DISS. ETH NO. 22775

To die or not to die:
Forest dynamics in Switzerland under climate change

A thesis submitted to attain the degree of

DOCTOR OF SCIENCES of ETH ZURICH

(Dr. sc. ETH Zurich)

presented by

NICOLAS BIRCHER

M.Sc. Environmental Sciences, ETH Zurich

born on 08.09.1985

citizen of Küttigen (AG)

accepted on the recommendation of

Prof. Dr. Harald Bugmann, examiner
Dr. Maxime Cailleret, co-examiner
Prof. Dr. Rupert Seidl, co-examiner

2015

Table of contents

Summary

A high diversity of forest ecosystems is found around the globe providing various ecosystem services to humans. Responses of forests to recent increases of drought events have given rise to serious concerns about future forest development. Since anthropogenic climate change is proceeding at an unprecedented rate, the forestry sector is challenged to swiftly develop and plan adaptive management measures that guarantee the sustainable provision of forest ecosystem services in the future. The planning of management strategies is strongly dependent on reliable knowledge on future forest dynamics. To this end, the Swiss government has launched an extensive research program to examine the impact of climate change on Swiss forests. One aim among others is to assess the sensitivity of common forest types of Switzerland to climate change.

Dynamic vegetation models (DVMs) are suitable to provide quantitative assessments of forest sensitivity to climate change, as their flexibility allows considering dynamic vegetation transitions under conditions that do not represent a steady state. Among DVMs, forest gap models portray long-term forest dynamics at the stand scale taking biotic interactions such as competition into account. Recent integration of sophisticated management techniques has substantially extended their range of application from unmanaged to complex mixed-species forests under management, thus making them interesting tools for the assessment of climate change impacts on forest ecosystems. However, forest gap models integrate a large number of ecological processes that still lack an empirical base. This is particularly true for tree mortality – a key demographic process in forest dynamics – where increasing empirical research has been followed by little action in DVMs. Thus, although it is widely acknowledged that empirical functions should be integrated into DVMs to enhance ecological realism, little is known about whether this approach leads to an increased robustness of model projections.

Given this background, my thesis includes two major objectives: 1) to examine the potential of empirical mortality functions in dynamic vegetation models and 2) to assess the sensitivity of common Swiss forests to climate change.

In *Chapter 1* of this thesis, I implemented an inventory- and a tree-ring based mortality function in the forest gap model ForClim and combined them with a stochastic and a deterministic approach for the determination of tree status (alive vs. dead). These four new model versions were tested for two Norway spruces stands, one of which was managed (inventory time series of 72 years) and the other was unmanaged (41 years). Furthermore, I ran long-term simulations (~400 years) into the future to test model behavior under three climate scenarios. I showed that three out of the four model versions showed good agreement for stand basal area and stem numbers when compared against inventory data of both forest sites. Due to very similar model behavior, an unambiguous choice of a “best” model version was, however, not possible. In contrast, long-term simulations revealed very different behavior of the mortality models, indicating that the choice of the mortality function is crucial for simulated forest dynamics. Based on these results, I concluded that 1) empirical mortality functions are valuable replacements for current theoretical mortality algorithms in dynamic vegetation models 2) but further tests would be needed to rigorously assess their potential and to better understand interactions of the mortality function with other model processes.

Enhanced use of empirical data in dynamic vegetation models is widely advocated. However, it is largely unknown whether empirically derived functions are compatible with the wide range of processes and interactions that are usually found in DVMs and thus, whether they lead to an better model performance. In *Chapter 2*, I addressed this question with the focus on the inventory-based mortality function that has already been used in *Chapter 1*. I used Bayesian methods to recalibrate its mortality parameters within ForClim. I compared its performance with the ForClim version containing the original, empirically fitted mortality parameters and with the current ForClim v3.3 that included a theoretical mortality function. Calibration and subsequent validation was based on inventory data of 30 Swiss natural forest reserves. Similarities between the calibrated and the empirically fitted mortality parameters suggest that the general structure of ForClim is appropriate to integrate empirical mortality functions. However, I found some discrepancies that indicate necessary improvements regarding the role of species’ shade tolerance in growth-mortality relationships and an optimal balance between growth and mortality. Bayesian calibration led to best performance both at calibration and validation sites. Furthermore, it revealed that the sensitivity of ForClim to parametric uncertainty is particularly high for trees in low dbh classes but surprisingly small for standard model outputs such as basal area.

