of growth. This pattern is characteristic of some evergreen species in Mediterranean climates (Cherubini et al. 2003; Camarero et al. 2010) and was also observed in Scots pine (Primicia et al. 2013). At sites where autumn rainfall may not be sufficient to refill the soil, e.g., in Sion, the simulated growth response started to decrease in late spring (Eilmann et al. 2011).

The high inter-seasonal variability in the averaged $M1$ and $M2$ parameters reflects the ability of VS-Lite to reproduce the strategy of Scots pine to cope with drought (Irvine et al. 1998; Llorens et al. 2010), illustrating the importance of the timing of drought within the year for tree growth. In dry inner-Alpine valley (e.g., Sion) the lowest percentage of soil moisture under which growth is not limited ($M2$) was lower in summer than in spring (28% vs. 66%), suggesting that water deficit in spring reduces Scots pine growth more strongly than in summer. This is in line with studies that emphasized the dependence of ring width on the duration and rate of cell production in the early growing period (without drought; Cuny et al. 2012; Michelot et al. 2012), and the great importance of spring for root and shoot growth of Scots pine (Oberhuber et al. 1998; Rigling et al. 2002; Eilmann et al. 2011). In Navacerrada, the $M1$ and $M2$ parameters for spring were similar to those in Sion, but their values for summer were much higher. As little precipitation occurs in July and August in Navacerrada, the simulated growth response during these months is close to null. However, trees growing in Navacerrada may benefit from high precipitation in fall, as shown by the peak of growth response in September and the low values of $M1$ and $M2$ for that season (Fig. 2b).

The large inter-site variability in modeled $M1$ and $M2$ parameters may arise from differences in environmental conditions between sites and/or in different drought tolerance among populations due to local adaptation and phenotypic plasticity (Schütt and Stimm 2006; Benito Garzón et al. 2011; Taeger et al. 2013; Sánchez-Salguero et al. 2015). Across sites, Scots pine is known to adjust its hydraulic system and phenology to the specific moisture conditions to avoid drought or at least reduce its vulnerability (Berninger 1997; Martinez-Vilalta et al. 2009). We did not find, however, a clear relationship between both parameters and the climatic characteristics of the sites investigated. The high variability may further arise from the different sampling designs among studies, as climate-growth relationships depend on tree size and social status (Martín-Benito et al. 2008; Merian and Lebourgeois 2011).

Finally, detecting significant changes in $M1$ and $M2$ parameters along geographical and environmental gradients would require the use of an appropriate and consistent methodology and the consideration of a higher number of sites. Further studies to study the relationship between climate and parameter estimates may be beneficial in this context. Because of the large inter-seasonal and inter-site variability in moisture parameters (Fig. A2), our study highlights the need of averaging procedures using (i) hundreds of optimization iterations, (ii) long-term data (e.g.,

time series beyond 100 years), and (iii) as many sites as possible along a large environmental gradient. The latter point is key as the response of growth to drought was quasi-binary (due to very close $M1$ and $M2$ values; Table A1) for most of the sites and seasons, which is not biologically realistic if we use climatic data at monthly resolution. This behavior was due to the fact that we only considered the high frequency in the ring-width chronology to maximize the inter-annual variability in the residuals of the series.

Implementing intra-annual growth response to drought in the forest succession model ForClim

Enhancing the simulated impact of drought in forest succession models can be achieved either by integrating more ecophysiological and ‘mechanistic’ components (e.g., Gustafson et al. 2015), or by implementing better empirical functions that are derived from long-term observations such as tree-ring data. We included intra-annual growth responses to drought without increasing the structural complexity, calibration efforts or computation time of a forest succession model. Although processes that might be important at small temporal and spatial scales (e.g., stomatal conductance) are not included, this level of detail may not need to be represented in models that are built for long-term projections, thus avoiding the need for an extensive site-specific parameterization, as is often the case with more complex physiological models (e.g., Grant et al. 2006). This compromise renders forest succession models suitable for exploring the future long-term dynamics of mixed-species stands in response to climate change along environmental gradients, and for evaluating the suitability of management practices (Lindner et al. 2000; Rasche et al. 2013). In addition, ForClim – and most similar succession models (Bugmann 2001) – is based on the principle of growth-limiting factors (Moore 1989), which simplifies its coupling with a forward model of ring-width such as VS-Lite.

Simulations performed for water-limited Scots pine sites showed that the current ForClim (v3.3; cf. Mina et al. 2017) underestimated basal area and stem numbers compared to measured data. The major reason for this was the divergence between the months in which the highest values of the drought index were calculated (July-August) and the actual period with the highest influence of drought on Scots pine radial growth (e.g., spring; cf. Eilmann et al. 2011; Lévesque et al. 2014). This resulted in an underestimation of annual $SMGF$, which considerably reduced diameter increment in the simulations (Fig. 4). The new drought formulation was able to fully correct this.

In addition to model limitations, the remaining discrepancies between observations and simulation results may be due to (1) the use of different time intervals for calibrating the $M1$ and $M2$ parameters and for simulating forest dynamics in Pfywald, (2) limitations of the inventorying methodology, and (3) the functions used for simulating multiple management interventions. First, because of because of slightly different periods used for calibrating the modified VS-Lite and for running ForClim simulations, the non-stationarity of climate could affect the climate-growth functions over time and thus the $M1$ and $M2$ parameters may not be representative of the entire

range of growing conditions during the simulation period. However, since these parameters were determined to accurately reproduce the inter-annual variability in ring-width indices, we believe that using the longest available climate time-series for parameter calibration was more appropriate than using the same period for calibration and validation. Second, because of the calliper limit (4 cm in Pfywald, 10 cm in Valsaín), an undetermined number of small trees present in the first inventory year could not be included in the initial state of the stand, producing an artificial underestimation of stem numbers throughout the simulation. In addition, the sampling method for the last inventory in Valsaín was different than for previous inventories, which may strongly hamper the comparability of the data along time (cf. Appendix B). Third, in the simulation the stems removed in each thinning intervention were selected randomly based on a Weibull function fitted to the current DBH distribution and on the percentage of basal area to harvest (Rasche et al. 2011). Undoubtedly this is the best approach for simulating harvesting in DVMs (Mina et al. 2017), but it may still under- or overestimate the number of stems removed in reality, while harvested basal area that simulated is accurate (cf. the overestimation of removed stems in 1966 in Pfywald, medium thinning; Fig. 4).

Site-specific growth responses to drought

The comparison between simulation results derived from the new ForClim versions, the one including site-specific optimized sets of moisture parameters (v3.3-LOC) and seasonal parameters averaged across the gradient (v3.3-AVG), allowed us to investigate the importance of including site- and species-specific responses to drought in simulations of forest dynamics. Basal area was simulated more accurately with ForClim v3.3-LOC compared to v3.3-AVG. For stem numbers, however, the two new model versions (v3.3-LOC and v3.3-AVG) gave nearly indistinguishable results (Table 2). This was because the values of annual *SMGF* (cf. section 3.2) were not low enough to induce tree mortality, as was the case with the standard v3.3. The minor differences between v3.3-LOC and v3.3-AVG in both locations in Central Spain and Switzerland show that including site-specific growth responses to drought – with our model and methodology – has little influence on simulated forest dynamics in Scots pine stands. We therefore suggest that, in the absence of local tree-ring chronologies, the model version including only the species-specific (rather than site-specific) intra-annual response to drought can be used faithfully for simulating forest growth in Scots pine stands.

Modeling growth responses to drought: research recommendations

We presented the first attempt to use a forward model of tree-ring width for improving a forest succession model. The superior performance of the upgraded ForClim versions highlight the importance of including intra-annual growth strategies in models that aim to simulate forest dynamics in areas where drought is important (cf. Allen et al. 2015). The large inter-site variability observed in the moisture parameters suggests that intra-specific variability in drought tolerance is an

important aspect that should be considered for simulating species distributional shifts at the continental scale (Snell et al. 2014).

The parameters derived with the modified VS-Lite are applicable only to ForClim, but given the availability of tree-ring width chronologies worldwide (i.e., ITRDB) a similar approach could be applied with a new calibration scheme with other DVMs and other tree species. Unfortunately, tree-ring data are mostly available for mature trees, which prevent their use to better simulate the effect of drought on regeneration, a crucial process influencing simulated forest composition and productivity in the long term (Price et al. 2001). Common garden experiments on recruitment and seedling establishment could be a useful source for validating model processes and species parameters (Richter et al. 2012; Taeger et al. 2013). In addition, further studies would be useful to improve the modeling of tree phenology, which is strongly influenced by climate change (Buntgen et al. 2013; Richardson et al. 2013). Also in this context, the use of forward models such as VS-Lite coupled with tree-ring data could be of high interest.

By implementing the intra-annual growth response to drought in a forest succession model, we were able to reflect the ability of Scots pine to withstand severe, periodic water stress during part of the year. This does not imply, however, that the species will be able to cope with increasing prolonged dry periods in the future (Bigler et al. 2006; Lévesque et al. 2014). While the global increase of temperature may boost growth rates on fertile and cool sites (i.e., boreal and some temperate) due to an extended growing season (Menzel and Fabian 1999; Pretzsch et al. 2014), more intense competition and more frequent drought and heat events (Fischer and Schar 2010) may accelerate the observed replacement of Scots pine by other, more drought-tolerant species (Weber et al. 2007; Galiano et al. 2010; Gea-Izquierdo et al. 2014). Projecting future drought events under climate change remain a challenge (Dai 2011), but also further efforts are required by ecological modelers towards better assessing the impacts of drought on future forest dynamics, and for producing reliable projections that will help to evaluate, improve and adapt current ecosystem management practices.

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Appendix A

Additional figures

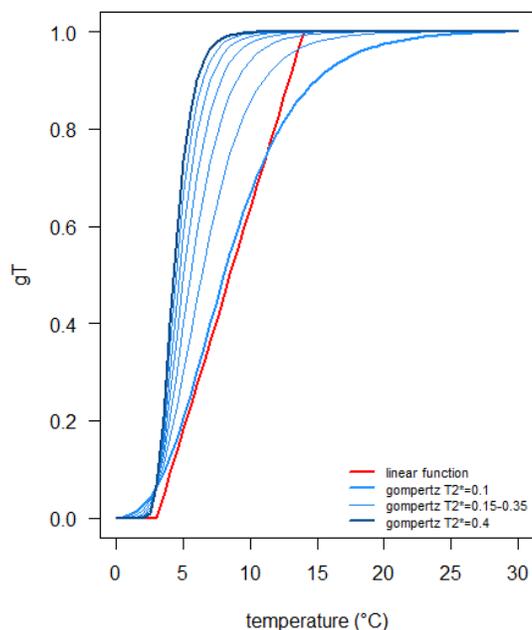


Fig. A1: Gompertz equation for modeling the growth response to temperature (gT) in the modified version of VS-Lite compared with a linear function (in red). The different curves (dashed, gray, dotted) were calculated with the same T1 parameter as for the linear function (in this case 3°C) but different T2* values (see legend). We constrained T2* from a minimum value of 0.1 (below gT would not reach one within the range of temperatures typically observed at our sites, e.g., 0-30°C), to a maximal of 0.4 (above which the response function would be binary).

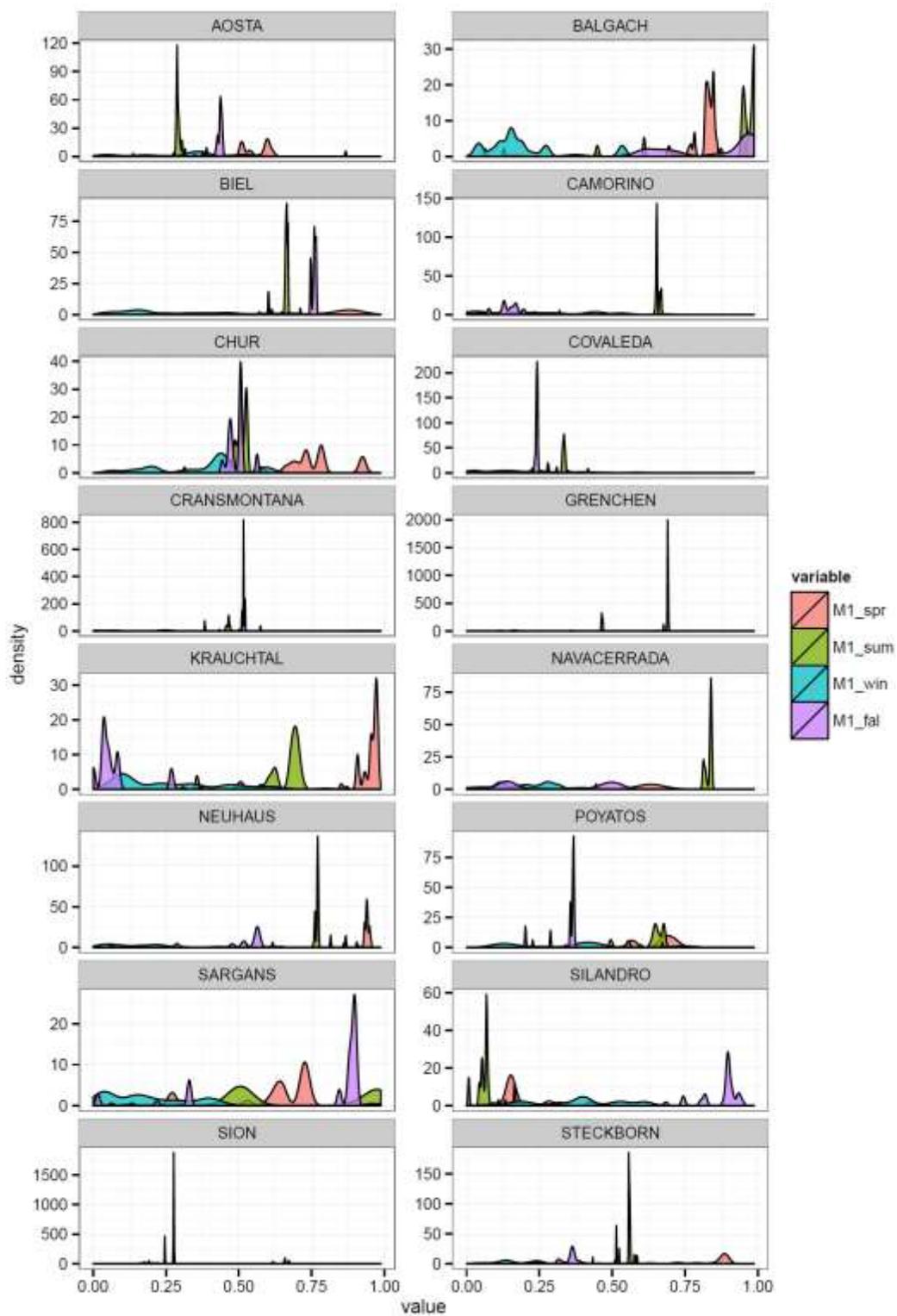


Fig. A2a: Distribution for each site of the seasonal MI parameters from the 100 iterations within the optimization procedure.

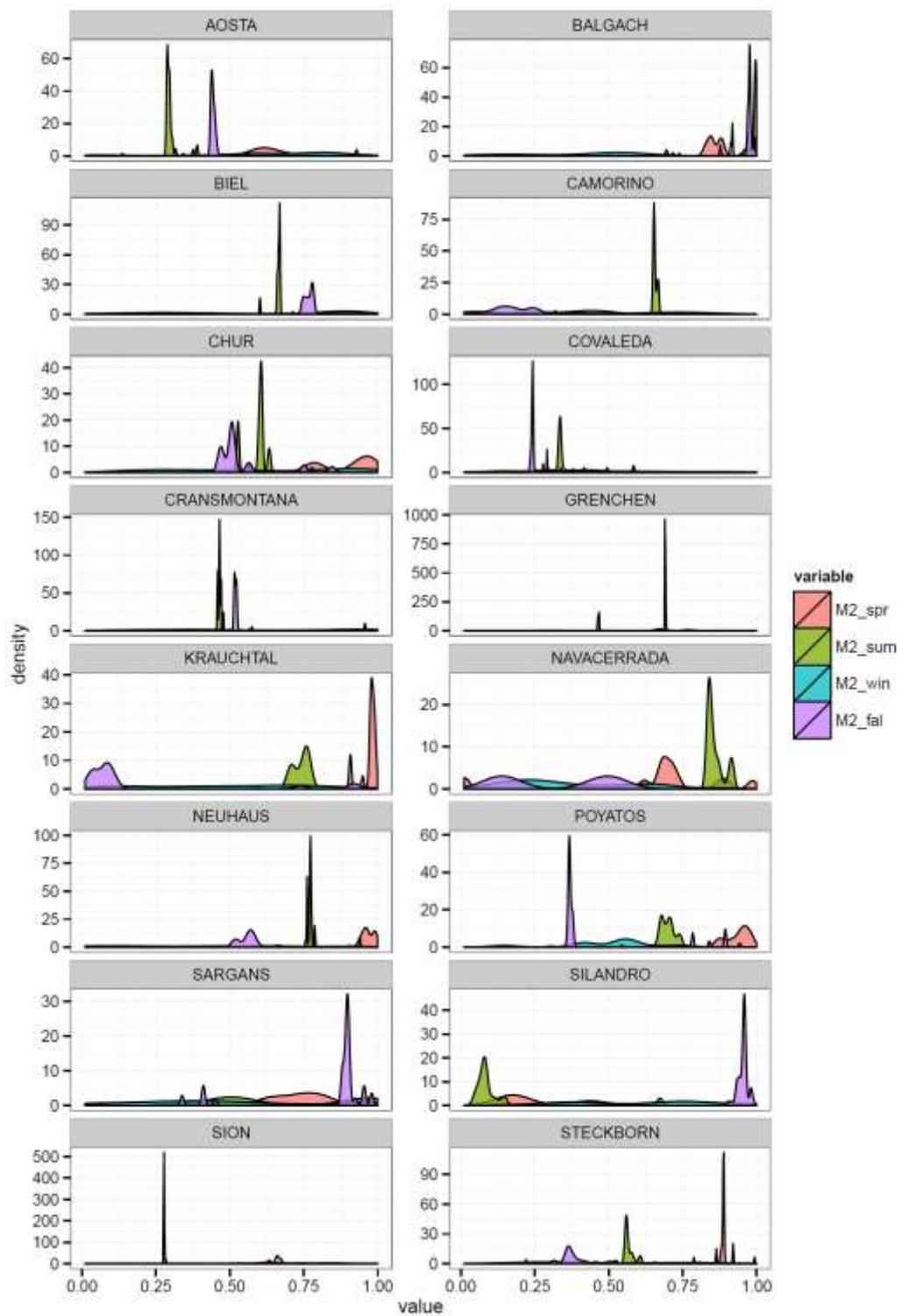


Fig. A2b: Distribution for each site of the seasonal $M2$ parameters from the 100 iterations within the optimization procedure.