Assessing the sensitivity of common forest stands in Switzerland with a forest gap model makes it necessary 1) to know which forest stands are common and 2) to have suitable data for model initialization. In *Chapter 3*, I developed a stratification of the Swiss forest area to identify those forest types of Switzerland that, in terms of their stand structure and tree species composition, are most common in different eco-regions and elevation zones. I used plot data form the third Swiss National Forest Inventory (NFI3) that contained both stand attributes and single-tree data. NFI plots were grouped into eco-regions and elevation zones according to the “Guide for sustainability in protection forests” (NaiS). I further segregated NFI plots into more groups based on two forest stand attributes: vertical stand structure and developmental stage. In a last step, I relied on recommendations of sylvicultural experts for dividing some groups into more strata to strengthen a realistic tree species composition. The stratification resulted in 71 strata that contained 25% of all NFI forest plots. Single-tree data of all NFI plots associated to one stratum were aggregated. Although the final result is a somewhat “artificial” forest stand, it has the tremendous advantage that NFI plot data can be used directly for stand initialization in the forest gap model ForClim.

In Switzerland, studies on forest sensitivity to climate change often focus on extreme sites where shifts in tree species composition are already visible while less attention is paid to the fate of common forest stands that are most important for Swiss forestry. In *Chapter 4*, I ran simulations for 71 strata that had been identified in the previous chapter using two model versions to examine their development until the end of the 21st century (year 2100). Simulations were run with common Swiss forest management strategies and without management. I considered forest development under current climate (1980-2009) and under 11 different climate change scenarios assuming an A2 greenhouse gas emission scenario. According to these simulation results, shifts in structure and composition of Swiss forests have to be expected for the second half of this century. However, high variability among the strata was found due to drivers of small-scaled forest dynamics such as regional climate, elevation gradients and current species composition. I showed that current management regimes can alleviate the negative impacts of climate change but adaptive measures are necessary to be applied at a site-specific and objective-oriented base. In conclusion, model-based assessments on forest sensitivity can only provide reliable decision-making support for forest managers if small-scaled drivers of forest stand dynamics are taken into consideration.

In the *Synthesis*, I reflect the findings of the previous chapters by discussing the potential of empirical mortality functions in DVMs and the use of forest gap models – as one type of DVM – as tools for decision-support regarding forest management under climate change. I come to the conclusion that empirical mortality functions are capable to further improve the performance of DVMs and to increase our confidence in their projections. However, empirical functions come with limitations, which might constrain a valid applicability. For this reason, I advocate not to focus on one individual function but to aggregate knowledge on mortality mechanism and data from various sources to enhance the validity of the tree mortality mechanism in DVMs beyond individual empirical data sets. Climate change is expected to have strong effects on future development of current Swiss forests at various sites. High variability in forest response to a changing environment underlines the need to plan future forest strategies at the local scale. Forest gap models have limitations that need to be discussed and tackled. Still, I am convinced that they have the potential to play a key role in decision-making processes as they can provide what decision makers need: a comprehensive reflection of essential processes and an adequate spatial resolution.

Zusammenfassung

Rund um den Globus findet sich eine hohe Vielfalt an Waldökosystemen, die dem Menschen zahlreiche Ökosystemleistungen zur Verfügung stellen. Zunahmen von Trockenheitsereignissen in der jüngsten Vergangenheit haben bereits zu Reaktionen in verschiedensten Wäldern geführt und damit ernste Besorgnis über die zukünftige Waldentwicklung ausgelöst. Da der anthropogene Klimawandel mit beispielloser Geschwindigkeit voranschreitet, ist die Forstwirtschaft gefordert, sich möglichst rasch um die Entwicklung und Planung von adaptiven Massnahmen zu bemühen, welche die nachhaltige Sicherstellung von Waldökosystemleistungen auch in Zukunft gewährleisten sollen. Für die waldbauliche Planung sind jedoch zuverlässige Kenntnisse über die zukünftige Walddynamik zwingend erforderlich. Aus diesem Grund hat die Bundesregierung der Schweiz ein umfangreiches Forschungsprogramm lanciert um die Auswirkungen des Klimawandels auf Schweizer Wälder zu untersuchen. Ein wesentliches Ziel dabei ist es, die Empfindlichkeit von häufigen Waldtypen der Schweiz auf den Klimawandel abschätzen zu können.

Dynamische Vegetationsmodelle (DVMs) sind gut für solche quantitativen Abschätzungen geeignet. Ihre Flexibilität erlaubt es dynamische Übergänge von Vegetationssystemen auch ausserhalb von konstanten Bedingungen zu berücksichtigen. Innerhalb der DVM-Familie zielen Waldsukzessionsmodelle auf die Abbildung der langfristigen Walddynamik auf Bestandesebene ab. Dabei berücksichtigen sie auch biotische Interaktionen wie die Konkurrenz zwischen den Baumarten. Der jüngste Einbau von komplexeren Bewirtschaftungstechniken hat ihren Anwendungsbereich von unbewirtschafteten Naturwäldern zu Wirtschafts- und Mischwäldern beträchtlich erweitert. Damit sind sie auch zu einem interessanten Werkzeug für die Abschätzung von Auswirkungen des Klimawandels auf heutige Wälder geworden. Viele dieser Sukzessionsmodelle beinhalten jedoch immer noch eine hohe Anzahl an ökologischen Prozessen, denen eine empirische Basis fehlt. Dies trifft vor allem auf die Baummortalität zu, einem demographischen Schlüsselprozess der Walddynamik, welcher zwar zunehmend untersucht wird, empirische Erkenntnis bisher jedoch kaum in Sukzessionsmodelle eingeflossen ist. Es ist zwar weitgehend anerkannt, dass empirische Funktionen vermehrt in DVMs integriert werden sollen, um so deren ökologische

Glaubwürdigkeit zu erhöhen. Hingegen weiss man wenig darüber, ob dies ein sinnvoller Ansatz ist um die Robustheit von Modellprojektionen zu verbessern.

Basierend auf diesem Hintergrund hatte diese Dissertation zum Ziel 1) das Potenzial von empirischen Mortalitätsfunktionen in dynamischen Vegetationsmodellen zu untersuchen und 2) die Empfindlichkeit von häufigen Schweizer Waldbeständen auf den Klimawandel abzuschätzen.

Im *Kapitel 1* dieser Arbeit wurden eine Inventur- und eine Jahrring-basierte Mortalitätsfunktion in das Waldsukzessionsmodell ForClim eingebaut. Weiter wurden diese mit einem stochastischen bzw. deterministischen Ansatz zur Bestimmung des Baumzustands (lebend vs. tot) kombiniert. Diese vier neuen Modellversionen wurden in zwei reinen Fichtenbeständen, einem bewirtschafteten (Inventurzeitreihe von 72 Jahren) und einem unbewirtschafteten (42 Jahre) getestet. Ausserdem wurden Langzeitsimulationen (~400 Jahre) in die Zukunft durchgeführt um das Modellverhalten unter drei verschiedenen Klimaszenarien zu prüfen. Es wurde gezeigt, dass drei von vier Modellversionen gute Übereinstimmung bezüglich totaler Basalfläche und Stammzahl mit den Inventurdaten der beiden Standorte erzielten. Die eindeutige Identifikation einer „besten“ Modellversion war aufgrund sehr ähnlichen Modellverhaltens jedoch nicht möglich. Im Gegensatz zeigten die Langzeitsimulationen ein sehr unterschiedliches Verhalten der Mortalitätsfunktionen auf. Dies weist darauf hin, dass die Wahl der Mortalitätsfunktion massgeblich die simulierte Walddynamik beeinflusst. Anhand dieser Resultate wurden die Schlussfolgerungen gezogen, dass 1) empirische Mortalitätsfunktionen bestehende, theoretische Mortalitätsalgorithmen in DVMs angemessen ersetzen können, 2) es jedoch weiterer Tests gebraucht um ihr Potential gründlich zu prüfen und Interaktionen der Mortalitätsfunktion mit anderen Modellprozessen besser zu verstehen.