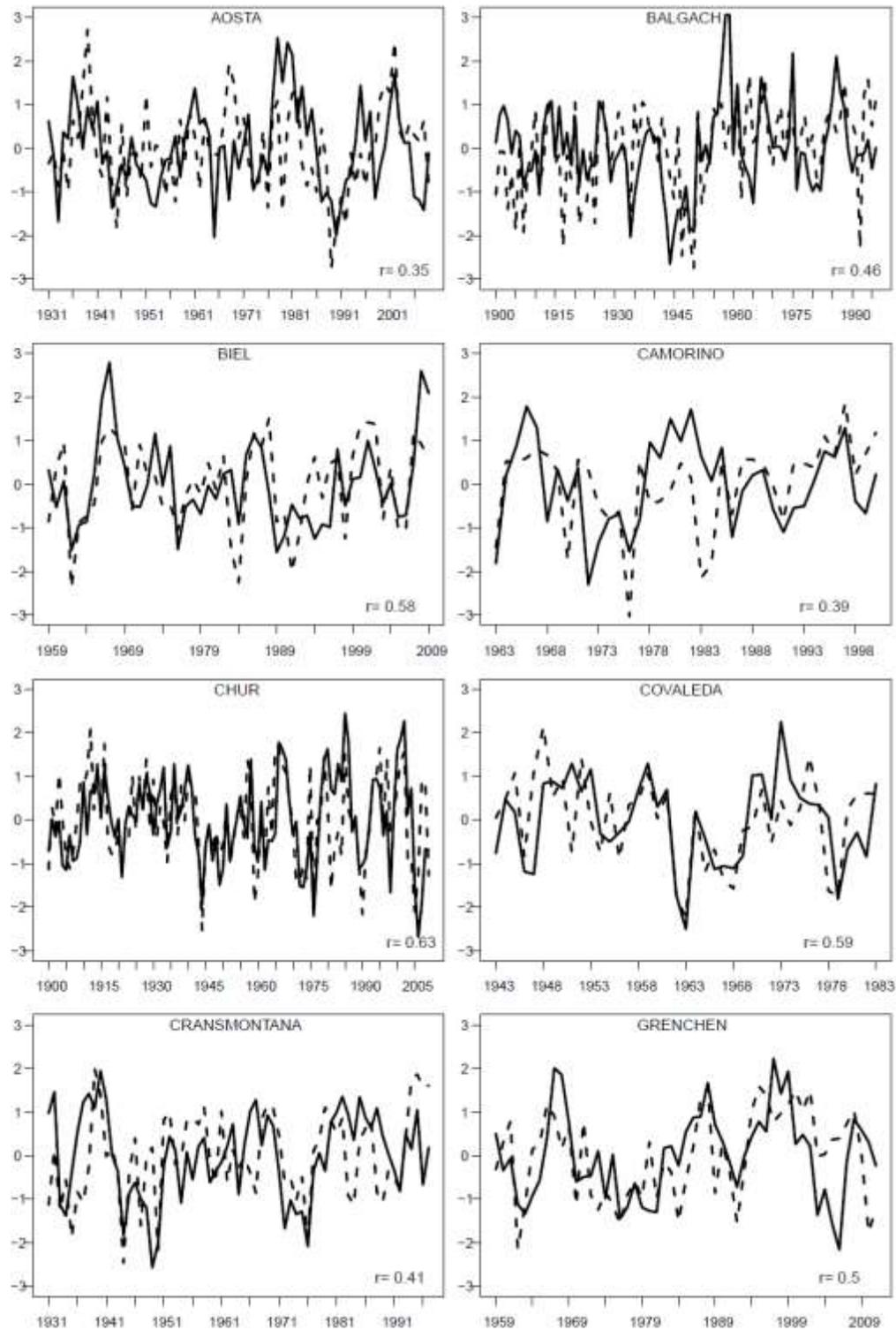


Fig. A3: Observed (solid) and simulated (dashed) ring width indices for the 16 studied sites, with respective correlation values. Note that different periods are shown depending on the available temporal data.

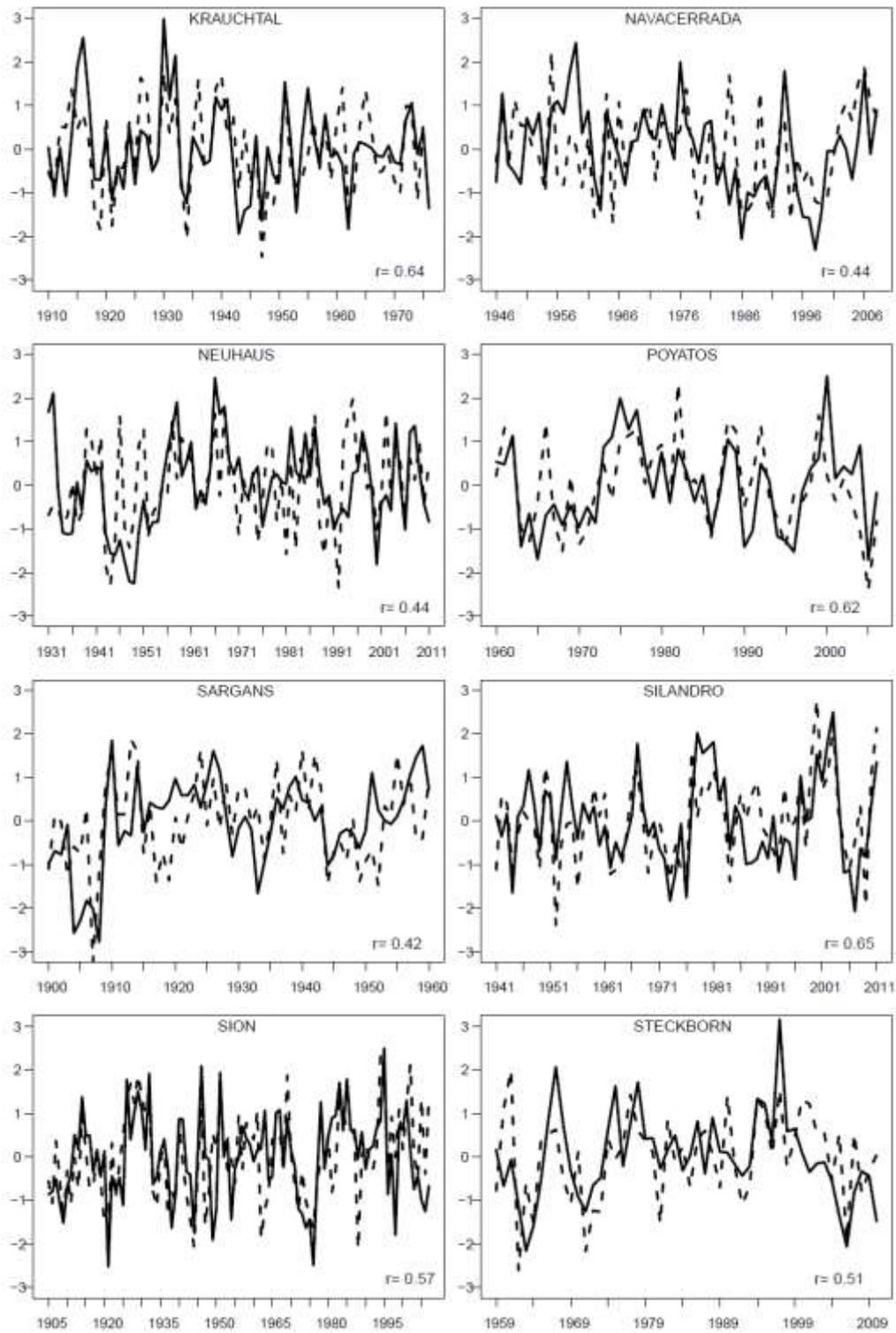


Fig. A3: (Continued)

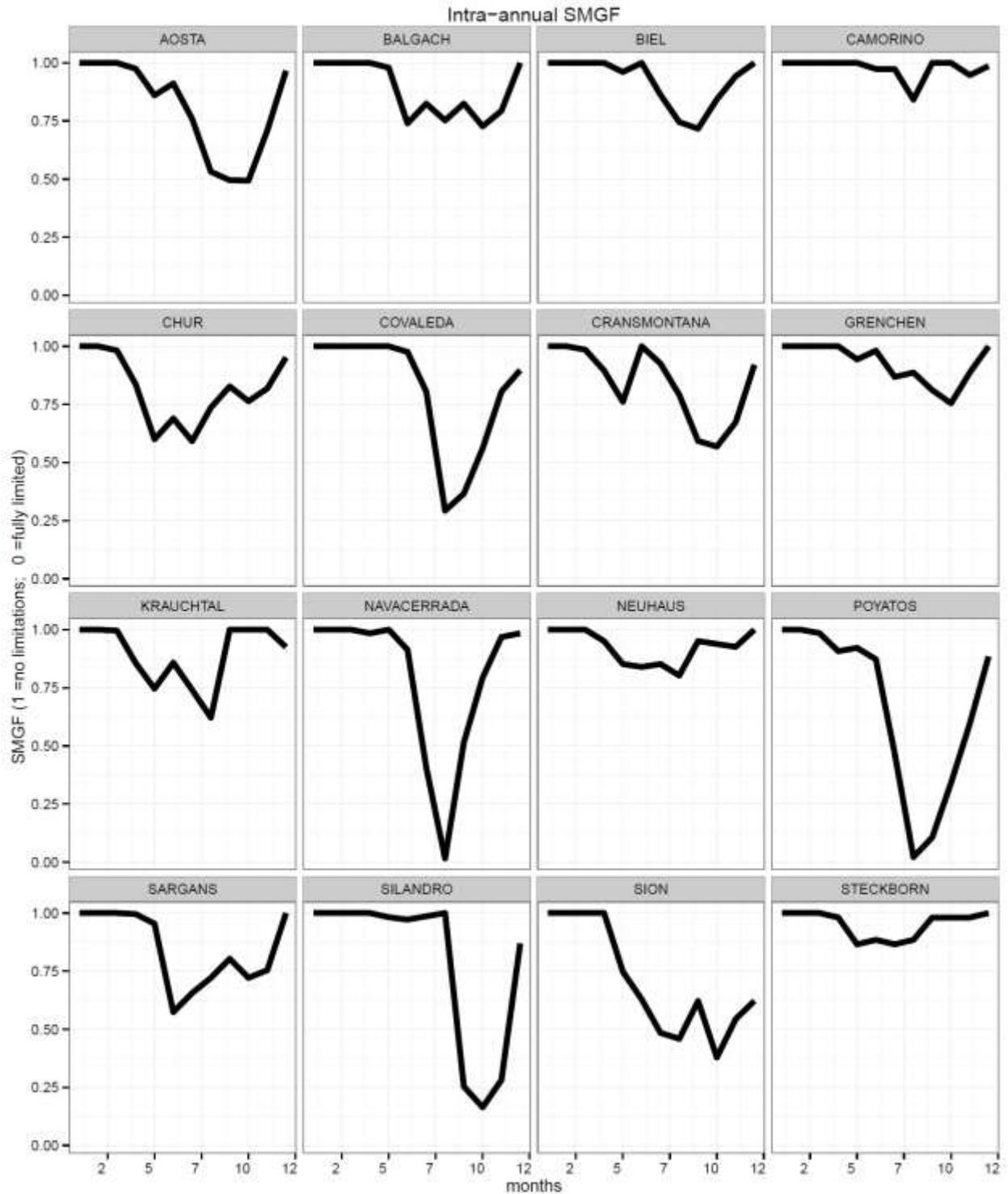


Fig. A4: Intra-annual change in *SMGF* (i.e., growth response to moisture *gM*) calculated with site-specific seasonal *M1* and *M2* parameters (Fig.3) and averaged over the period of data availability (see Table 1).

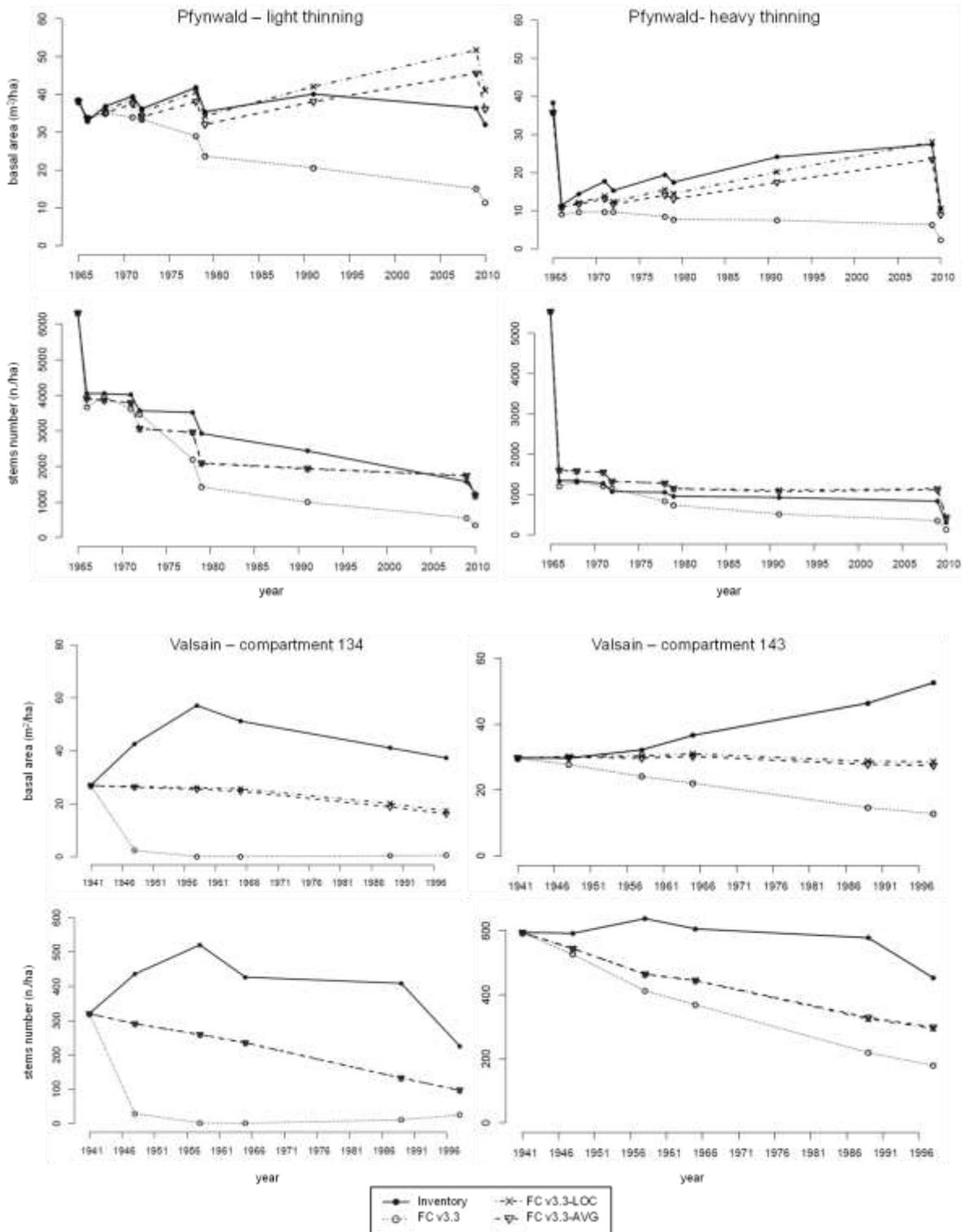


Fig. A5: Simulated stand basal area (m²/ha) and stem numbers (per ha) compared with observed inventory data for the remaining four stands not shown in Fig.4.

Additional tables

Table A1: Temperature (T) and soil moisture (M) parameters in the modified VS-Lite model (see main text for description) estimated with the optimization procedure using differential evolution algorithms (100 iterations) for each site across the precipitation gradient. T1 is expressed in °C, T2* is unitless (shape of the Gompertz curve), seasonal M1 and M2 parameters are expressed as percentages of the site-specific soil water holding capacity (sp=spring, su=summer, wi=winter, fa=fall). The last column (r) reports the correlation coefficient between observed and simulated tree-ring width chronology maximized in the optimization procedure. We did not observe a systematic change of the seasonal parameters across the gradient.

Site	T1	T2*	M1sp	M2sp	M1su	M2su	M1wi	M2wi	M1fa	M2fa	r
Sion	3.42	0.40	0.66	0.66	0.27	0.28	0.19	0.84	0.29	0.29	0.57
Silandro	3.00	0.40	0.15	0.17	0.06	0.08	0.09	0.68	0.90	0.95	0.65
Poyatos	3.13	0.19	0.67	0.92	0.68	0.68	0.38	0.56	0.37	0.37	0.62
Coaleda	3.00	0.40	0.22	0.28	0.33	0.33	0.36	0.60	0.24	0.24	0.59
Aosta	7.76	0.40	0.60	0.60	0.29	0.29	0.01	0.29	0.43	0.44	0.35
Cransmontana	3.04	0.37	0.98	0.98	0.46	0.47	0.13	0.72	0.52	0.52	0.41
Chur	3.04	0.38	0.92	0.92	0.50	0.60	0.44	0.50	0.47	0.47	0.63
Navacerrada	7.99	0.34	0.71	0.71	0.82	0.89	0.04	0.64	0.14	0.14	0.44
Krauchtal	3.00	0.40	0.97	0.98	0.71	0.76	0.63	0.98	0.05	0.08	0.64
Steckborn	3.00	0.40	0.88	0.88	0.56	0.56	0.12	0.95	0.38	0.38	0.51
Grenchen	6.76	0.32	0.67	0.67	0.46	0.46	0.13	0.23	0.69	0.69	0.50
Sargans	5.61	0.39	0.73	0.83	0.98	0.98	0.32	0.32	0.88	0.88	0.42
Neuhaus	6.36	0.40	0.94	0.94	0.77	0.78	0.23	0.23	0.56	0.57	0.44
Biel	7.60	0.40	0.89	0.89	0.66	0.67	0.34	0.39	0.76	0.78	0.58
Balgach	3.66	0.10	0.85	0.85	0.99	1.00	0.09	0.25	0.97	0.98	0.46
Camorino	7.91	0.40	0.45	0.45	0.65	0.66	0.35	0.63	0.13	0.13	0.39

Table A2: Summary statistics of the moisture parameters in the modified VS-Lite model (see main text for description) over the gradient sites and all DEoptim iterations. Mean values were used in the calculation of SMGF in ForClim v3.3-AVG.

parameter	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
M1sp	0.01	0.28	0.66	0.58	0.84	0.98
M2sp	0.01	0.54	0.77	0.70	0.92	1.00
M1su	0.01	0.36	0.54	0.55	0.68	0.99
M2su	0.04	0.46	0.61	0.58	0.74	1.00
M1wi	0.00	0.13	0.23	0.27	0.39	0.97
M2wi	0.01	0.29	0.53	0.52	0.75	1.00
M1fa	0.00	0.24	0.47	0.47	0.69	0.99
M2fa	0.01	0.37	0.52	0.55	0.76	0.99

Appendix B

Additional information on the calculation of maximum tree height

Site-specific maximum tree height in ForClim was modeled considering the reduction due to the effect of unfavorable temperature and drought (see Rasche et al. 2012 for a complete description of the implementation). Regarding limitations due to temperature, the annual – seasonal for deciduous species – sum of degree days (uDD) was used for calculating a percentage reduction of species-specific maximal height ($RedFacDD$) caused by degree days:

$$RedFacDD = 100 - \left[(DD_{OPT} - uDD) * \frac{100 - kRedMax}{DD_{OPT} - kDD_{MIN}} \right] \quad (B1)$$

where kDD_{MIN} is a species-specific parameter denoting the minimum degree-day sum required for growth, $kRedMax$ is the species-specific maximum maximum reduction parameter (Rasche 2012) and DD_{OPT} is the value after which degree days are no longer limiting calculates as follows:

$$DD_{OPT} = \begin{cases} kDD_{MIN} + 471 & \text{for deciduous species} \\ kDD_{MIN} + 353 & \text{for evergreen species} \end{cases} \quad (B2)$$

In the case of limitation caused by drought, the site- and species-specific maximum height ($Hmax$) was directly related to the soil moisture growth-reducing factor ($SMGF$) using the factor $RedFacDR$, which indicates the percentage reduction of $Hmax$ caused by drought:

$$RedFacDR = \frac{100 * \left(kHmax - \left\{ kHmax - \left[kHmax - \left(kHmax * \frac{kRedMax}{100} \right) * (1 - SMGF) \right] \right\} \right)}{kHmax} \quad (B3)$$

where $kHmax$ is the species-specific maximum height parameter (Bugmann 1994).

Finally the site- and species-specific maximum height $Hmax$ was calculated as follow:

$$H_{MAX} = \frac{kHmax}{100} * \min(RedFacDD, RedFacDR) \quad (B3)$$

For Scots pine $kHmax = 45$ m and $kRedMax = 38\%$ (Rasche et al. 2012).

Additional information for ForClim simulations

Forest inventory data for the three stands in Valsaín

Inventory data included the number of trees by diameters classes of 10 cm bins, for each inventoried year (1941, 1948, 1958, 1965, 1989 and 1998). For the inventories between 1941 and 1989 all trees with DBH greater than 10 cm were sampled. Since 1989, the inventory method followed a systematic sampling in rectangular grids, with identical diameter classes and callipering limit. Although this could lead to some uncertainties for the last inventory point, we decided to include the 1998 inventory in the model evaluation. For each observed year we calculated diameter distribution, total basal area and stem numbers per hectare (Table B2). Data from management plans and their revisions were available at the website of the Spanish National Parks Agency (<http://www.magrama.gob.es/es/parques-nacionales-oapn/centros-fincas/valsain/ordenaciones.aspx>; accessed on 11/08/2015).

Model initialization

We initialized each of the six forest stands using DBH data from the first inventory. Each tree was randomly allocated to the number of patches obtained by dividing site area by the default patch size used in ForClim (800 m²). The patches were then replicated to 200 in order to reduce stochastic noise in the simulations. Details about this methodology can be found in Wehrli et al. (2005) and Didion et al. (2009). For initializing tree height, we used species-specific relationships between height and diameter available from local forest inventory data.

Additional inputs required for ForClim

ForClim simulations require site-specific parameters that are typically derived from measurements - if available - or site descriptions for each stand, such as bucket size (kBS , in cm), available nitrogen ($kAvN$, in kg/ha*yr) and browsing probability ($kBrPr$, in %). For the Pfywald stands, measured data of soil water holding capacity were not available. Therefore, we estimated the values of bucket size and available nitrogen based on site descriptions from Brunner et al. (2009). For all the three stands we assigned a value of 10 cm for kBS and 60 kg/ha*yr for $kAvN$. All the three stands in Valsaín were located at an elevation range between 1360 and 1710 m a.s.l. For them we used information of soil data provided within the framework of the ARANGE project (see Project Deliverable D1.2 at http://www.arange-project.eu/wp-content/uploads/ARANGE-Deliverable-D12_06092013.pdf; accessed on 03.08.2015). We estimated bucket size and available nitrogen values based on assessment of water storage capacity and plant available nitrogen for stands located at 1500 m a.s.l. in the Valsaín forests (kBS 10 cm, denoting soils with normal water storage capacity, and $kAvN$ 90 kg/ha*yr denoting standard nutrient-rich soils in ForClim). For all the stands in both locations browsing data were not available. Thus, we assigned the browsing probability $kBrPr$ to a standard value of 20%.

Management data and implementation of harvesting interventions

Inventory data for the three thinning experiments in Pfywald included the number of stems by DBH classes before and after each management intervention (Giuggiola et al. 2013; Elkin et al. 2015). Thus, we calculated the percentage of removed stems for each thinning intervention and we estimated the type of silvicultural operation based on the harvested stems by DBH classes (tending, thinning from below, and thinning from above). We then simulated harvesting using the ForClim thinning functions (Rasche et al. 2011). For Valsaín we obtained data for the management operation executed in each stand (large forest compartment) between 1941 and 1998 in the form of: type of silvicultural intervention (e.g., tending, thinning, shelterwood felling, sanitary felling and snags removal), number of trees harvested, volume harvested. Based on these indications, we calculated the cumulative volume harvested in percentage between two inventory years. Similarly to Pfywald, we then simulated harvesting using the thinning functions available with the management submodel of ForClim (Rasche et al. 2011).

Inventory data

Table B1: Stand basal area (BA, m²/ha) and stem numbers (TRS, stems/ha) for each inventory year for the three thinning treatments in Pfywald used for evaluating model performance. [p.t. = post thinning]

Pfywald						
	light		medium		heavy	
year	BA	TRS	BA	TRS	BA	TRS
1965	38.6	6085.0	40.0	5578.0	38.4	5541.0
1966 p.t.	32.9	4050.0	22.2	3008.0	11.4	1346.0
1968	36.9	4050.0	26.3	3008.0	14.4	1346.0
1971	39.5	4013.0	28.9	2917.0	17.7	1277.0
1971 p.t.	36.2	3566.0	25.1	2459.0	15.3	1078.0
1978	41.8	3518.0	30.7	2444.0	19.4	1053.0
1978 p.t.	35.4	2927.0	25.7	1895.0	17.5	959.0
1991	40.1	2438.0	33.2	1742.0	24.1	931.0
2009	36.4	1575.0	35.2	1379.0	27.4	837.0
2010 p.t.	32.0	1244.0	21.0	753.0	10.5	309.0

Table B2: Stand basal area (BA, m²/ha) and stem numbers (TRS, stems/ha) for each inventory year for the three stands in Valsáin used for evaluating model performance.

Valsáin						
	134		143		243	
year	BA	TRS	BA	TRS	BA	TRS
1941	27.0	321.0	29.9	595.0	46.9	317.0
1948	42.6	436.0	29.7	592.0	42.4	304.0
1958	57.1	521.0	32.2	638.0	42.1	328.0
1965	51.2	427.0	36.6	606.0	44.2	359.0
1989	41.1	409.0	46.4	578.0	36.3	453.0
1998	37.3	226.0	52.6	453.0	47.3	782.0

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Chapter IV

Future ecosystem services from European mountain forests under climate change

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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.

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

Introduction

The large array of ecosystem goods and services (ES) delivered by mountain ecosystems is fundamental for sustaining the wellbeing of people living in mountain and lowland areas (MEA 2005; Gret-Regamey et al. 2012). Currently, about half of the global human population depends on benefits delivered by mountain ecosystems (Körner and Ohsawa 2005). In Europe, mountain regions cover more than 40% of the continent (Price et al. 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 and Butt 2000), offer habitat for many species of plants and animals (Estreguil et al. 2012), contribute to climate regulation e.g. by storing carbon (Ciais et al. 2008) and have important recreational and cultural values (Peña et al. 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 et al. 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 et al. 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 and 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; Reyer 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. 2017). 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: (1) What is the impact of climate change on multiple ES in European mountain forests? (2) Will alternative management regimes be more suitable in providing multiple ES under climate change than current management? (3) 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 ‘ARANGE’ to cover the key forest types and governance settings in the main mountain ranges of central and southern Europe, and diverse climate regimes (see Table 1, Table 2 and Appendix S1 in 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, single-tree selection cuts, etc.) 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).

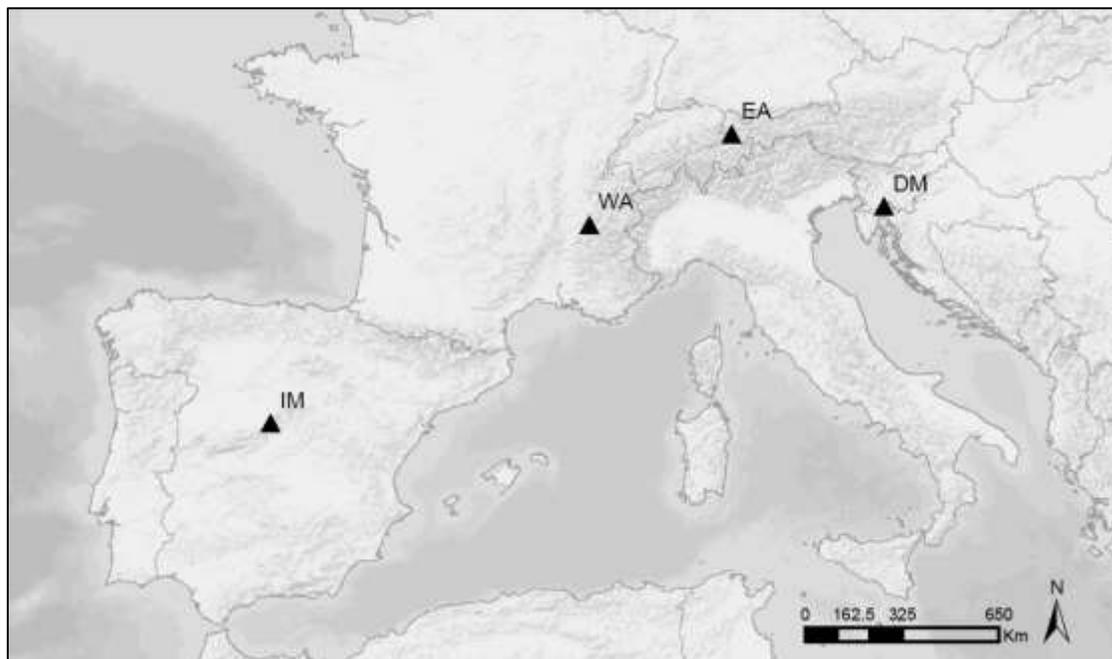


Fig. 1: Location of the case study areas (IM: Iberian Mountains; WA: Western Alps; EA: Eastern Alps; DM: Dinaric Mountains).

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

	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 tem- perature (°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> , Pyre- nean 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

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 and 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 of 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. 2016b; Mina et al. 2017), 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. (2017). For the scenario of non-intervention (NM), we did not simulate any harvesting operation until the end of the rotation.

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 (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. 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).

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 - Over-mature	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

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 et al. 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; Lafond et al. 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). Second, 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 (cf. Abdi et al. 2013). The analysis was performed with the software R (R Core Team 2014) using the package *FactoMineR* (Lê et al. 2008). Finally, a total of five indicators were selected: timber volume harvested for production (T), aboveground 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 (Fig. 2; Fig. 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, f, g, 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 (Fig. 2a; Fig. 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 of timber production in RSTs 13.0 (Fig. 2d) and 19.0 (Fig. S3.2).

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

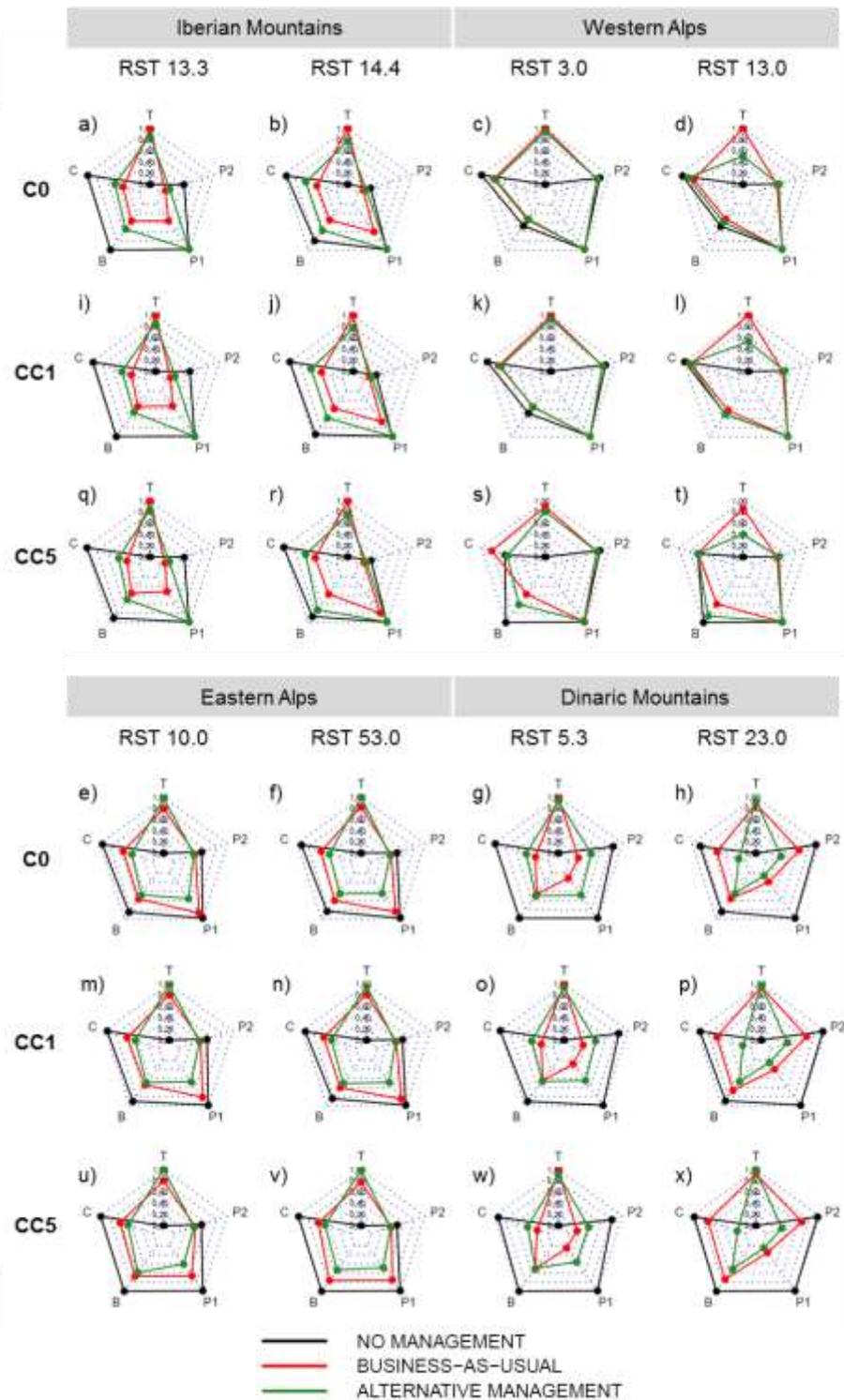


Fig. 2: Radar plots showing the projected future provision (2080-2100) of four ES (T: timber production; C: carbon storage; B: biodiversity; P1: protection against rockfall; P2: protection against avalanches) for selected RSTs in the four mountain regions (columns). Results for the different management regimes are shown as different lines for simulations under current climate conditions (C0) and two climate change scenarios (CC1 and CC5; rows). Results for all RSTs and climate scenarios are in Fig. S3.2.

Impacts of climate change

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 of biodiversity, but only under BAU and AM. At low elevations (RSTs 4.3 and 8.3, Fig. S3.2), however, a decrease of 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.

Table 3: F-values of the ANOVA on the multifunctionality index in each CSA; d.f. = degrees of freedom. Cell colors represent the significance level of the respective and interactive effects of the climate scenario (CLIMATE), management scenario (FM), and RST. Residuals d.f.: 40.

	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

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).

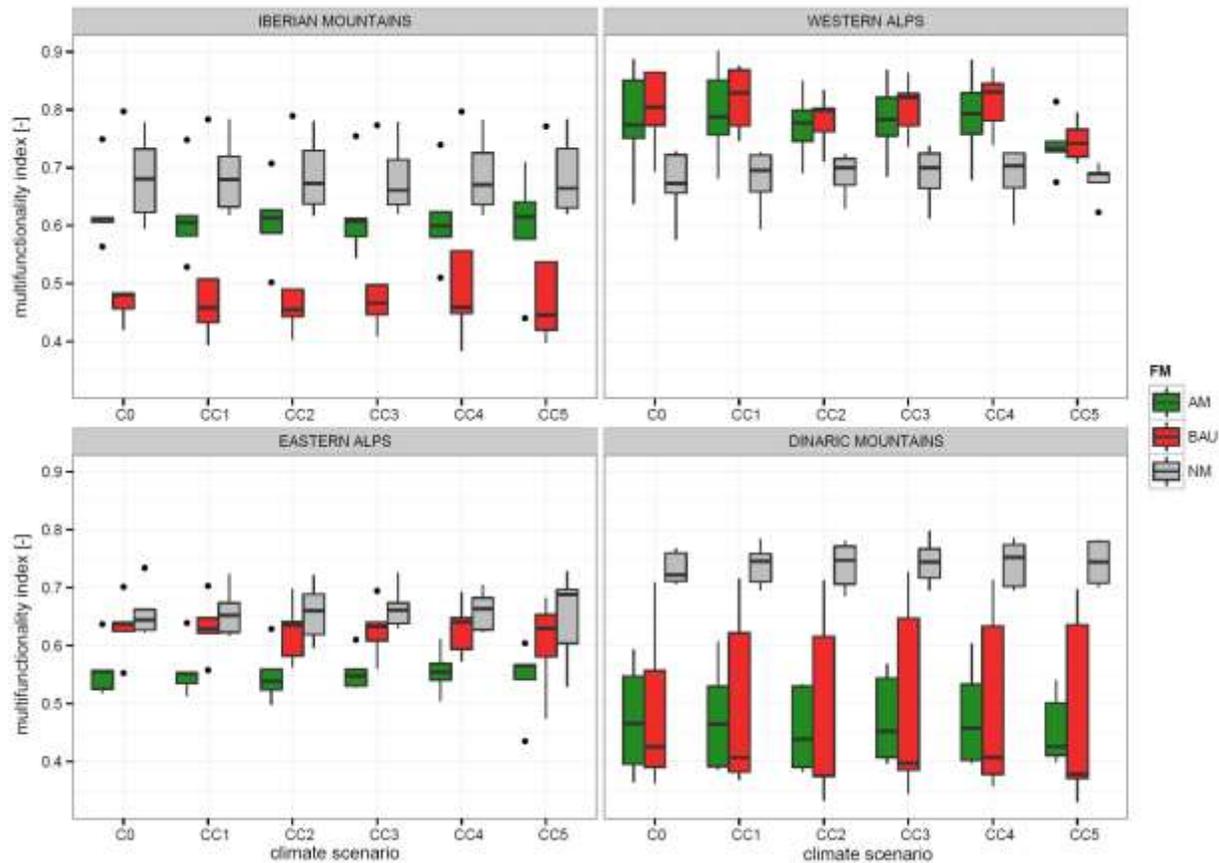


Fig. 3: Change in the multifunctionality index MFI in each CSA as a function of management and climate scenario. The range of MFI within a scenario represents the differences between RSTs.

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).