Auch wenn die vermehrte Verwendung von empirischen Daten in DVMs propagiert wird, ist es jedoch weitgehend unbekannt, ob empirisch hergeleitete Funktionen mit der breiten Palette an Modellprozessen in DVMs und deren Interaktionen kompatibel sind. Damit verbunden stellt sich die Frage ob sie tatsächlich zu optimalem Modellverhalten führen. Dieser Frage wurde in *Kapitel 2* dieser Arbeit nachgegangen, wobei das Augenmerk auf die Inventur-basierte Mortalitätsfunktion gelegt wurde, die bereits in *Kapitel 1* zum Einsatz kam. Mittels Bayes'scher Statistik wurden deren Parameter in ForClim rekalibriert. Die Leistung dieser Modellversion wurde mit derjenigen Version, welche die ursprünglichen, empirisch gefitteten Parameter beinhaltete und der gegenwärtigen ForClim-Version (v3.3), welche eine theoretische Mortalitätsfunktion beinhaltet, verglichen. Die Kalibrierung und die anschliessende Validierung beruhten auf Inventurdaten von 30 Schweizer Naturwaldreservaten. Ähnliche Werte für die kalibrierten und die empirische gefitteten Mortalitätsparametern legen den Schluss nahe, dass die generelle Modellstruktur von ForClim angemessen ist um empirische Mortalitätsfunktionen zu integrieren. Es wurde aber auch einige Abweichungen festgestellt, welche auf notwendige Verbesserungen bezüglich der Rolle von Schattentoleranzklassen in Wachstums-Mortalitäts-Beziehungen und bezüglich eines optimalen Gleichgewichts zwischen Baumwachstum und –mortalität im Modell hindeuten. Die Bayes'sche Kalibrierung führte zur besten Modelleistung sowohl an Kalibrierungs- als auch an Validierungstandorten. Weiter zeigte sich, dass die Empfindlichkeit von ForClim gegenüber Unsicherheiten in der Parametrisierung insbesondere für Bäume in den tieferen Durchmesserklassen deutlich ausgeprägt ist, für Standardergebnisse wie die totale Basalfläche jedoch erstaunlich gering ist.

Die Empfindlichkeit von häufigen Schweizer Waldbeständen mit dem Waldsukzessionsmodell ForClim abschätzen zu können, setzt voraus, einerseits zu wissen welche Waldtypen häufig sind und andererseits hierfür über passende Einzelbaumdaten zu verfügen um damit das Modell zu initialisieren. In *Kapitel 3* wurde eine Stratifizierung der Schweizer Waldfläche durchgeführt um diejenigen Waldtypen zu identifizieren, welche bezüglich ihrer Struktur und Zusammensetzung in verschiedenen Standortsregionen und Höhenstufen der Schweiz am häufigsten vorkommen. Hierfür wurden Untersuchungsflächen (Plots) des dritten Schweizerischen Landesforstinventars (LFI) verwendet, auf welchen nicht nur gängige Bestandesattribute sondern auch Einzelbaumdaten erhoben wurden. Die LFI-Plots wurden gemäss den Standortsregionen und Höhenstufen nach der Wegleitung „Nachhaltigkeit im Schutzwald“ (NaiS) in Gruppen eingeteilt. Diese Gruppen wurden unter Verwendung der Bestandesattribute „vertikale Bestandesstruktur“ und „Entwicklungsstufe“ weiter aufgeteilt. In einem letzten Schritt wurden einige Gruppen basierend auf Empfehlungen von Waldbauexperten zusätzlich getrennt, um eine möglichst realistische Baumartenzusammensetzung zu gewährleisten. Die Stratifizierung ergab 71 Straten, welche insgesamt 25% aller als „Normalwald“ klassifizierten LFI-Plots beinhalteten. Die Einzelbaumdaten aller zu einem Stratum zugehörigen LFI-Plots wurden aggregiert. Obwohl dies eine zu einem gewissen Grad künstliche Waldstruktur ergab, lag der Vorteil darin, dass die Einzelbaumdaten des LFI direkt für die Bestandesinitialisierung in ForClim verwendet werden konnten.