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

	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

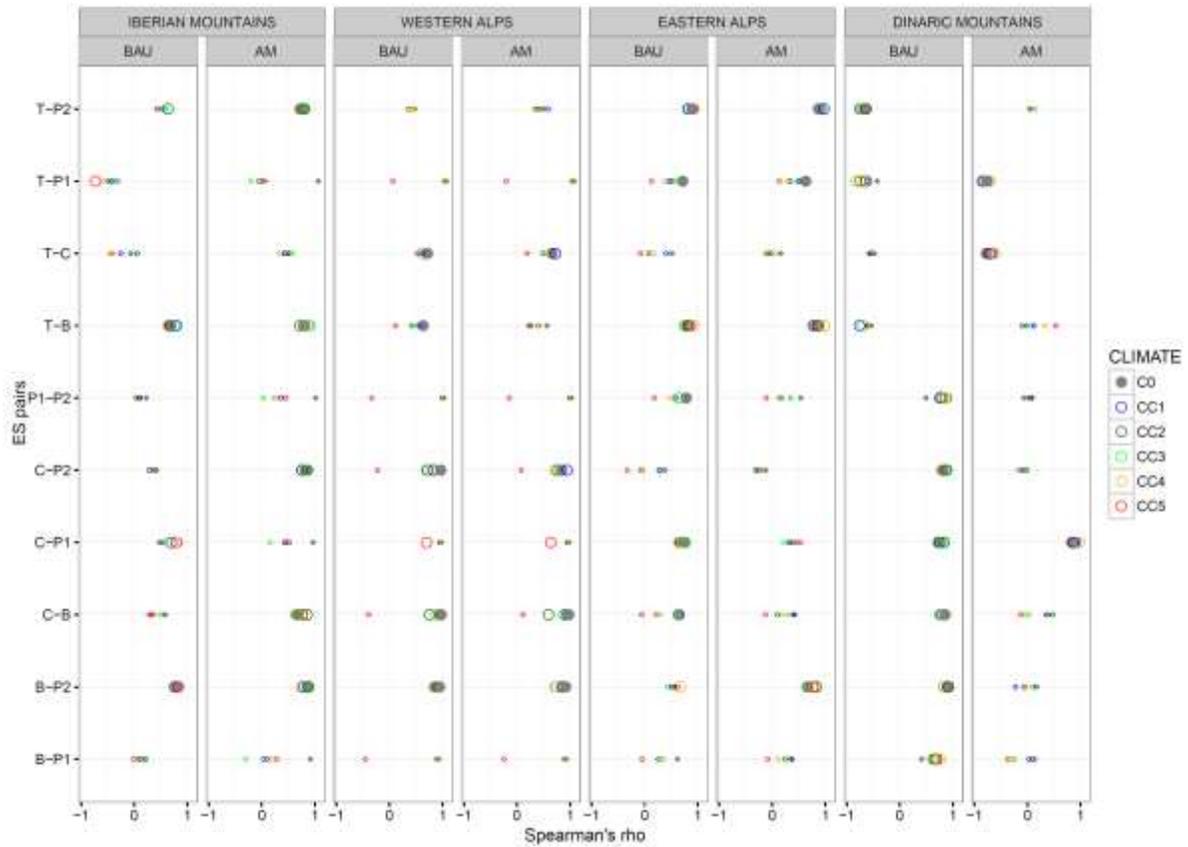


Fig. 4: Trade-offs and synergies between the five ES expressed as Spearman’s rho in the four CSAs and for the two active forest management scenarios. Non-significant correlations ($p < 0.05$) are shown with smaller circles.

Table 5: F-values of the ANOVA on Spearman’s rho calculated for the four CSAs; d.f. = degrees of freedom. Cell colors 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.

	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

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 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 of 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 and Piñol 2002; Rebetez and 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 of 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-yr 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 and 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; Fig. S1.2, Fig. 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 windthrow are considered (Seidl et al. 2011; Irauschek et al. 2015).

In the Dinaric Mountains, climate change would strongly affect ES, albeit differently depending on elevation, thus highlighting the necessity to consider the 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 and Kobler (2011), and confirms the pattern observed for a broader range of RSTs in the same region (Mina et al. 2017).

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 et al. 2015; Lutz et al. 2015), 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 et al. 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.

Second, 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).

Third, 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 et al. 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., aboveground 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 and 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 et al. 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 and 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 are 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 envi-

ronmental 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 and 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 et al. 2004; Lassauce et al. 2011), instead of other options such as tree size diversity or elements of structural diversity that are important e.g. 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.

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Data accessibility

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

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Appendix S1: Supplementary methods and data

Business-As-Usual (BAU) and alternative management (AM) scenarios

In the Iberian Mountains, thinnings from below executed in BAU for achieving timber production were replaced with heavier (40-50% of the standing volume removed instead of 15-30%) but less frequent thinnings from above to promote higher growth and vigor of quality timber, while keeping the same rotation length (120 years) and an irregular shelterwood system to regenerate stands. For the Western Alps, to simulate management intensification for both wood production and climate change adaptation objectives, but also specific compensatory practices to avoid loss of biodiversity, single-tree selection cuttings in uneven-aged stands were combined with the retention of a certain number of large trees at each felling while lowering harvested diameters (ca. - 10 cm). In the Eastern Alps, group selection fellings executed in different forest patches in uneven-aged stands (Irauschek et al. 2015) were increased in frequency to harvest near current observed volume increment rates as a strategy against over-aging forests. In the Dinaric Mountains, in order to promote conifers over broadleaves, thinning interventions were reduced in frequency and increased in intensity, and 3% of the standing volume was retained in the final cut. Here, uneven-aged RSTs were converted from single-tree selection fellings to even-aged regimes (i.e., thinnings and regeneration fellings).

Table S1.1: Description of the two active forest management regimes (FM) in the four case study areas (CSAs), with specification of the silvicultural interventions, rotation periods and regeneration systems. Further details can be found in Klopčič et al. (2013).

CSA	FM	Description
Iberian Mountains	BAU	Four thinning from below and selective thinning (removal of 15-30% standing volume). Regeneration phase with four irregular shelterwood interventions. Rotation period 120 years. Natural regeneration
	AM	Three thinning interventions from above (removal of 40-50% standing volume). Regeneration phase with four irregular shelterwood interventions. Rotation period 120 years. Natural regeneration.
Western Alps	BAU	Uneven-aged management. Single-tree selection cuttings each 8-10-12 years (depending on the RSTs), with removals of 15-20% basal area. Percentage of removals between the species proportional to their share in the stand. Natural regeneration.
	AM	Uneven-aged management. Individual selection with lower harvesting diameter and retention of large trees at each felling. Natural regeneration.
Eastern Alps	BAU	Uneven-aged management with specific group selection system carried out with skyline based logging techniques*. Harvesting intervention each 42 years, with subsequent removal on 25, 25, 15% area in irregular patches on the skyline working area; Felling turnover of the forest area: 250 years**. Natural regeneration.
	AM	Increased frequency of harvesting operations. Harvesting intervention each 25 years Removal on 25, 25, 15, 15% area in irregular patches along the skyline; Felling turnover of the forest area: 150 years**. Natural regeneration.
Dinaric Mountains	BAU	Combination of irregular shelterwood system with single-tree selection. Even-aged stands: three to four thinning interventions, two to three regeneration fellings, Management rotation: 135-140 years; uneven-aged stands: single tree or group selection harvesting interventions each 8-10 years. Natural regeneration
	AM	General protection and promotion of conifers. Shorter rotation periods (115-120 years), reduced frequency and increased intensity in thinning, retention of the 3% of the standing volume at the final cut. Uneven-aged stands managed with even-aged rotation. Natural regeneration

* Details of the forest management applied in the Eastern Alps area can be found in Irauschek et al. (2015).

** In absence of future climate scenario beyond the year 2100 and since ES were analysed for the period 2080-2100, the last simulation year in this CSA was set to 2110.

Baseline climate

An artificial 100-year time series for baseline climate, reflecting the climatic conditions of the period 1951-2011, was developed for each CSA. In the Iberian Mts, Western and Eastern Alps, time series were generated using data from weather stations located within the CSAs. In absence of available datasets from weather stations, in the Dinaric Mts the public E-OBS 0.25° grid point dataset was used (van den Besselaar et al. 2011). The description of the entire process used for deriving baseline climate records can be found in Thurnher (2013).

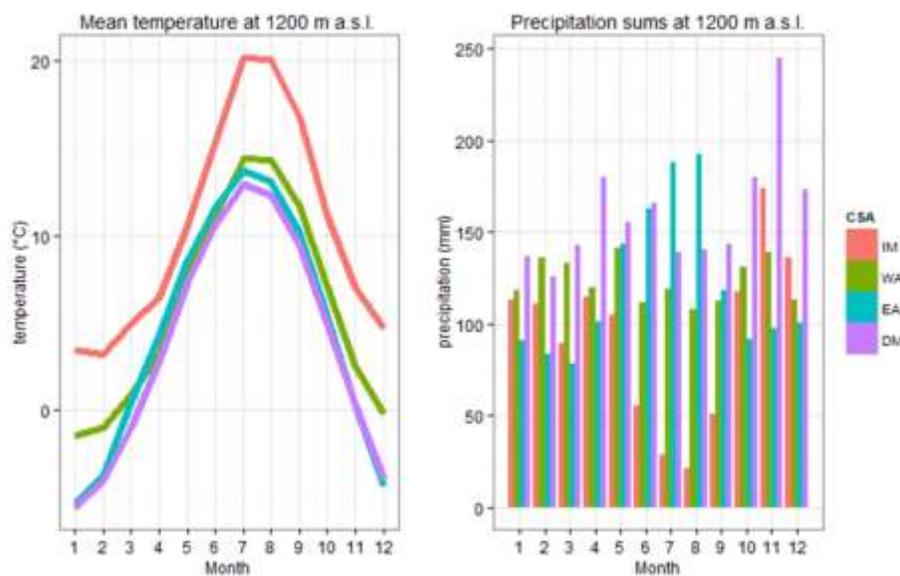


Fig. S1.1: Baseline climate expressed as averages of mean monthly temperature and monthly precipitation sums at 1200 m a.s.l. in the four case study areas (IM: Iberian Mountains; WA: Western Alps; EA: Eastern Alps; DM: Dinaric Mountains).

Climate change scenarios

Table S1.2: Ranking of the climate change scenarios for each case study area based on the increase of mean annual temperature. The first label in each cell denotes the regional climate simulation (e.g., DMI-HIRHAM5) while the second one indicates the General Circulation Model (e.g., BCM). Detailed information on the downscaling approach are available in Truhetz (2013) and Bugmann et al. (2016).

Climate scenario	CASE STUDY AREA			
	Iberian Mountains	Western Alps	Eastern Alps	Dinaric Mountains
CC1	DMI-HIRHAM5 BCM	DMI-HIRHAM5 BCM	DMI-HIRHAM5 BCM	DMI-HIRHAM5 BCM
CC2	SMHI-RCA HadCM3Q3	HC-HadRM3 HadCM3Q3	HC-HadRM3 HadCM3Q3	DMI-HIRHAM5 ARPEGE
CC3	ICTP-RegCM ECHAM5-r3	MPI-REMO ECHAM5-r3	SMHI-RCA HadCM3Q3	MPI-REMO ECHAM5-r3
CC4	MPI-REMO ECHAM5-r3	SMHI-RCA HadCM3Q3	HC-HadRM3 HadCM3Q0	SMHI-RCA HadCM3Q3
CC5	HC-HadRM3 HadCM3Q16	HC-HadRM3 HadCM3Q16	HC-HadRM3 HadCM3Q16	HC-HadRM3 HadCM3Q16

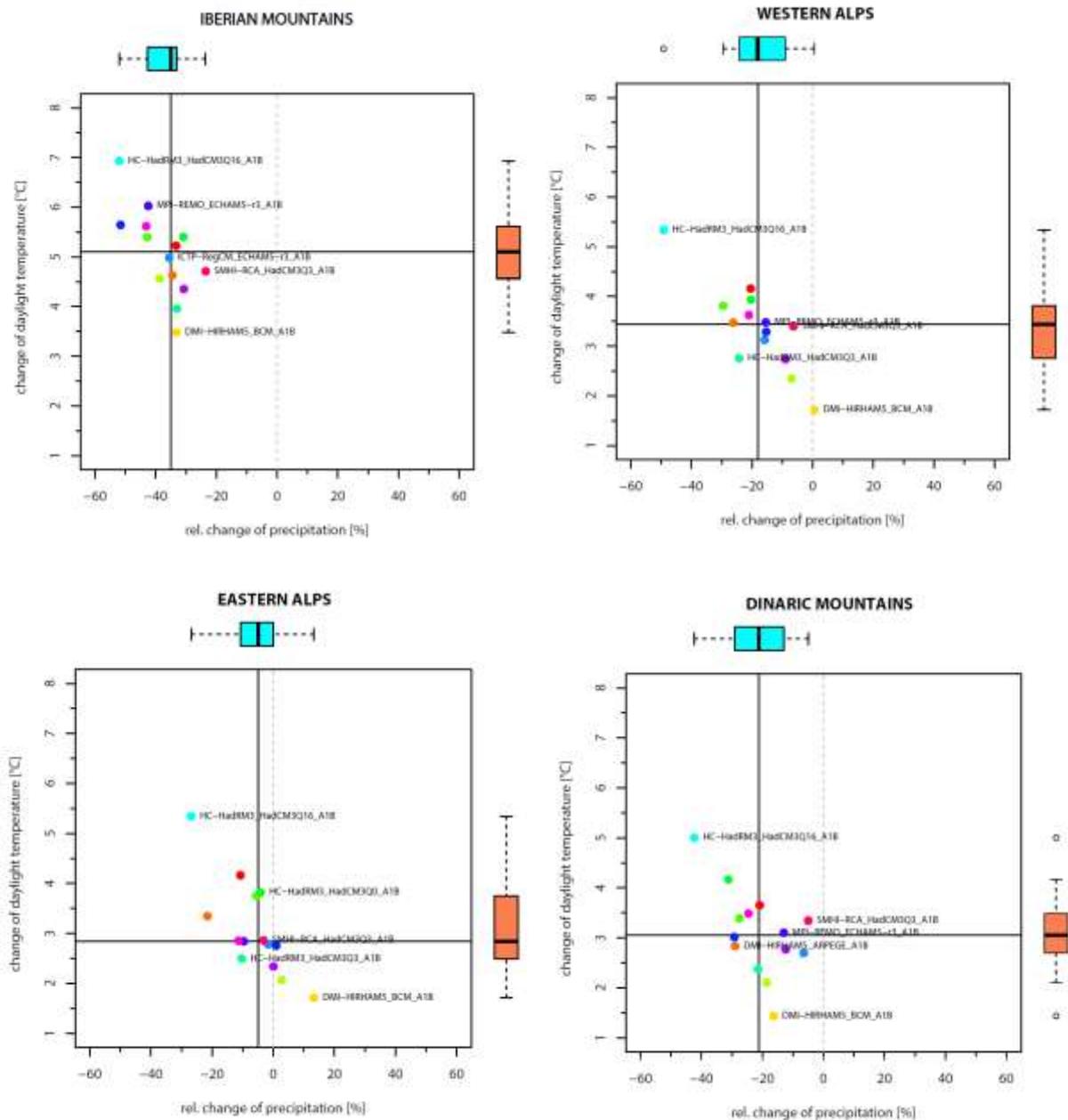


Fig. S1.2: Changes of temperature (°C) and precipitation (%) for the four case study areas, plotted as the change in the summer half-year (April-September) between the periods 1961 to 1990 and 2071 to 2100 for downscaled and bias-corrected ENSEMBLES simulations (Hewitt and Griggs 2004). Labeled points denote the five scenarios selected for the present study. Scenarios were subsequently ranked in each CSA based on the increase in mean annual temperature and renamed from CC1 (smallest increase) to CC5 (largest increase; see Table S1.2). Figure modified from Truhetz (2013).

Appendix S2: Ecosystem service indicators

Table S2.1: Multiple factor analysis on the initial 22 indicators, with values of coordinates (*coord.*) and contributions (*ctr.*) for the different variables for the first three dimensions. The rockfall protection indices depend on rock size and rock density (see Cordonnier et al. 2013). The five indicators that best explained each ES (bold face) were selected based on the sum of their contribution to the three dimensions proportioned to the percentage of variance expressed by each dimension and based on their correlation (e.g., API was selected instead of RPI9 because less correlated to RPI4; see Fig. S2.1). Symbols reported in braces are the ones used in the main text of the manuscript.

ES	Indicator	Symbol	Dim.1		Dim.2		Dim.3	
			Coord.	Ctr.	Coord.	Ctr.	Coord.	Ctr.
Timber	Volume increment (m ³ ha ⁻¹ yr ⁻¹)	VI	0.53	0.00	1.22	0.00	0.78	0.00
	Timber volume harvested (m³ ha⁻¹ yr⁻¹)	TVH [T]	-182.68	15.45	120.39	24.03	58.40	11.74
	Volume of living trees (m ³ ha ⁻¹)	V	166.71	12.87	27.31	1.24	56.56	11.01
Carbon	Aboveground carbon (t ha ⁻¹)	C_ab [C]	56.98	25.91	16.75	8.02	22.03	28.77
	Belowground carbon (t ha ⁻¹)	C_be	17.26	2.38	5.07	0.74	6.67	2.64
Biodiversity	Tree size diversity index (-)	H	0.20	0.00	0.14	0.00	0.09	0.00
	Dead wood volume (m³ ha⁻¹)	DWV [B]	38.63	13.40	24.85	19.86	-20.22	27.28
	Number large standing dead trees (n.ha ⁻¹)	LSDTN	10.12	0.92	6.33	1.29	-5.68	2.15
	Volume large standing dead trees (m ³ ha ⁻¹)	LSDTV	28.13	7.11	14.42	6.68	-14.84	14.70
	Number of large living trees (n.ha ⁻¹)	LLTN	3.38	0.10	0.88	0.03	1.43	0.14
	Bird habitat quality index (1-3)	BHQI	0.18	0.00	0.02	0.00	0.02	0.00
Protection	Rockfall protection index 1 (0-1)	RPI1	0.70	1.94	-0.40	2.29	0.13	0.53
	Rockfall protection index 2 (0-1)	RPI2	0.70	1.93	-0.45	2.90	0.09	0.26
	Rockfall protection index 3 (0-1)	RPI3	0.71	2.01	-0.54	4.15	0.00	0.00
	Rockfall protection index 4 (0-1)	RPI4 [P1]	0.73	2.15	-0.55	4.25	-0.04	0.04
	Rockfall protection index 5 (0-1)	RPI5	0.69	1.92	-0.56	4.42	-0.03	0.02
	Rockfall protection index 6 (0-1)	RPI6	0.70	1.94	-0.40	2.32	0.13	0.52
	Rockfall protection index 7 (0-1)	RPI7	0.69	1.92	-0.48	3.30	0.07	0.15
	Rockfall protection index 8 (0-1)	RPI8	0.72	2.06	-0.54	4.23	-0.01	0.01
	Rockfall protection index 9 (0-1)	RPI9	0.73	2.14	-0.55	4.26	-0.04	0.04
	Rockfall protection index 10 (0-1)	RPI10	0.63	1.59	-0.57	4.58	-0.01	0.00
Avalanche protection index (0-1)	API [P2]	0.76	2.28	0.32	1.42	0.01	0.01	
Percentage of variance explained			61.17		17.08		8.23	
Cumulative percentage of variance explained			61.17		78.25		86.48	

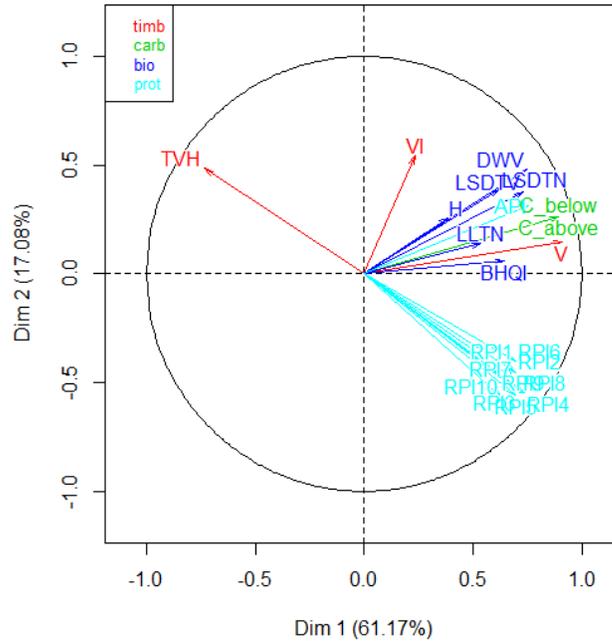


Fig. S2.1: First two dimensions from the Multiple Factor Analysis performed with the initial 22 indicators characterizing the four ES.