Die Klimaempfindlichkeit von Schweizer Wäldern wird oftmals nur an Extremstandorten untersucht, wo sich Veränderungen der Baumartenzusammensetzung bereits beobachten lassen. Den häufigen Waldstandorten wird weniger Aufmerksamkeit geschenkt, obwohl sie für die Forstwirtschaft von höchster Bedeutung sind. Aus diesem Grund wurden in *Kapitel 4* mittels zweier ForClim-Versionen Simulationen für die 71 im vorherigen Kapitel identifizierten Straten durchgeführt, um so deren Entwicklung bis Ende des 21. Jahrhunderts abzuschätzen. Dabei wurden Simulationen ohne sowie mit Waldbewirtschaftung durchgeführt wobei gängige Schweizer Waldbewirtschaftungspraktiken zur Anwendung kamen. Die zukünftige Waldentwicklung wurde sowohl unter heutigem Klima (1980-2009) als auch unter Anwendung von 11 verschieden Klimaszenarien basierend auf einem A2 Emissionsszenario untersucht. Gemäss den Resultaten zeigen Schweizer Wälder klimabedingte Veränderungen insbesondere in der zweiten Hälfte dieses Jahrhunderts. Dabei zeigte sich jedoch eine hohe Variabilität zwischen den verschiedenen Straten bedingt durch Faktoren wie regionales Klima, Höhengradienten und Baumartenzusammensetzung, welche die Walddynamik auf kleinräumiger Ebene steuern. Gegenwärtige Bewirtschaftungspraktiken waren in der Lage negative Einflüsse des Klimawandels auf die Bestandesdynamik abzumildern. Gleichzeitig zeigte sich auch, dass es neuer, adaptiver Massnahmen bedarf, welche aber standortsspezifisch und zielorientiert geplant und angewandt werden müssen. Diese Studie zeigt klar, dass modell-basierte Abschätzungen über Auswirkungen des Klimawandels auf Wälder nur dann einen zuverlässigen Beitrag für die Forstwirtschaft leisten können, wenn sie diejenigen Faktoren in Betracht ziehen, welche die Walddynamik auf Bestandesebene steuern.

In der *Synthese* werden die Ergebnisse aus den einzelnen Kapiteln reflektiert und insbesondere bezüglich der Frage nach dem Potential von empirischen Mortalitätsfunktionen in DVMs und nach dem Nutzen von Waldsukzessionsmodellen als Entscheidungsgrundlage für die zukünftige Waldbewirtschaftung diskutiert. Empirische Mortalitätsfunktionen zeigen sich in der Lage die Leistung von DVMs zu verbessern und unser Vertrauen in Modellprojektionen zu erhöhen. Sie sind jedoch auch mit Einschränkungen verbunden, welche ihre Gültigkeit und Zuverlässigkeit in Anwendungen begrenzen. Aus diesem Grund sollte der Fokus weniger auf eine einzige Funktion gelegt werden sondern vielmehr darauf, das Wissen über Mortalitätsmechanismen und Daten aus verschiedene Quellen zu kombinieren um damit die gültige Abbildung der Baumortalität in DVMs über einzelne Datensätze hinaus zu erweitern. Der Klimawandel wird voraussichtlich an verschiedenen Standorten eine starke Wirkung auf die zukünftige Waldentwicklung heutiger Schweizer Wälder haben. Die hohe Variabilität in der Reaktion auf den Klimawandel unterstreicht die Notwendigkeit zukünftige Waldbaustrategien auf lokaler Ebene zu planen. Waldsukzessionsmodelle beinhalten Unsicherheiten, die diskutiert und angegangen werden müssen, dennoch sind sie in der Lage eine Schlüsselrolle bei der Entscheidungsfindung der waldbaulichen Planung zu übernehmen. Denn sie beinhalten die notwendigen Vorgaben, dies es für die Entscheidungsfindung auf lokaler Ebene braucht: Eine weitgehende Abdeckung der erforderlichen Prozesse und Faktoren sowie eine angemessene räumliche Auflösung.

General introduction

Forests under climate change

Forest ecosystems have been shaped by changing climates, natural disturbances, and human land-use for thousands of years (Tinner and Theurillat, 2003; Colombaroli and Tinner, 2013; Fyfe *et al.*, 2015). In this process, forests have shown remarkable resilience to changes in their abiotic and biotic environment (e.g., Feurdean *et al.*, 2011; Lopez-Merino *et al.*, 2012). Land-use and climate change are expected to remain major natural drivers of ecosystems in the future (Sala *et al.*, 2000), but the present-day situation is unique as, for the first time, climate change is and will be human-induced to a large degree (IPCC, 2014). Greenhouse gas emissions are rising at an unprecedented rate (World Meteorological Organisation, 2014), resulting in projected increases of global average temperature of 2 to 4 °C by the end of this century (IPCC, 2014). Although forests are known to respond to altered climatic conditions (e.g., Schwörer *et al.*, 2014), their rate of adaption is limited due to the longevity of trees (Lindner *et al.*, 2010; Milad *et al.*, 2011). Given the high rate of recent and predicted future climate change, many forest systems around the globe have already shown a response to recent increases of drought (Allen *et al.*, 2010) and will most likely face drastic shifts regarding their structure, composition, and dynamics (e.g., Ciais *et al.*, 2005). Hence, the resistance and resilience of forests to climate change is of high concern (e.g., Bonan, 2008).