Description of ES indicators

All 22 indicators were calculated from ForClim outputs following Cordonnier et al. (2013), where additional information on the single indicators can be found. A description of the five indicators analyzed in the present manuscript is given here below.

Timber volume harvested

The total annual volume of timber harvested in the forest stand. Since management interventions were not simulated with the same time intervals among the different CSAs and RSTs timber volume harvested was calculated as cumulative sum along the simulation. In ForClim, only living trees were harvested (i.e., dead trees are automatically included in the deadwood pool during the simulation).

Aboveground carbon:

The dry mass of carbon contained in aboveground living trees, as calculated with ForClim (Bugmann 1994). A detailed description (with equations) of the representation of the species-specific biomass in ForClim v.3.3 can be found in Mina (2015).

Deadwood volume

The deadwood volume includes the volume per hectare of standing and lying trees with DBH ≥ 5 cm that die naturally (Cordonnier et al. 2013). Naturally-dead trees were included in deadwood volume irrespective of the decomposition stage. As ForClim does not simulate deadwood decomposition and carbon turnover, the amount of deadwood in the stand accumulates over time in the simulations.

Rockfall protection index

The index expressing protection against rockfall is calculated based on the *Probable Residual Hazards (PRH)*, which is the percentage of rocks that are able to pass through a forested slope (Cordonnier et al. 2013). The 10 indices differ depending on the diameter and density of the rock for which they express protection (five types of boulders and two rock densities; see below) and are calculated as a function of:

1. slope angle (in degree; specific input for each RST; see Table 2 in the main paper);
2. initial free fall height of the rock (F_{ih} ; value set to 20 m for all RSTs);
3. diameter and density of the rock (different depending on the RPI considered; for the selected RPI4, rock diameter $\Phi_{rock} = 1.68$ m and rock density $\rho = 2400$ kg/m³; volumes, rock diameters and densities for the other nine RPI can be found in Cordonnier *et al.* 2013);
4. stem density and average DBH of the current stand (given in stems/ha and cm respectively; both simulated by ForClim);
5. percentage of evergreen and deciduous species in the stand (simulated by ForClim).

$$A = \frac{(\Phi_{rock} \times N \times 250 \times \cos(\text{slope}^\circ)) \times (EvG + (DeD \times 1.7)) \times 38.7 \times \overline{DbH}^{2.21}}{3.352 \times 10^4 \times \left[0.5 \times \rho \times \pi \times \left(\frac{\Phi_{rock}}{2} \right)^2 \times \left[\min \left(\sqrt{\left(2 \times 9.81 \times \left(F_{ih} + \left(\frac{250}{\cos(\text{slope}^\circ)} \right) \times \max(\tan(\text{slope}) - 0.6; 0.00086) \right)} \right) \times 0.64 \times \text{slope}^\circ \right]^2 + 0.25 \times \rho \times \pi \times \left(\frac{\Phi_{rock}}{2} \right)^2 \times F_{ih} \right]}$$

$$B = \frac{(\Phi_{rock} \times N \times 250 \times \cos(\text{slope}^\circ)) \times (EvG + (DeD \times 1.7)) \times 38.7 \times \overline{DbH}^{2.21}}{3.352 \times 10^4 \times \left[0.5 \times \rho \times \pi \times \left(\frac{\Phi_{rock}}{2} \right)^2 \times \left[\min \left(\sqrt{\left(2 \times 9.81 \times \left(F_{ih} + \left(\frac{250}{\cos(\text{slope}^\circ)} \right) \times \max(\tan(\text{slope}) - 0.6; 0.00086) \right)} \right) \times 0.8 \times \text{slope}^\circ \right]^2 + 0.25 \times \rho \times \pi \times \left(\frac{\Phi_{rock}}{2} \right)^2 \times F_{ih} \right]}$$

If the basal area of the stand > 10 m²/ha:

$$RPH = \max(0.01; 1 - A);$$

If the basal area of the stand < 10 m²/ha:

$$RPH = \max(0.01; 1 - B)$$

$$RPI = 1 - RPH \quad (\text{between } 0 \text{ and } 1)$$

An *RPI* of 0.99 expresses very efficient protection against rockfall (99% of rocks are stopped).

Avalanche protection index

Similarly as for rockfall, the index of protection against avalanches was calculated based on current stand parameters and slope of the site. Input data for the calculation of the index were:

1. stand basal area (G, in m²/ha; simulated by ForClim);
2. average DBH of the current stand (in cm; simulated by ForClim);
3. slope angle (in degree; specific input for each RST; see Table 2 in the main paper).

For pure evergreen stands (> 70% evergreen species):

$$API = \min \left[\frac{G}{(0.2901 * \overline{DBH} + 1.494) \times (0.1333 * slope^{\circ} - 3)} ; 1 \right]$$

For mixed and pure deciduous (incl. *Larix decidua*) stands (<70% evergreen species):

$$API = \min \left[\frac{G}{(0.528 * \overline{DBH} + 1.5566) \times (0.1333 * slope^{\circ} - 3)} ; 1 \right]$$

The value of API is included between 0 and 1. API = 1 indicate very efficient protection against avalanches.

Appendix S3: Additional simulation outputs

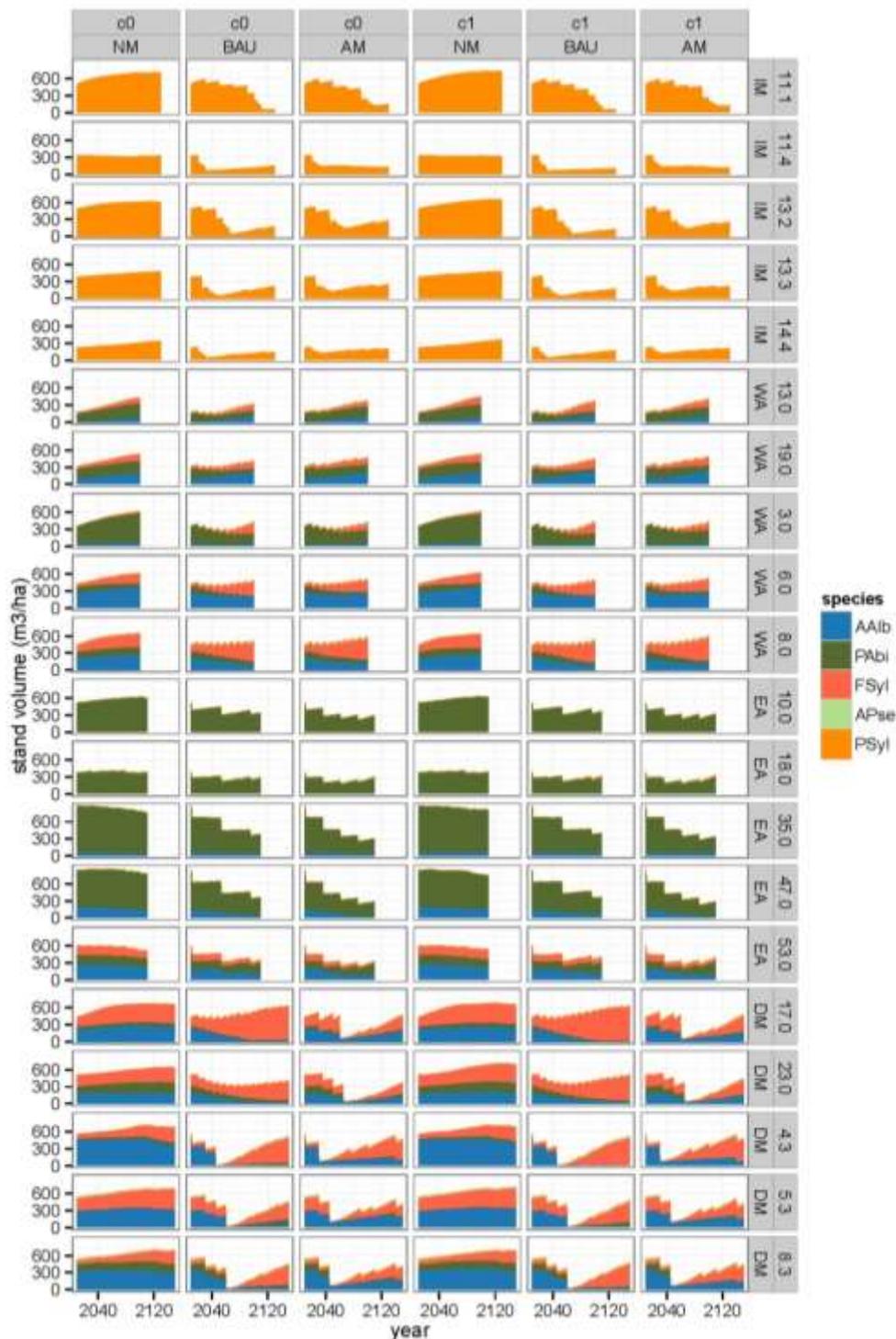


Fig. S3.1: Simulated volume by species for each RST in the four CSAs (IM: Iberian Mountains; WA: Western Alps; EA: Eastern Alps; DM: Dinaric Mountains) under the three management scenarios (NM: no Management; BAU: Business-As-Usual; AM: alternative management) and the five climate scenarios (c0: current climate; c1 to c5: climate change). Species: AA1b = Silver fir; PA1b = Norway spruce; FSyl = European beech; APse = Sycamore maple; PSyl = Scots pine.

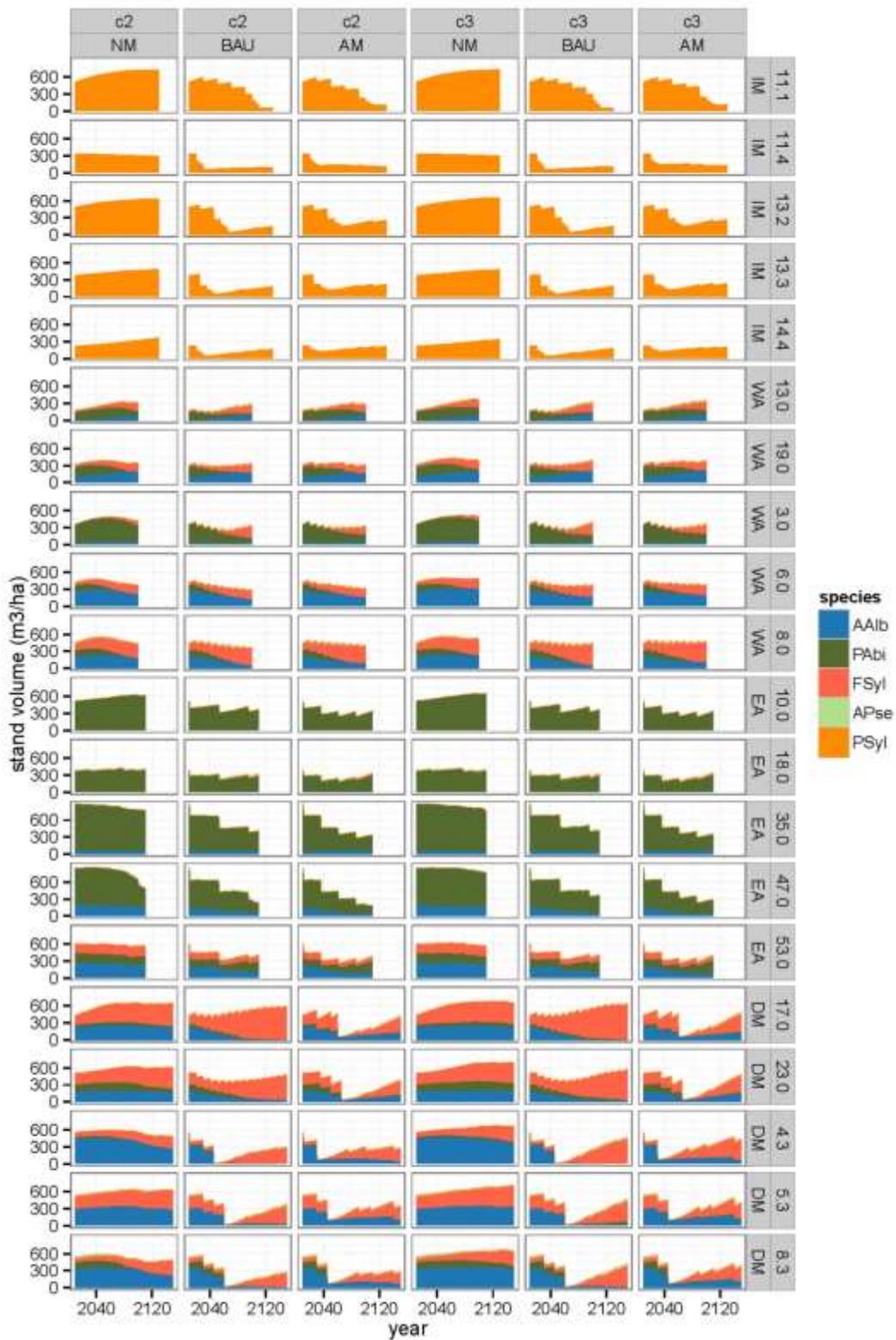


Fig. S3.1 (continued).

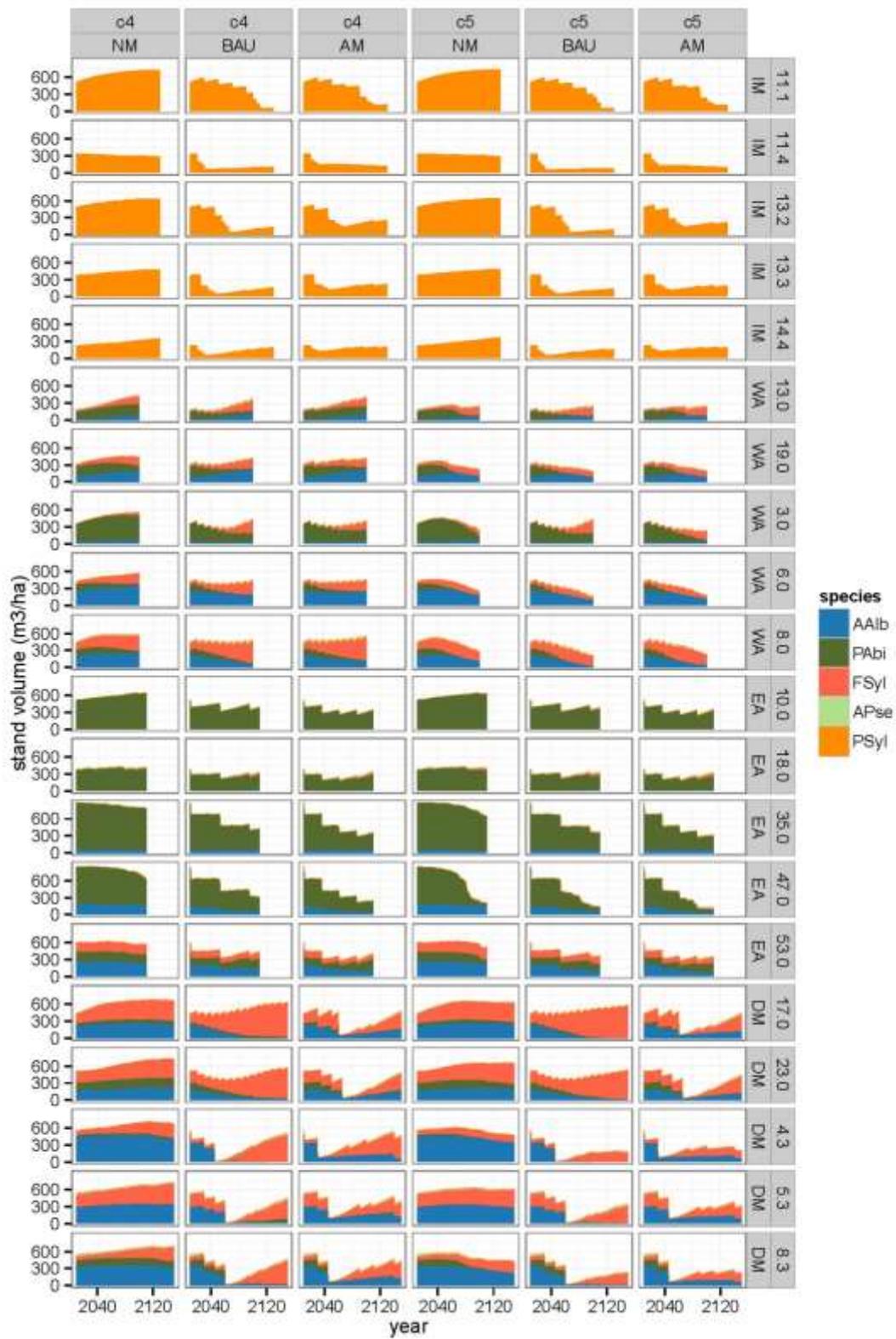


Fig. S3.1 (continued).