Forests provide a wide array of ecosystem services (ES) to humans including resources, amenities, social, biospheric, and ecological aspects (MEA, 2005). Failing to provide these services due to the impacts of climate change would mean, if nothing else, a high economical loss (Hanewinkel *et al.*, 2013). This alone places high pressure on the forestry sector (Lindner *et al.*, 2010). If forest management is to maintain adaptive and disturbance-resistant forests under climate change (Brang *et al.*, 2008), possible adjustments of sylvicultural interventions and measures need to be developed and implemented quickly, as the management of long-living organisms like trees requires long-term strategies (Seidl *et al.*, 2011). However, the development of efficient, adaptive forest management is only possible if sound, regional knowledge on future forest dynamics is available (Rigling *et al.*, 2008).

In Switzerland, forests cover around 30% of the land area, providing a variety of ES including timber production, protection from natural hazards, conservation and recreation, to name just the most important ones (Brändli, 2010). The country is characterized by a complex topography, a high proportion of mountain areas, and steep bioclimatic gradients that are driving a high habitat diversity along different elevation zones (OcCC, 2007). Due to this wide spectrum of sites differing in climate and geology, around 120 types of natural forests have been defined (Frehner *et al.*, 2005).

Swiss forests have experienced a 1.5 °C increase of average annual temperatures since 1970 (OcCC, 2008), which reflects a rate of change that is 1.5x higher compared to the terrestrial surface of the northern hemisphere (IPCC, 2007). Responses of Swiss forests to recent climate extremes and changes have already become visible for example during the hot summer of 2003 (e.g., Jolly *et al.*, 2005) or at dry sites in the inner-Alpine valleys (e.g., Rigling *et al.*, 2013). Current climate projections for Switzerland suggest a further increase of temperature particularly in the summer season by about 2.7 °C to 4.8 °C, possibly coupled with a decrease of summer precipitation by about 20% to 28% compared to the reference period of 1980 to 2009 (CH2011, 2011). Such climatic changes will most likely lead to strong reactions by the country's forests (Bugmann *et al.*, 2014), although high uncertainty about its magnitude presents a substantial challenge regarding the development of novel sylvicultural strategies (Brang *et al.*, 2008).

Model-based studies have been conducted for a few decades to quantitatively assess the impacts of climate change on Swiss forests (cf. Bolliger, 2002). However, earlier studies have either worked with zonal forest communities (Brzeziecki *et al.*, 1995), neglected population dynamics such as competition (e.g., Bolliger *et al.*, 2000), and/or not considered actual forest stand data but simulated potential natural vegetation (e.g., Kienast, 1991; Kräuchi and Kienast, 1993; Kienast *et al.*, 1996; Bugmann, 1997; Fischlin and Gyalistras, 1997; Lischke and Zierl, 2002). In addition, climatic scenarios have been rather coarse and realistic management regimes missing. Overall, none of these studies were very supportive in terms of decision-making for Swiss forestry.

More recent studies, both empirical and model-based, are usually lacking a comprehensive approach as they, on the one hand, often focus on a few objects only representing sites that experience climatic extremes already today (e.g., Bigler *et al.*, 2006; Rigling *et al.*, 2013), and thus are not representative for the majority of Swiss forest sites; or they represent case studies that only allow for limited conclusions regarding the entire country (e.g., Elkin *et al.*, 2013). On the other hand, studies on the adaptability of tree species to increased drought (e.g., Levesque *et al.*, 2014) or about their future potential distribution ranges (e.g., Zimmermann and Bugmann, 2008) are often restricted to a few species only and/or do not consider important aspects of forest dynamics such as competition. Thus, there is an urgent need for a quantitative assessment on the national scale (1) to focus on forest stands that are typical for the Swiss forest area regarding structure and composition and, hence, form the backbone of today's forestry, and (2) to include bioclimatic effects and interactions among tree species.

To provide decision makers in policy and forestry with a solid foundation regarding future forest dynamics, the Swiss Government has launched an extensive research program "Forests and Climate Change" (BAFU, 2009; Brang *et al.*, 2011) to (1) examine the impacts of climate change on Swiss forests, (2) to assess consequences for the future provision of forest ecosystem services and (3) to identify and derive suitable adaptive management solutions to guarantee their provision in the future.

My PhD thesis, as part of the research program "Forests and Climate Change", is a contribution to fill this knowledge gap. The questions which forest types are typical for

Switzerland and how sensitively they will react to climate change are addressed in *Chapters 3* and *4* of my thesis, respectively.

Modeling forest dynamics

The quantitative assessment of forest ecosystem shifts under climate change requires the extrapolation of current knowledge and strongly relies on the specific assumptions on forest dynamics (Bugmann *et al.*, 2014). To this end, mathematical and simulation models are needed and useful (Busing and Mailly, 2004; Botkin *et al.*, 2007). Dynamic vegetation models (DVMs) are particularly suited for this purpose as they allow considering dynamic transitions of plant populations (Prentice *et al.*, 2007; Fontes *et al.*, 2010) under non steady-state conditions (Botkin *et al.*, 2007).

A wide range of DVMs has been developed over the last decades (Bugmann, 2001; Cramer *et al.*, 2001; Sitch *et al.*, 2008) that usually share many similarities regarding their architecture (Cramer *et al.*, 2001; Prentice *et al.*, 2007). In principle, these models predict temporal trajectories of plant response to biotic (e.g., competition, disturbances) and abiotic (e.g., soil, climate) factors (Jeltsch *et al.*, 2008; Hartig *et al.*, 2012). They differ, however, regarding the degree of complexity and their field of application (Sitch *et al.*, 2003).

At large scales, dynamic global vegetation models (DGVMs) couple processes related to vegetation dynamics (e.g., plant establishment, growth and mortality) with biogeochemical fluxes (e.g., carbon cycle; Cramer *et al.*, 2001). Large-scale applications with coarse resolution and/or considerable computational and parameterization constraints are addressed by using the presence/absence of so-called plant functional types, not individuals, as the primary entity to be modeled (Cramer *et al.*, 2001). Thus, these models do normally not consider processes and interactions (e.g., competition) that are occurring at the individual level (e.g., Sato *et al.*, 2007).

At the other end of the spatial scale axis, individual-based models such as forest gap models are usually applied at the level of a forest stand (Bugmann, 2001). Here, processes of vegetation dynamics are calculated for individuals (but see cohort-approach in Bugmann, 1996) and tree responses to environmental conditions differ based on species-specific physical and physiological requirements. While most forest gap models do not explicitly reflect biogeochemical cycles (Reynolds *et al.*, 2001), they are capable of accounting for more detailed species-specific, individual-based responses to resource availability, competition and other processes regarding succession, which are driving forest stand dynamics (Shugart, 1984; Bugmann, 2001).

Below, I expand on the underlying concept, history and development of forest gap models since their approach has recently also been embodied in DGVMs so as to increase their ecological realism by more detailed formulations of physiological processes at the stand level (i.e. individual-based hybrid models; e.g., Moorcroft *et al.*, 2001; Smith *et al.*, 2001; Sato *et al.*, 2007; Hickler *et al.*, 2012; Naudts *et al.*, 2014).

The fundamental concept underlying forest gap models to explain vegetation dynamics is attributed to Watt's (1947) theory of "gap phases". On a small-scaled forest patch, the death of a large canopy tree creates a gap, resulting in enhanced resource availability and thus better growth of suppressed trees as well as a wave of tree recruitment (see also Shugart, 1984; Bugmann, 2001). From a landscape perspective, such events of canopy tree mortality occur with spatial and temporal heterogeneity, leading to a mosaic of forest patches that differ regarding their successional state. With the words of Watt (1947, pp.1-2): "*…these patches form a mosaic and together constitute the community*". Accordingly, forest gap models simulate vegetation dynamics on small patches that comprise an area that is potentially dominated by one large canopy tree (often, 1/12 ha; Shugart, 1984). The successional pattern at the forest stand or at larger scale is obtained by averaging simulation results across many patches (Bugmann, 2001).