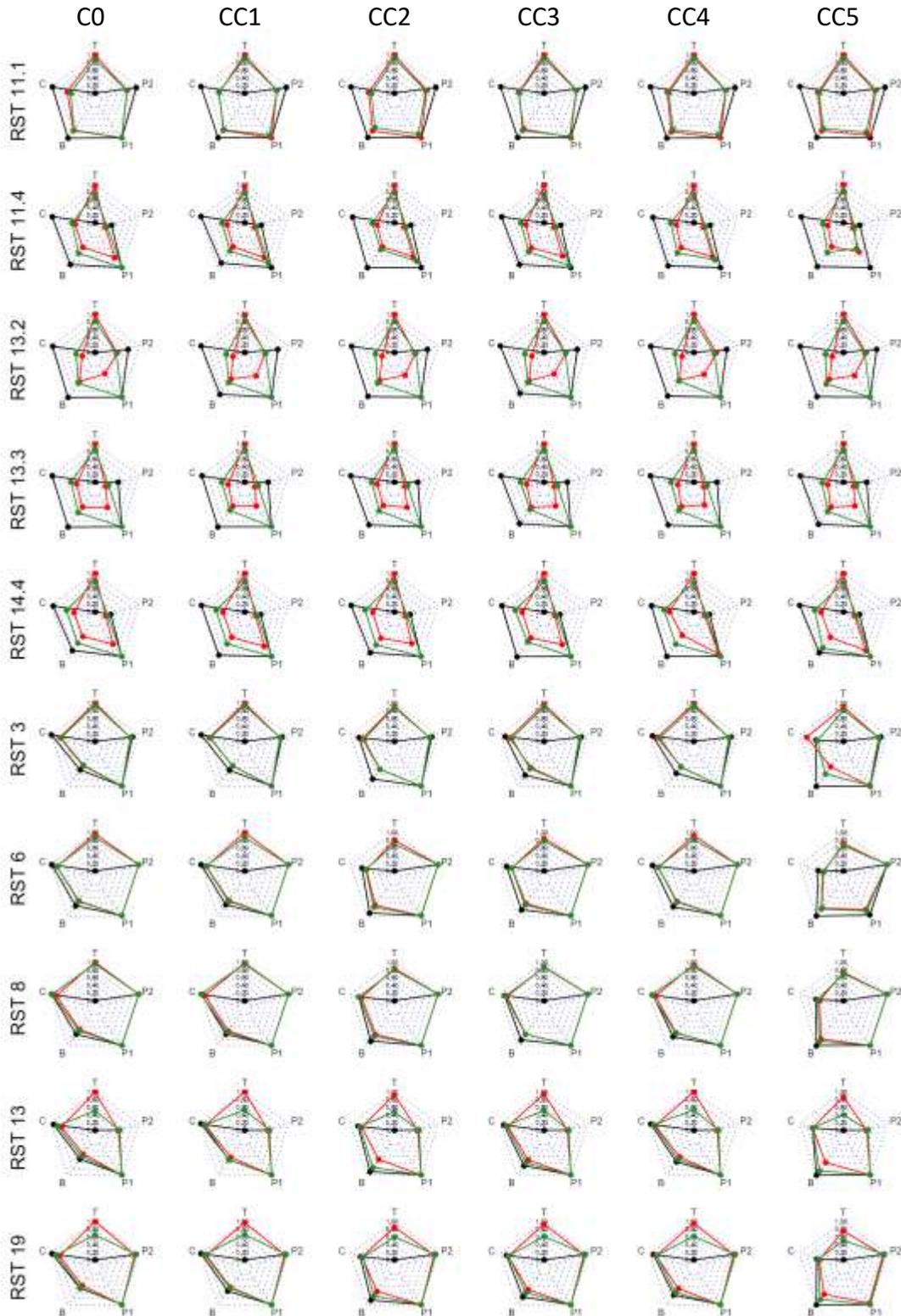


Fig. S3.2: Radar plots of the projected future provision of the four ES (T: timber production; C: carbon storage; B: biodiversity conservation; P1: protection against rockfall; P2: protection against avalanches). Results for the different management regimes are shown for simulations under current climate conditions (c0) and all five climate change scenarios (CC1 to CC5) for all RSTs included in the study.

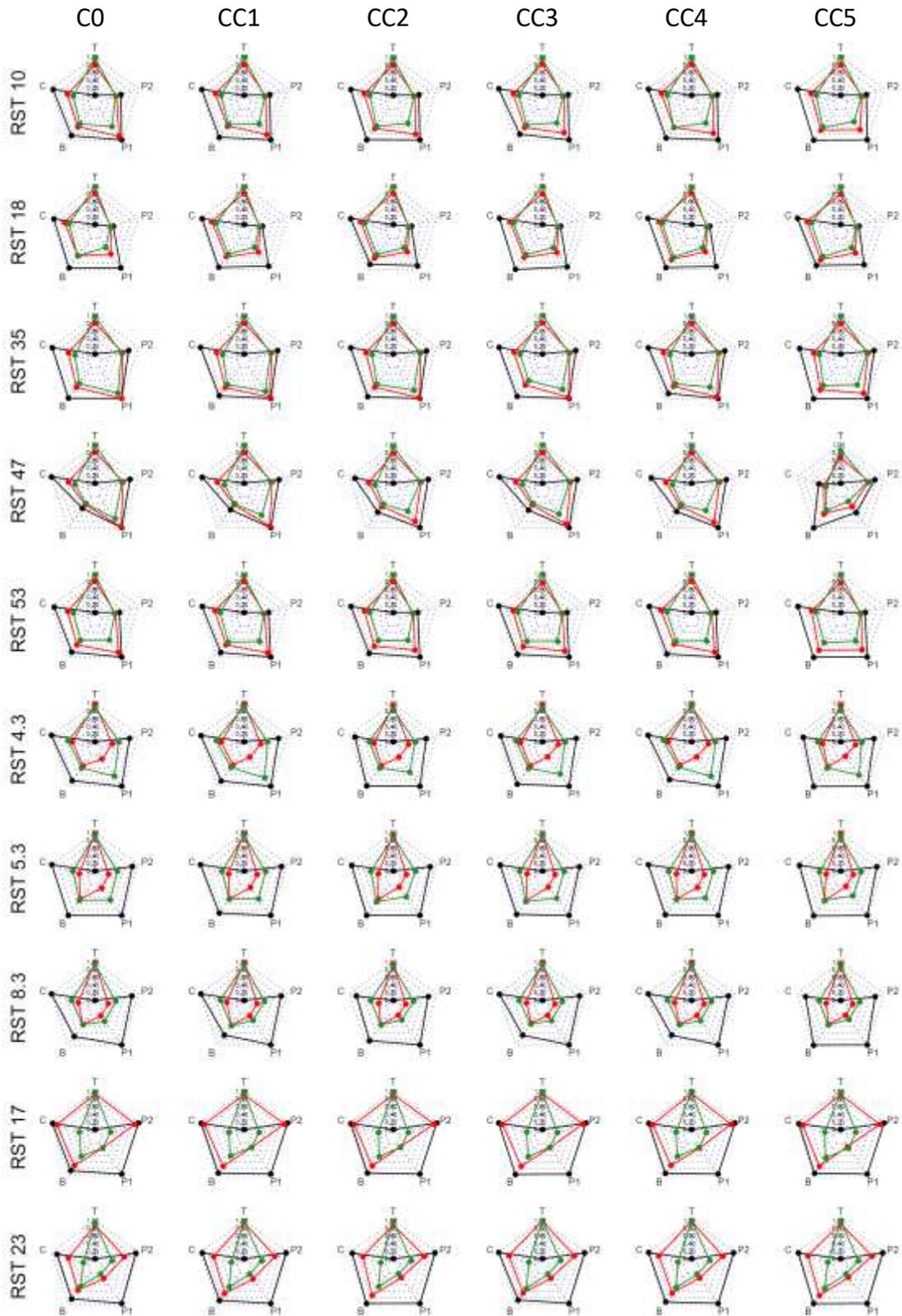


Fig. S3.2 (continued).

Appendix S4: Supplementary Discussion

Additional discussion on methodological aspects

We used the climate-sensitive forest gap model ForClim, which had been tested and validated in multiple studies (Didion et al. 2009; Rasche et al. 2011; Mina et al. 2017) and was found to be a valuable tool for studying stand dynamics along environmental gradients (Bugmann and Solomon 2000) and for decision support in forestry (Rasche et al. 2013). For simulating forest development in the Iberian Mts, we used a modified formulation of the model (see section 2.2 in the main paper) that better captures the influence of summer drought on Scots pine growth (Mina et al. 2016). Although simulations using the original v.3.3 in the RSTs of the Iberian Mts may have led to different results and that the robustness of forest gap models under climate change scenarios may need further investigations, we are confident that using a locally adapted and mechanistically refined model was preferable for simulating forest dynamics in this CSA.

It is important to take into account that albeit we presented a multi-faceted assessment of the future provision of multiple ES in multiple case study regions under a wide range of climate scenarios and several management regimes, we chose to analyze the potential relative average changes between indicators in the long term, rather than evaluating their quantitative variation over time. Thus, further studies should elucidate such additional, potentially very important aspects because it is often the extreme conditions that are of concern for forest management (e.g. regarding protection from natural hazards), rather than long-term averages (cf. Smith 2011; Reichstein et al. 2013).

We also did not evaluate the importance of ES for each CSA based on regional societal demand. Clearly, some ES will be of higher importance in specific mountain regions and some of the ES demands are likely to change in the future as well. For example, protection against rockfall and avalanches are not very important in stands characterized by gentle slopes (e.g., Western Alps) or at low elevations (e.g., Dinaric Mountains) but they are crucial in steep stands at medium-high elevation (e.g., Eastern Alps; cf. Maroschek et al. 2014). Thus, we acknowledge the importance of regional studies incorporating different perceptions of ES functions based on stakeholders, decision-makers and the involvement of local experts (e.g., Haida et al. 2015), so as to balance our supply-oriented perspective on ES provision by the actual demand.

Moreover, we acknowledge that timber production may not be a perfect indicator of economic provisioning services, which would have required a detailed market analysis of harvesting costs and timber prices at both local and regional scales (cf. Hahn et al. 2014). We also did not account for the impacts of forest management operations and the storage of wood-based products over the entire carbon cycle when calculating the quantity of carbon stored by the forest. A throughout quantification of the ‘carbon impacts’ associated with forestry operations, transport of wood material (e.g., using Life Cycle Assessment methods; cf. Mirabella et al. 2014) combined with an evaluation of different allocation scenario of wood-based products which contribute in the carbon

storage (Jungmeier et al. 2002) would have been needed. The inclusion of these aspects were clearly beyond our study on forest dynamics and ES provision under climate change but we recommend further investigations on these aspects.

Lastly, our evaluation study was based on a series of management scenarios that were defined by local forestry experts prior the simulation runs (Klopčič et al. 2013). Since we wanted to explore potentially applicable management regimes in order to deliver clear recommendations to practitioners in the different regions, we preferred to use this data-driven approach based on expert knowledge. However, different approaches for such as multi-criteria decision analysis (Uhde et al. 2015) and financial optimizations using bioeconomic models (Knoke and Seifert 2008) could be applied as decision support tool in forest management planning (e.g., see Hahn et al. 2014 for a study in the framework of the ARANGE project).

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Synthesis

In this thesis, I aimed to assess the potentials and limitations of current and alternative forest management strategies for the provision of ecosystem services by European mountain forests under future climate. To this end, I further developed and evaluated the forest gap model ForClim, and focused on two aspects that are crucial when attempting to simulate long-term forest dynamics: the modeling of harvesting and of growth response to drought. I applied a first version of the model to study current and alternative forest management strategies in a regional case study under climate change (*Chapters I and II*). Thereafter, I developed a novel approach for considering intra-annual variations of growth response to drought (*Chapter III*), a feature that is not considered in most dynamic vegetation models but that is of high relevance when such models are applied in sites where drought is the main growth limitation (e.g., Mediterranean forests). Finally, I applied the model in four European mountain ranges and investigated the potential impacts of climate change – and management regimes – on the provision and relationships of multiple ecosystem services (*Chapter IV*).

Below, I discuss the main findings and provide recommendations for future research. I divide the topics addressed in the different chapters of the thesis in two main parts: (1) development and applicability of ForClim, and of gap models in general, in particular related to the topics discussed in the first part of *Chapter I* and in *Chapter III*; (2) projections of future forest dynamics and evaluation of ecosystem services in European mountain forests under scenarios of climate change and management (second part of *Chapter I*; *Chapters II and IV*). Lastly, I draw general conclusions on the relevance of the results for the scientific modeling and forest management communities.

Model development and applicability

General discussion of the results

Simulation of accurate values of basal area

In earlier studies, anomalous behavior of ForClim has been pointed out (cf. Rasche 2012), particularly with respect to overcome a strong underestimation of growth rates (and therefore also basal area). Prior to the development of ForClim v3.3 (*Chapter I*), I performed a series of simulations at multiple sites in a range of European mountain forests (e.g., Austrian Alps, Dinaric Mountains, Swiss Alps) followed by sensitivity tests of the model parameters for the most dominant species (i.e., Norway spruce, silver fir, European beech). These tests revealed that the underestimation of growth was not caused by climate-related limiting factors, but most likely by the feedback on growth that is exerted by the “crown length” growth factor, which had been introduced by Didion et al. (2009) to take into account the self-pruning of tree crowns under heavy shade. In ForClim v3.0, this growth reduction factor acted as an independent multiplier in the equation describing diameter increment (Didion et al. 2009), i.e. it had a very strong and direct effect on simulated growth rate. This made the model incapable of producing high volume and basal area, contrary to what is often observed in inventory data of both managed and unmanaged stands.

With ForClim v3.3 as developed in this thesis, no systematic underestimation of basal area was observed any more, especially in subalpine conifer-dominated stands where the problems were most evident (see Appendix 4 in Rasche 2012). ForClim reproduced stand basal area and diameter distributions remarkably well, not only at the Swiss sites previously used for evaluating model performance (Rasche et al. 2011) but also in stands located outside the Alps, such as in the Slovenian Dinaric Mountains, an area for which the model had never been applied before. Further applications of ForClim v3.3 in the framework of this dissertation (*Chapter IV*) confirmed the capability of the model to reproduce high values of basal area and standing volume at very diverse sites across the Alpine region. Although ForClim – as any other ecological model – has unavoidable limitations and trade-offs between realism, accuracy and generality (Bugmann et al. 2010), these encouraging results confirm that ForClim is a broadly applicable forest model indeed, and it can successfully be employed under a wide range of conditions of climate and species composition.

Simulation of forest harvesting

Several studies evaluated the effects of management on forest growth using modeling approaches (Lindner 2000; Taylor et al. 2008; Guillemot et al. 2014). In the majority of these investigations, the harvesting functions were not described in sufficient detail. Moreover, the management algorithms were rarely tested whether the simulation results are sensitive to the choice of the ap-

proach for simulating harvesting (Rasche et al. 2011). Interestingly, my analysis in *Chapter I* revealed that empirical harvesting algorithms, such as removals of single stems using static diameter classes, may fail to correctly capture management interventions and can lead to sharply different results compared to analytical harvesting functions (e.g., thinning algorithms that stochastically distribute stems to be removed based on the simulated diameter distribution); this is in stark contrast to the recommendation by Rasche et al. (2011), who suggested that “generic” functions will normally be sufficient. In my model evaluation exercise, these differences depended largely on initial stand structure. Thus, while recommending that in general analytical harvesting algorithms should be preferred for simulating forest dynamics with gap models, my results clearly indicate that the choice of management algorithms is a key aspect when such models are employed for projecting the dynamics of managed forests. Although simulating management interventions is typically viewed as being less complex and sensitive than modeling natural tree mortality (e.g., Bircher et al. 2015), the choice of the harvesting function should be done with great care, as mismatches between simulated stand structure and prescribed removals can jeopardize the reliability of any projections.

Simulation of the effect of drought on tree growth

Prior to this thesis, ForClim has never been evaluated in detail and applied in drought-prone regions such as the sub-Mediterranean forests of Europe. Bugmann (1994) briefly discussed the problem of capturing drought in the Insubrian and Mediterranean bioclimatic zones, where annual precipitation can be higher than 1000 mm (e.g., in the southern range of the Alps, but also in the mountains of Central Spain), but strong drought periods may still occur during the growing season. Later, Bugmann & Cramer (1998) proposed a refined definition of both the soil moisture balance and the representation of drought in ForClim, a formulation that is still used in ForClim v3.3. However, the effect of drought is the same in each month of the growing season; furthermore, the performance of this new model version was not tested in the Mediterranean area.

In *Chapter III*, I proposed a method for considering intra-annual growth responses to drought in ForClim, but as a matter of fact the new algorithm is also applicable to other dynamic vegetation models. My goal was to create a model version that could be used for reliable simulations in both Mediterranean and temperate biomes while retaining the same order of complexity as the current version, which has been found to have broad applicability, as discussed above. It is clear that similar model performance could have been achieved for Central Spain and the Valais simply by modifying (“tuning”) species parameters, e.g. by increasing the drought tolerance parameter for Scots pine. However, in my opinion such modifications would not have treated the “disease” of the model (i.e., inability to capture intra-annual growth responses to drought) but only the “symptoms” (i.e., underestimation of forest properties in drought-prone sites). In addition, if parameters are “tuned” to match locally measured patterns of vegetation, it is likely that the predictive ability of the model is lost when environmental conditions are changing; hence this approach typically is self-defeating in the context of global change impacts on ecosystems.

I acknowledge that improvements to the modeling of (1) the water balance, for example by enhancing the representation of soil properties (e.g., by implementing multi-layer soil profile; cf. Manusch et al. 2014) and (2) water uptake may have been helpful to further increase model accuracy in dry sites (see recommendations below). Since ForClim assumes a very simple soil scheme that is based on a single soil layer (Bugmann and Cramer 1998) and that modeling rooting depth and soil hydrology at high resolution has been recognized to be pivotal in dynamic vegetation models (Ostle et al. 2009; Manusch et al. 2014), future studies focusing on this aspect in ForClim would be highly welcome.

Although for this work I focused on single-species stands of Scots pine only, I was able to demonstrate the better performance of the new formulation of ForClim for matching observed basal area and stem numbers when intra-annual growth patterns are considered. The outcomes presented in the chapter clearly demonstrate that the annual drought index based on an arithmetic average over the growing season (Bugmann and Cramer 1998) cannot capture the season-specific influence of drought and thus should not be used for simulating forest dynamics in sites where highly seasonal drought plays a key role for determining forest composition and productivity. This is not only valid in Mediterranean climates, but also in dry inner-alpine regions (e.g., Valais area in Switzerland), where the model produced unsatisfactory results unless species parameters were calibrated to local conditions (Weber et al. 2008).

In addition, the results from *Chapter III* highlighted the potential of tree-ring data for improving the simulation of drought effects on tree growth in forest gap models, other than for calibrating the growth response to temperature (Rickebusch et al., 2007) or for implementing empirical growth-mortality functions (Bircher et al., 2015). This method was powerful for improving ForClim, but it could be used in other gap and possibly even in dynamic vegetation models that aim to simulate species distributional shifts at continental to global scales (e.g., Hickler et al. 2012). Given the large availability of tree-ring data worldwide, I believe that this novel methodology could be expanded for many tree species to develop a version of ForClim that could be successfully employed to simulate forest dynamics in both temperate and Mediterranean climatic zones for a wide range of species.

Model applicability

During the last two decades, ForClim have been applied in numerous studies. The model was employed for simulating forest dynamics at sites in Central Europe (Bugmann and Cramer 1998; Morin et al. 2011), the Alps (Risch et al. 2005; Wehrli et al. 2005) or in the Pacific Northwest of North America (Bugmann and Solomon 2000; Gutiérrez et al. 2016). Other areas of application included eastern North America (Bugmann and Solomon 1995), northeast China (Shao et al. 2001) and the Colorado Front Range of the Rocky Mountains (Bugmann 2001). In most of these studies, however, the model was used for simulating potential natural vegetation or forest dynamics under unmanaged conditions (but see Rasche et al. 2013). With the exception of the recent

study by Bircher (2015) for forests in Switzerland, ForClim has never been initialized with high resolution stand data and consequently applied for simulating multiple management regimes under different climate scenarios. In this context, *Chapter IV* of this dissertation represented an important step forward in the applicability of ForClim, where I demonstrated that the model can be applied for these purposes at multiple locations throughout Europe.

For the model applications in the Alps and the Dinaric Mountains, I used ForClim v3.3, which is based on the classical approach of gap models for modeling drought (Bugmann and Cramer 1998). For simulating Scots pine stands in Central Spain, ForClim v3.3 failed, and thus I applied the novel formulation developed in *Chapter III*. Although this version works well for this type of forest stands, it can be used for simulations in pure Scots pine forests only. In addition, the Iberian sites were located in the mountains of Central Spain, i.e. at the southern distribution edge of this species. Although characterized by strong summer drought, these pure Scots pine stands cannot be considered typically Mediterranean as they experience a continental climate that features rather high amounts of annual precipitation compared with other, more typical Mediterranean sites (Camarero et al. 2010; Henne et al. 2015).

Thus, we are still far from having a ForClim version that can be applied consistently in both the temperate forests of Central Europe and in Mediterranean woodlands. Although simulations using the classic version of ForClim (v3.3) in Iberian mountain forests may have led to very different results, I am confident that using the new version was preferable for modeling forest dynamics in this region and thus I was able to include an additional case study area within this comprehensive European study.

Modeling stand dynamics under management and climate change: outlook and research needs

Every mathematical and computer model, whether built on a few empirical regression functions or on process-based algorithms that result in complex numerical simulations, is a strong simplification of reality that, if well conceived, can help scientists – and not only them – to know, understand and predict system behavior (Kimmins et al. 2010). Since the full range of components and processes operating at different temporal and spatial scales in a real (eco)system cannot be taken into account in any model, every model is always imperfect and leaves space for further development. Below, I report the most important research needs for further improving ForClim that I identified during this dissertation, especially if we aim at using the model as a forestry decision-support tool in the context of climate change.

Tree mortality

Simulation results in *Chapters I, II and IV* clearly indicate that the modeling of individual tree mortality (Keane et al. 2001) and sapling establishment (Price et al. 2001) need to be improved for simulations of managed stands. Mortality functions in forest gap models typically combine “background” and stress-related algorithms (see Bircher 2015) and were initially developed for simulating potential natural vegetation and “undisturbed” forest dynamics. These formulations, however, tend to fail reproducing natural mortality in managed growth-and-yield plots, and consequently the model cannot accurately depict forest properties such as basal area and stem number (Bircher et al. 2015). In intensively managed stands, natural mortality rates and deadwood pools are usually lower than under unmanaged conditions, as timber harvesting usually removes trees before they die naturally (Hura and Crow 2004; Gibb et al. 2005; Powers et al. 2012). It would be valuable to implement in the model a mechanism by which the trees that have a higher probability of mortality (e.g., individuals experiencing slower growth) would be removed first during a harvesting intervention. This would better emulate the choices that forest managers make during harvesting interventions, and it would enhance the representation of the amount of deadwood in intensively managed stands. Additionally, I suggest improving the representation of standing and lying dead trees, such that it would become possible to simulate snag removals and salvage logging (Irauschek et al. in prep).

Regeneration

Most forest gap models represent regeneration as the appearance of a number of saplings in the patch based on environmental filters, and they assume a constant seed rain without dispersal limitation and feedback from the upper canopy (Price et al. 2001). In ForClim, the only difference to this classic approach is described in Risch et al. (2005), where species-specific shade tolerance (kLa) was included as a multiplier to the number of newly established trees in a patch. This was made to account for the different regeneration strategies of shade-tolerant vs. -intolerant species (i.e., pioneer species typically produce more seeds under favorable conditions). This may be suitable for investigating the long-term dynamics of natural vegetation along environmental gradients. However, I believe that this approach is likely to be inappropriate to project future stand properties in intensively managed forests, in which – most of the time – harvesting intends to favor the regeneration of the most economically valued species, which typically are present in the canopy already (e.g., shelterwood fellings or regeneration cuts; see Wagner et al. 2010 for silvicultural systems in beech-dominated forests). If in the future ForClim should be applied prevalently in management-oriented studies as a decision support tool, it would be highly beneficial to modify the modeling of sapling proportions according to the abundance and the species composition of the overstorey (e.g., Lexer and Honninger 2001). This would help to obtain more realistic simulations of species composition without the need for calibrating the establishment potential of the species based on inventory data (as done in *Chapters I and II*) or excluding pio-

neer species from the list of simulated tree species. In addition, many deciduous species are able to prolong their presence in the stand via sprouting when seedlings would be incapable to establish due to adverse environmental conditions (Price et al. 2001). Thus, modeling of vegetative reproduction would be valuable as this feature is observed in about one-third of all temperate tree species (Price et al. 2001). Although the implementation of vegetative reproduction in ForClim would be possible, I think it may not be straightforward since the resprouting ability of the different species depends on several factors such as stump diameter and age of the parent tree (Matula et al. 2012). Although this would require the estimation of several additional species-specific parameters, it appears feasible with some effort (cf. Kienast 1987).

Tree height

The implementation of a site-specific maximum tree height in ForClim substantially improved predictions of tree heights without the need to calibrate the model using locally-derived diameter-height relationships (Rasche et al. 2012). Nevertheless, when the environmental factors that are limiting growth (i.e., drought index, growing degree-days) approach the species-specific maximum tolerance, which may occur when running simulations under climate change, maximum height rapidly decreases, thus inducing a reduction or even a complete halt of diameter growth and an increase of growth-induced mortality (see Appendix B of *Chapter III*). Similarly as Bircher (2015), the simulations that I ran in this dissertation projected a large decrease of basal area for drought-intolerant species, particularly at low elevations (e.g., Norway spruce in the Dinaric Mountains and in the Alps, but in some cases also European beech). Even though on the one hand I believe that some species are particularly sensitive to changing climatic conditions, on the other hand I doubt that the declines in basal area that are induced by drought-related mortality events in the simulations would actually occur with the same magnitude in reality, especially in the case of well-established individuals. Further investigations are needed to better model the reduction of maximum height and particularly its consequences on growth rates and stress-induced mortality. Among others, I would recommend revising the linear relationship between environmental factors and height reduction, for example by using asymptotic functions, or by linking maximum height reduction to the growth-reducing factors directly, as proposed in *Chapter III*.

Applicability at the southern and northern edge of temperate forests

Currently, with the exception of Holm oak (*Quercus ilex*), no other Mediterranean species are parameterized in ForClim (e.g., Mediterranean pines such as *Pinus halepensis*, *P. pinaster*, *P. pinea*; or *Juniperus spp.*, *Quercus cerris*, *Ostrya carpinifolia* and *Pinus nigra*, etc.). Mediterranean pines and oaks are better adapted to drought than Central European species and thus may be able to replace current species at their lower altitudinal and latitudinal distribution limits (Hanewinkel et al. 2013). Including these species in ForClim would therefore be beneficial, alt-

though the process of estimating species-specific parameters based on field data and physiological experiments can be quite difficult and time demanding. In addition, given the number of processes that are explicitly modeled in the current version of ForClim (e.g., dynamic height/diameter relationship, dynamic crown structure; cf. Didion et al. 2009, Rasche et al. 2012), the parameterization procedure may be more challenging than for the earlier model versions (e.g., see Appendix II in Bugmann 1994).

During this dissertation I also performed explorative simulations at the northern edge of temperate forests and in the boreal zone (Mina and Bugmann 2013). These tests revealed strong deficiencies of ForClim to reproduce potential natural vegetation and realistic amounts of basal area at Vilhelmina (Sweden) and Hyytiälä (Finland). Most species were unable to establish due to limitations by temperature (winter temperature and growing degree-days), and those species that were able to establish exhibited strong limitations due to drought. I believe that major modifications would be required for successfully applying ForClim in boreal forests, and this is why the northern European mountain ranges were not considered in my thesis. I would recommend: (i) a reconsideration of the one-layer soil submodel and its conversion to a two- or multi-layer model, also accounting for vertical root distribution and varying water uptake rates (Manusch et al. 2014), (ii) the inclusion of a submodel that takes into consideration snow accumulation and melting (e.g., Rutter et al. 2009), and (iii) a revision of the species-specific parameters expressing limitations to minimum winter temperature and growing degree-days for those species that grow in both temperate and boreal forests (e.g., Scots pine, Norway spruce, European larch, birch).

Natural disturbances

The consideration of natural disturbances (e.g., wildfire, windthrow, pests and insect outbreaks) in ForClim would be advantageous as well, especially in the context of climate change where these agents are predicted to become more frequent and severe in the future (Millar and Stephenson 2015). A possible approach would be to change the structure of the model towards a hybrid simulation tool that is based on cells that are defined in a spatially explicit manner with neighbor interactions and with the possibility to expand the simulation area to a (small) landscape (e.g., the model SORTIE in Pacala et al. 1996; or PICUS in Lexer and Honninger 2001). Although this would be technically feasible, I believe that such disturbance processes should be evaluated at the (true) landscape scale rather than at the level of a few stands. Therefore, I would rather suggest complementing the stand-scale simulations of ForClim with those from a larger-scale model, for example LandClim (Schumacher et al. 2004), iLand (Seidl et al. 2012) or other forest landscape models (Perera et al. 2015). This multi-model approach could add robustness to the results of climate impact assessments and would allow for exploring different spatial scales and research questions within the same study (Elkin et al. 2013).

Nonetheless, I am of the opinion that adding further ecological feedbacks between processes in the model should be done carefully, as increasing model complexity is likely to amplify the demand for species- and site-specific parameters, calibration data and computer power (Bugmann et al. 2010), and it may lead to pathological behavior in case of positive feedbacks within the model in which errors can amplify. This may have strong consequences for the “out-of-the-box” applicability (i.e., without particular needs for re-parameterization to specific site conditions), which I think is the finest strength of ForClim and similar models.

Lastly, for promoting the use of the model beyond the scientific community (i.e., for forest practitioners, stakeholders and decision makers), a visualization tool and an intuitive graphical user interface (GUI) are a prerequisite. Considerable progress has been made for ForClim with the integration of the GUI “ForSim” but, in my opinion, the preparation of input files and model initialization with measure stand data, as well as the integration of management interventions is still not a straightforward process. It is unlikely that these tasks could be accomplished independently and without major efforts by first-time users. Thus, further work aimed at simplifying the initialization and implementation processes is certainly needed for boosting the use of the model beyond researcher’s offices. I believe that further advantages could result from the increasing diffusion of mobile technologies (e.g., Rosset et al. 2015).

Evaluating current and alternative forests management strategies under climate change

General discussion of the results

This dissertation provided insights that should be useful for researchers interested in developing and applying simulation models of forest dynamics (e.g., simulating management interventions and drought effects). Beyond this, I contributed to a comprehensive assessment of multifunctional forest management strategies in European mountain forests in the context of a large collaborative project (Bugmann et al. 2016). Furthermore, I believe that the model-based projections that I presented will be helpful for forest practitioners regarding the future impacts of climate change and management regimes. Hereafter, I discuss the implications of my results first for the Dinaric mountain forests (*Chapter I, II* but also part of *Chapter IV*) and then for the other three mountain regions (Iberian Mountains, Eastern and Western Alps; *Chapter IV*).

Dinaric mountain forests

In the Dinaric Mountain region, forest management has a long tradition to promote timber production and nature conservation, which are the most important ecosystem services for local communities. The presence of conifers (silver fir and Norway spruce) in the Dinaric fir-beech

forests has high economic and ecological importance. This is mainly because of their economic value, but also because mixed stands are likely to be more resistant to natural disturbances than monocultures (Knoke et al. 2008; Neuner et al. 2015). In addition, mixed forests provide higher habitat diversity (Cavard et al. 2011), are more productive (Pretzsch and Schutze 2009) and generally promote higher levels of multiple ecosystem services than pure forest stands (Gamfeldt et al. 2013). The regional climate change projections in the Dinaric Mountain area indicate an overall increase of mean temperature and a decrease of precipitation, the latter particularly pronounced during the summer months (see *Chapter II*). These forecasted changes are expected to induce substantial shifts in species composition (e.g., increase proportions of beech; cf. Poljanec et al. 2010) and productivity in the Dinaric Mountains.

Until the work presented in my dissertation, the projected impacts of climate change on productivity and species composition in this region were mostly discussed only indirectly, based on the analysis of inventory data (Ficko et al. 2011) and regeneration rates (Boncina et al. 2009). The few modeling studies suggested very pessimistic scenarios for Dinaric fir-beech forests, forecasting their complete disappearance from the Slovenian territory by the end of the 21st century under the most severe climate change scenario (Kutnar et al. 2009; Kutnar and Kobler 2011). However, these projections were based on shifts of potential natural vegetation; they considered neither current stand properties such as species composition or tree size distribution, nor the dynamic behavior of forest stands including lag effects and the role of forest management. The simulations performed in this thesis considered all these aspects and delivered practically relevant recommendations for multifunctional forest management in this region.

Under business-as-usual management (BAU) and climate change, my results showed that the decline of conifers, especially the currently dominant silver fir, and their replacement by European beech would continue in the future, in line with the observed trend during the last decades (Ficko et al. 2011). Ecosystem services such as timber production and biodiversity conservation, as well as carbon storage and protection against natural hazards (*Chapter IV*) would not be threatened by climate change if we consider the entire mountain region. However, my results identified strong differences between stands at low and high elevations. The results clearly showed that stands at lower elevations would be particularly sensitive to climate change, and that forest management (both BAU and alternative regimes) cannot counteract the negative impact of the changing climate on the abundance of conifers in these forests. As a matter of (simulated) fact, the combined effect of management and climate change at these elevations would lead to an absence of conifers by the end of the 21st century. Simulations for stands at middle elevations indicated that European beech would become more dominant, mainly because beech regeneration is more competitive and less sensitive to browsing damage than silver fir (Motta 1996; Klopčič et al. 2010). At high elevations, however, the rise of temperature and the extension of the growing season would favor tree growth, as demonstrated in other empirical and modeling studies (Pretzsch et al. 2014; Tegel et al. 2014). Here, the establishment and growth of conifers would

not be limited by climate change, thus promoting better species mixtures, higher carbon storage and better biodiversity conservation.

The outcomes from my simulations came without major surprises, as studies for other areas had already projected changes in species composition and showed an advantage of broadleaves over conifers under scenarios of climate change (Hanewinkel et al. 2013; CH2014-Impacts 2014). However, the originality of my results lies in the demonstration that forest management interventions are crucial and may foster changes in species composition and cause further decline processes of certain species (Oliva and Colinas 2007). Importantly, the application of alternative management strategies (AM) did not show any advantages for the conservation of conifers and particularly of silver fir, but I was still able to highlight some promising techniques that can be taken into consideration for future conservation practices, such as decreasing fir removals in the low diameter classes and reducing browsing intensity by ungulates. I also showed that, in some cases (e.g., at middle elevations) alternative management regimes could help to achieve a higher provision of multiple ecosystem services (*Chapter IV*). Ultimately, my results confirmed that uneven-aged management regimes in Dinaric mountain forests would deliver higher multifunctionality than even-aged rotations, as the continuous canopy cover promotes carbon storage, biodiversity conservation and protective functions (Boncina 2011; O'Hara and Ramage 2013).

Other European mountain forests

In the other three regions, climate change is expected to induce a strong increase of mean temperatures (from +4.8 to +6.8 °C in summer under the most severe climate change projection) and a reduction of precipitation, particularly during the summer months (from -21% to -59% in summer under the same scenarios). The simulation study presented in *Chapter IV* revealed that the effects of climate change on the provision of multiple ecosystem services are highly heterogeneous among and within the four European mountain regions.

The only region in which I identified strong impacts of climate change in all forest stands, at all elevations and under any management scenario was the Western Alps. Here, forests are mainly composed of Norway spruce, which for economic reasons was promoted strongly over European beech and silver fir by past forest management. The simulation results revealed that a changing climate would induce large alterations in the supply of some ecosystem services, and overall to the provision of multiple ES. Under BAU, model projections indicated a decrease in carbon storage and an increase in the biodiversity index (linked to the amount of simulated deadwood), caused by the intensification of the mortality of drought-intolerant Norway spruce. Alternative management regimes would not be efficient to counteract these effects. For this reason, I recommend that management actions should be directed towards favoring the presence of more drought-tolerant species, which would foster resistance for sustaining a wider array of ES (Knoke et al. 2008; Gamfeldt et al. 2013) and increase resilience by enhancing recovery after disturbance events (Dale et al. 2001). To my knowledge, no other model-based studies on the impact of cli-

mate change and management have been carried out for this region, thus hopefully making the results presented in *Chapter IV* valuable for regional forest management. However, as previously discussed in this *Synthesis*, I acknowledge that mortality of Norway spruce may have been over-estimated, as it is possible that the species is more drought-tolerant than its current representation in ForClim.

Simulations for Scots pine forests in the Iberian Mountains indicated that climate change would not affect the provision of multiple ES but that their changes are mostly attributable to the management regime. These results were rather unexpected, since the region features the typical Mediterranean summer drought, and previous studies have reported strongly negative impacts of recent climate change on Scots pine (Martínez-Vilalta and Piñol 2002; Sánchez-Salguero et al. 2015). Under climate change, simulation results showed that Scots pine growth would not be affected by increased summer drought, whereas regeneration would be impacted strongly by higher winter temperatures. In this case, the simulations showed that AM would be more suitable than BAU to achieve higher multifunctionality, but changes in the management regime would not be urgently needed to compensate for climate change effects. However, given the fact that Scots pine regeneration may be threatened by future climate change, I suggest that this aspect should be considered when planning future management interventions (e.g., promote higher canopy cover during the regeneration phase of a stand for reducing seedling sensitivity to drought events).

The simulations for this region were performed with the variant of ForClim developed in *Chapter III*, which is capable of capturing the intra-annual response of Scots pine growth to summer drought, as tested against empirical data and clearly performing better than the previous model version. Several studies found that spring and summer precipitation is the main limiting factor on Scots pine growth in Central Spain and in other parts of Europe (Eilmann et al. 2011; Génova 2012; Lévesque et al. 2014). However, they also confirmed that the southernmost Scots pine populations are more adapted to dry conditions than northern populations (Herrero et al. 2013) and that there are phenological differences even between sites at different elevations within a region (Sánchez-Salguero et al. 2015). Since the variant of ForClim used in *Chapter III* was calibrated with local tree-ring data, it reflected the adaptation to drought of adult trees of this specific population. As recommended by Sánchez-Salguero et al. (2015), I believe that the inclusion of the local adaptation to site conditions was important for running the model in this area, as observed in the better performance against empirical data, although model projections under climate change are still subject to uncertainty that unfortunately cannot be quantified at the present time.

In the Eastern Alps case study region, forests are mainly composed of Norway spruce and are typically growing on steep slopes; therefore ES such as protection against avalanches and rockfall are very important. My results showed that climate change will not significantly affect ES provision from these forest stands and that BAU is more appropriate than AM for achieving multifunctionality. Related studies basically agree with these findings, but suggest that this region is highly vulnerable to natural disturbances such as bark beetle outbreaks (Maroschek et al. 2014), which were not included in my approach. Triggered by changes in climatic conditions, disturbance

events may strongly affect the future supply of ES from these forests (Seidl et al. 2011; Irauschek et al. in revision). Although certainly useful for assessing differences in ES provision under different management scenarios in the absence of large-scale disturbances, my results for the Eastern Alps would have been more robust and also more useful for practical management if disturbances had been considered (see *Recommendations for future research*).

Beyond assessing the future provision of multiple ES, results in *Chapter IV* showed that climate change is likely to induce changes of synergies and trade-offs between ecosystem services. Changes induced by climate, however, were not as consistent for most of the ES pairs as alterations caused by changes in forest management regimes or changes due to the different region and its biogeographical setting. This confirms that (i) there are profound differences between European mountain forests, which can be detected in the relationships between ES, and (ii) differences in management regimes have higher impacts than changes in the climate. The number of studies focusing on synergies and trade-offs between forest ES has recently increased strongly (Seidl et al. 2007; Dickie et al. 2011; Lafond et al. 2015; Lutz et al. 2015), but only few of them evaluated differences between regions (Biber et al. 2015), within a landscape (Duncker et al. 2012), or under different climate and forest management scenarios (Temperli et al. 2012). I acknowledge that the results in *Chapter IV* had limitations regarding the choice of ES indicators and their analysis (see further below), but I am convinced that with this study I was able to provide both a comprehensive and a fine-scale evaluation of the effects of climate change and management on multiple ES, and also to deliver useful insights on potential changes in the relationships among ES.

In contrast to other studies that have illustrated similar impacts and changes in species suitability under scenarios of climate change on European forests (e.g., Reyer et al. 2014), I think that a distinct advantage of my approach was the inclusion of high-resolution local stand properties as a starting point for the evaluation, thus taking into account the management history of these forests (Temperli et al. 2012). In addition, I simulated management regimes that were developed locally in each case study area, and thus they accurately reflected the current (BAU) and potentially applicable (AM) management practices. Consistently for all four European mountain regions, my results showed that impacts of climate change on the multiple provision and relationships between forest ecosystem services would be lower than the effect of management as a key human-induced disturbance. Only few other studies have focused on the combined impact of local-scale management and different climate change scenarios, and, interestingly, they drew similar conclusions (Köhl et al. 2010; Horemans et al. 2016).

Since the large majority of forests in Europe are managed at least to some degree (Lindner et al. 2014) and only 4% of the woodlands are free of human disturbances (Dominguez et al. 2015), I conclude that past, current and future management regimes must be taken into account when investigating and analyzing the impacts of a changing climate on European forests. This allows us to assess possible measure to reduce their sensitivity and to increase their adaptive capacity to rapid changes in climate (Fitzgerald and Lindner 2013). My model-based results could be used by local practitioners and decision-makers to guide management decisions. Regardless, the simula-

tion studies presented here are undoubtedly an advancement in assessing the potential impacts of climate change and species shifts in mountain forests, despite some model limitations that were discussed in each chapter as well as in this *Synthesis*.

Recommendations for future research

As mentioned above as well as in the individual chapters of this thesis, I think that the major limitation of my applied research studies was the absence of the consideration of natural disturbances such as windthrow events, insect outbreaks or other perturbations (Thom and Seidl 2015), which are likely to be quite important at larger scales in the four mountain regions. As damages due to stochastic disturbance events are likely to increase in the coming decades (Seidl et al. 2014), assessing disturbance vulnerability in a particular forest region can be fundamental in the context of forest management planning. Management interventions may promote the conversion to more adapted forest composition and structure, thus strongly impacting the provision of ES (Attiwill 1994; Millar and Stephenson 2015). Hence, I recommend that future studies be performed using a set of models that operate on different spatial scales, as already proposed by some authors (Elkin et al. 2013; Seidl et al. 2013; Zlatanov et al. 2015).

Even if including disturbance events would have added robustness to the results, expanding the analysis to more stands and simulating additional management strategies would have been beneficial as well. In *Chapter IV*, in order to provide a comprehensive assessment across multiple cases study regions I chose to limit the analysis to the most representative stands (RSTs), and I selected only one alternative management strategy. The RSTs accounted for a large number of stands, as they were identified based on a region-specific stratification of real stands (e.g., the 23 RSTs in the Dinaric Mountains used in Chapter I and II represented a total of 1438 forest stands; cf. Lexer 2013). Yet, further investigations on the provision of ES could be performed specifically in each regional case study area, for example by considering additional, locally important stand types or including further alternative management regimes (e.g., as shown in *Chapter II* for the Dinaric Mountains). In this context, I would recommend to also consider the region-specific societal demands for the different ecosystem services including their perception by local stakeholders (Haida et al. 2015; Huber et al. 2015); this may modify the calculation of ES provisioning, and particularly the valuation of trade-offs and synergies.

The choice of the number and the type of stands and management regimes in my analysis had a high influence on the overall conclusion, but it is important to recognize that the results in *Chapter IV* also depended strongly on the choice of indicators. I selected a restricted number of indicators that best explained each ES based on a multiple factor analysis. For example, the biodiversity conservation index was uniquely based on deadwood in the stand, which, as deadwood decomposition is not explicitly modeled in ForClim, accumulated over time during the simulation period. Follow-up studies should focus on combining multiple indicators for expressing a single ES function, or using region-specific trait-based approaches for their quantification (van Bodegom and

Price 2015), thus assessing the sensitivity of the results to the choice of linker functions, which was neglected in my study.

In addition to the choice of indicators, the methodology used for examining the trade-offs and synergies between them is also quite influential for the final outcomes. In *Chapter IV* I used linear correlation coefficients, which is a common approach for this type of studies (Chan et al. 2006; Beier et al. 2008; Egoh et al. 2008; Zhun et al. in prep). I am confident that in the context of my investigation this was a very practical solution, since I had a large number of scenarios that needed to be compared with each other for the same site (e.g., four case study regions times two management regimes times six transient climate scenarios). In other circumstances, however, other methodologies could be explored for taking into consideration possible non-linear interactions between ES, such as ranked cumulative correlation coefficients and bag-plots (Jopke et al. 2015) or Pareto frontiers (Kennedy et al. 2008; Castelletti et al. 2010).

Conclusions

This dissertation provided a concrete contribution to the assessment of ecosystem services in the framework of a large collaborative EU project and provided insights on processes driving forest dynamics in four European mountain regions. It is noteworthy that most of the simulation studies contained in this thesis led to implications and recommendations for forest management, which – as I believe – highlights the usefulness of this work not only for the ecological modeling community or forest ecologists, but also for forest practitioners and resource managers.

From the modeling perspective, this thesis showed that the accurate simulation of management interventions is key for obtaining reliable model-based predictions of forest dynamics, and that dynamic vegetation models should consider the intra-annual growth responses for better modeling the impacts of drought on tree growth. These types of models certainly deserve further development efforts in order to reduce their uncertainty and increase the reliability of their projections, but I firmly believe that they are important and useful tools for assessing the impacts of anthropogenic climate change, provided that their outcomes are not interpreted as certified predictions but rather as possible future trends given the range of limitations and assumptions.

This work showed that impacts of climate change on forests are likely to vary strongly not only among, but also within European mountain regions due to the local variability of stand structure, composition, and climate. Hence, there is a need in impact studies to carefully consider local and regional differences between European forests, as well as the role of small-scale forest management, since the impact of management is likely to be more important for the future of European mountain forests than the direct effects of climate change.

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Appendix I

Improving the representation of biomass and volume in ForClim

Introduction

In the first chapter of this thesis, I reported improvements of ForClim related to the effect of available light on tree growth and advancements of the management module. In Chapter III, I described how species- and site-specific intra-annual growth responses to drought could be implemented for better simulating drought impacts in dynamic vegetation and forest gap models. In this appendix, I report additional improvements to ForClim that were not described elsewhere, related to the development of its version 3.3. These enhancements focused on further developing model outputs using allometric equations, such as the calculation of stem volume, the estimation of volume and biomass of large and small branches, and improving the biomass equation. Although these modifications did not alter the internal model dynamics (i.e., simulated establishment, growth and mortality were not affected), I believe that having such variables directly calculated by the model is highly useful for application studies, for example when estimating a series of indicators that assess the provision of ecosystem goods and services (Chapter IV).

Implementing volume functions

For estimating forest productivity, Rasche et al. (2012) introduced the calculation of stand volume increment (in $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$) in ForClim. The direct calculation of the stem volume of each cohort, however, has never been implemented in the model code. Since the volume of living, dead and harvested trees are frequently needed for assessing timber production and biodiversity indices, equations for calculating stem volume were implemented in the code of ForClim v3.3. In addition, since the demand for wood energy is increasing in many countries, and evaluating the future provision of this ecosystem service with a model such as ForClim might be useful, I added equations for the calculation of the volume of wood that is typically allocated as fuel-wood, such as small and large branches.

Calculation of stem volume

A wide range of allometric equations for calculating stem volume from different tree-level explanatory variable is available from the literature (e.g., Lehtonen et al. 2004; Zianis et al. 2005). These functions typically derive from tree and stand measurements on forest plots, and the pa-

parameters required are usually species- and site-specific. To avoid adding a series of new species parameters and reduce the general applicability of ForClim, stem volume was calculated using the Denzin formula (Kramer and Akça 1995) following the rationale of Schmid (2014). The Denzin equation is based on the theoretical approach of the stem volume as an irregular cone. The calculation follows the equation:

$$V_{STEM} = \frac{\pi}{4} * D^2 * f * H \quad (1)$$

where stem volume (V_{STEM}) depends on tree diameter (D), tree height (H) and a shape factor (f), which typically varies between different species and stand site. This formula is often simplified (see Kramer and Akça 1995) following the assumptions that $\pi/4 \approx 0.8$; $f \approx 0.5$ and $h \approx 25$ m. Although this simplification may induce some under- and over-estimations of stem volume – especially for very small and large diameter classes – the resulting formula is an easy and universal formulation which is ideal for a rapid estimation of stem volume using only tree diameter as explanatory variable. As the simplified formulation does not require adjustments for tree size and location, the following equation was implemented in the code of ForClim v3.3:

$$V_{STEM} = \frac{D^2}{1000} \quad (2)$$

where stem volume (V_{STEM}) is expressed in m^3 , while diameter at breast height (D) is given in cm (see graphical representation in Fig.AI.1).

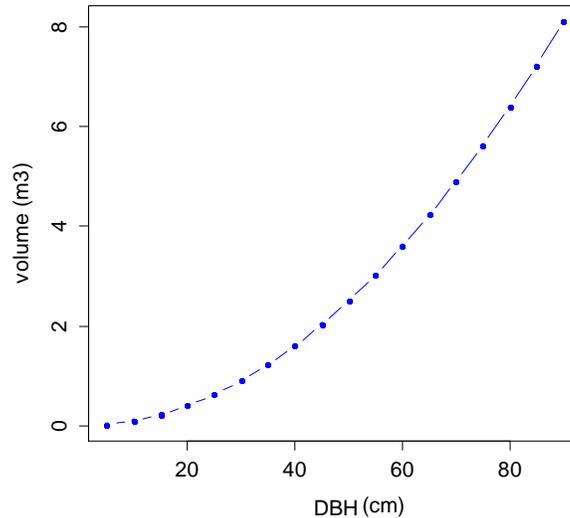


Fig.AI.1: Relationship between stem volume (in m^3) and diameter at breast height (in cm) as implemented in ForClim v3.3.

Calculation of large and small branches volume (i.e., wood energy volume)

Stem volume represents the largest component of the volume of a tree. Apart from the stem, merchantable timber often include the volume of large branches (Brassel and Lischke 2001; Meyer and Mina 2012). Depending on the wood market (national or local) and on the quality, wood from large branches is processed as material for industry and construction or it could be allocated as fuel wood. Wood that derives from small branches, if not left in the forest, could also be used in the wood energy industry in the form of wood chips (Meyer and Mina 2012). Taking these components into account using simple but yet efficient allometric equations for estimating the future supply of wood energy with ForClim would be advantageous.

The formula for calculating volume of large and small branches was implemented following the modeling approach proposed by Meyer and Mina (2012). They used regression coefficients derived from the Swiss National Forest Inventory (NFI; cf. Brassel and Lischke 2001) to calculate volume of branches as a function of a corresponding stem volume and DBH. This was achieved as follows:

$$V_{BRANCHES} = \left(\frac{\omega}{1 + \omega} \right) * V_{STEM} \quad (3)$$

where parameter ω is calculated with the following equation:

$$\omega = e^{k1+k2*DBH} \quad (3.1)$$

Coefficients $k1$ and $k2$ differ between large (diameter >7 cm) and small branches (diameter < 7 cm, without leaves or needles; Table AI-1). Regression coefficients were derived from measurements on a total of 12.000 trees from forest yield research plots in Switzerland (Brassel and Lischke 2001; E. Thurig, personal communication 2011).

Table AI-1: Regression coefficients used for calculating volume of large and small branches in ForClim v3.3. Large branches coefficients for conifers were obtained from measurements on silver fir (*Abies alba*) while for broadleaves from beech (*Fagus sylvatica*) from Brassel and Lischke (2001). Small branches coefficients were derived from NFI measurements on multiple tree species (Thurig 2010).

component	species	k1	k2
Large branches	Broadleaves	-4.939	0.061
	Conifers	-8.733	0.059
Small branches	Broadleaves	-1.206	-0.019
	Conifers	-1.933	-0.017

The relationships between calculated stem volume, wood-energy volume (i.e., sum of volume for large and small branches) and diameter at breast height (DBH) are shown in Fig. AI.2.

As described in Brassel and Lischke (2001), the proportion of large branches for conifer species if compared with broadleaves is negligibly small. This explains the large difference of wood-energy volume between the two categories of species above a certain diameter (Fig. AI.2).

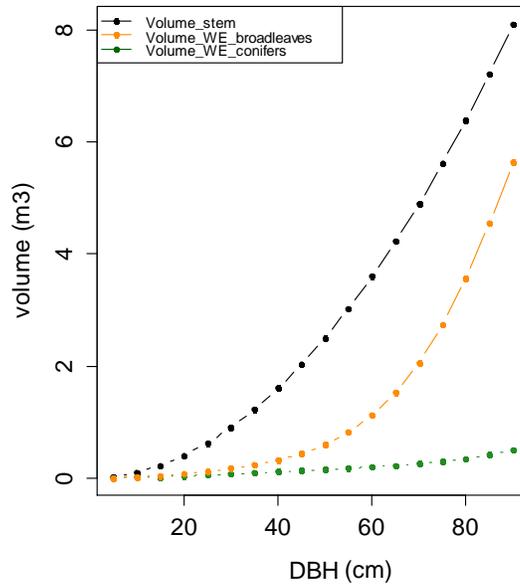


Fig.AI.2: Relationship between diameter at breast height, stem volume (black line), wood-energy volume for broadleaves (yellow line) and conifers (green line) as implemented in ForClim v3.3.

Implementing a species-specific biomass

In former versions of ForClim (v2.9.5 in Didion et al., 2009; v3.0 in Rasche et al., 2013) dry stemwood biomass of each cohort was calculated from diameter at breast height (D) with the following equation:

$$B_{stem} = 0.12 * D^{2.4} \quad (4)$$

This formulation derived from Bugmann (1994) and was based on allometric relationships from Burger (1945-53). This approach did not consider that stem biomass could differ considerably between tree species with equal DBH but having different wood densities. For example, species with higher wood density (e.g, slow growing species such as *Taxus baccata*) typically have higher dry stem weight than fast growing species with low wood density (e.g., *Populus spp.*).

Following Cordonnier et al. (2013) and IPCC (2006), I related the calculation of stem biomass (B_{stem} , in kg) with wood density as follows:

$$B_{stem} = [(V_{stem} * kWD * BEF) * CDF] * 1000 \quad (5)$$

where V_{stem} is the stem volume calculated in Eq.2, kWD the species-specific parameter denoting wood density (t dry matter * m⁻³ fresh volume, see description below and Table AI-3), BEF is a factor of biomass expansion which converts volume to aboveground biomass and CDF is the carbon dry fraction value (t C * t d.m.⁻¹). BEF and CDF have different values for broadleaves and for evergreen species (Table AI-2). For the estimation of the wood density parameter (kWD) for the different European tree species, data from different sources was used, as reported in Table AI-3.

Table AI-2: Biomass expansion factor and dry carbon fraction values used in the calculation of stem biomass. Values were obtained from Cordonnier et al. (2013) and IPCC (2006).

Tree type	BEF	CDF
Broadleaf	1.4	0.48
Conifers or evergreen broadleaf	1.3	0.51

Table AI-3: List of wood density values of the European tree species included in ForClim.

Species	kWD	Source	Species	kWD	Source
Abies alba	0.4	1	Corylus avellana	0.58	3
Larix decidua	0.46	1	Fagus sylvatica	0.58	1
Picea abies	0.4	1	Fraxinus excelsior	0.57	1
Pinus cembra	0.42	1	Populus nigra	0.35	1
Pinus montana	0.42	1	Populus tremula	0.35	1
Pinus sylvestris	0.42	1	Quercus ilex	0.69	4
Taxus baccata	0.67	2	Quercus petraea	0.58	1
Acer campestre	0.52	1	Quercus pubescens	0.58	1
Acer platanoides	0.52	1	Quercus robur	0.58	1
Acer pseudoplatanus	0.52	1	Salix alba	0.35	1
Alnus glutinosa	0.45	1	Sorbus aria	0.64	5

<i>Alnus incana</i>	0.45	1	<i>Sorbus aucuparia</i>	0.64	1
<i>Alnus viridis</i>	0.45	1	<i>Tilia cordata</i>	0.43	1
<i>Betula pendula</i>	0.51	1	<i>Tilia platyphyllos</i>	0.43	1
<i>Carpinus betulus</i>	0.63	1	<i>Ulmus glabra</i>	0.56	6
<i>Castanea sativa</i>	0.48	1			

Sources: 1) IPCC (2006); 2) http://www.engineeringtoolbox.com/wood-density-d_40.html; 3) <http://delta-intkey.com/wood/en/www/betcoave.htm>; 4) http://www.proforbiomed.eu/sites/default/files/Forest_biomass_end_users.pdf ; 5) <http://delta-intkey.com/wood/en/www/rossoauc.htm>; 6) <http://www.nichetimbers.co.uk/native-hardwood/elm/>.

A value of total biomass (B_{TOT} , in kg) of each cohort was then obtained as follows:

$$B_{TOT} = B_{stem} + B_{br1} + B_{br2} + B_{fol} \quad (6)$$

where B_{stem} is the stem biomass, B_{br1} is the biomass of large branches, B_{br2} is the biomass of small branches, and B_{fol} is the foliage weight (Didion et al. 2009). Biomass of both large and small branches was obtained with identical procedure as described for calculating stem biomass.

Recommendation for further developments

By implementing the direct calculation of volume and biomass for the different components of the simulated trees substantially simplified the post-process calculation of ecosystem service indicators (e.g., provision of wood energy biomass and aboveground carbon stock). I acknowledge, however, that further improvement would be needed for a better representation of these outputs in ForClim. For example, a better estimate of stem volume could be achieved by replacing the Denzin formula with a different equation that take into account both tree diameter and height. In my opinion, it is important that such formulation do not increase demands for additional parameters and coefficients, to the detriment of the broad applicability of the model. Another approach for calculating volume and biomass from diameter and height could be the use of empirically-derived allometric equations for the different species (e.g., Zianis et al. 2005; Falster et al. 2015). I believe that such formulas could be successfully applied to achieve precise estimate of species-specific volume and biomass in the context of application studies at specific regions or sites. However, as they would require using a series of site-specific parameters, there is the risk of sacrificing model generality.

Although the described approach for estimating volume of the branches is quite simplistic, I am confident that it can be used for obtaining estimates of wood energy production under different scenarios of forest management with ForClim. I recognize that the regression coefficients that were used in this method were obtained from measurement made only on few tree species within

the Swiss National Forest Inventory (see Brassel and Lischke 2001). The use of species-specific coefficients would be advantageous, but it might require a careful literature research. In addition, since the development of large branches also depends on the available light experienced by each cohort, a more realistic approach would be to link this calculation with the crown length factor (Didion et al. 2009), thus considering self-pruning effect along crown length.

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