The JABOWA model by Botkin *et al.* (1972a,b) was the first to use this concept for simulating tree establishment, growth and mortality, based on a few key simplifications (Bugmann, 2001): (1) forests are considered to be abstractions of many small patches (with a size of 100-1000 m^2), (2) there is horizontal homogeneity across a patch, i.e. tree position is not considered, (3) leaves are placed as an indefinitely thin disk at the top of the stem (i.e., no 2- or 3-dimensional crown structure), and (4) there is independence between patches (i.e., no interactions). A wide variety of forest gap models has evolved from this JABOWA model, addressing forest ecosystem dynamics from the boreal to the tropical zone (Shugart and Smith, 1996). In a still ongoing process, more mechanistic functions have been formulated or new assumptions introduced, such as the consideration of tree position (SORTIE; Pacala *et al.*, 1993, 1996), patch interactions (cf. Urban *et al.*, 1991, ZELIG), crown length calculation (Leemans and Prentice, 1989, FORSKA; Weishampel and Urban, 1996, ZELIG; Pacala *et al.*, 1993, 1996, SORTIE; Didion *et al.*, 2009, ForClim), seed dispersal (Pacala *et al.*, 1993, 1996, SORTIE; Lexer and Hönninger, 1998, PICUS), a cohort approach (Bugmann, 1996, ForClim), different life forms (Keane *et al.*, FIRE-BGC; Friend *et al.*, 1997, HYBRID), stress responses (i.e. new state variable; Solomon, 1986, FORENA) or belowground dynamics (Aber *et al.*, 1979, FORTNITE), to name just a few examples. In addition to changes targeting the physical and physiological elements of gap models, recent integration of management techniques (e.g., Rasche *et al.*, 2011, ForClim) and a more sophisticated consideration of natural disturbances (e.g., Seidl *et al.*, 2008, Picus) have substantially extended the range of model applications from originally unmanaged forests (Badeck *et al.*, 2001) to complex mixed-species stands that are under heavy management (cf. Pabst *et al.*, 2008; Larocque *et al.*, 2011).

The call for more empirical accuracy

In combination with increasing availability of long-term measured forest stand data, testing of forest gap models has experienced a remarkable shift from rather qualitative assessments (e.g., potential natural vegetation (PNV) or pollen data; Bugmann, 2001) to quantitative comparisons of model predictions against field data (e.g., Lindner *et al.*, 1997; Didion *et al.*, 2009a). The latter approach allows us to examine model behavior regarding, for example, forest stand structure (i.e., species-specific distribution of diameter at breast height, DBH) in a very rigorous manner (Wehrli *et al.*, 2005), rather than based on the "plausibility" or "realism" of the simulation results alone (e.g., Bugmann, 1994).

Since forest gap models were found to reproduce measured data of unmanaged (e.g., Larocque *et al.*, 2006) and managed (e.g., Pabst *et al.*, 2008; Rasche *et al.*, 2011) stands reasonably well, they have evolved from pure scientific instruments that were geared towards better understanding forest dynamics, into tools to investigate the sustainability of managed forest ecosystems under changing environmental conditions (Larocque *et al.*, 2006). In this context, they have already been applied to assess the impacts of climate change (e.g., Seidl *et al.*, 2008; Seidl *et al.*, 2011; Elkin *et al.*, 2013).

However, quantitative model tests have revealed considerable shortcomings in the formulation of ecological processes in forest gap models (cf. Lindner *et al.*, 1997; Monserud, 2003; Pabst *et al.*, 2008), and criticism had been expressed particularly regarding the poor empirical foundation of many processes (Loehle and LeBlanc, 1996; Keane *et al.*, 2001). Indeed, while some processes in forest gap models such as tree growth rely on a fairly sound empirical basis already (e.g., growth and yield plots, tree-ring records; Bugmann, 2001), other processes like tree recruitment and mortality reflect possibly realistic but not necessarily accurate theoretical assumptions (Keane *et al.*, 2001; Larocque *et al.*, 2011).

While the scarcity of suitable empirical data has often been used to explain the absence of more sophisticated algorithms in the past, such an explanation is difficult to maintain nowadays, as the availability of suitable forest data sets and statistical techniques for their interpretation is increasing rapidly. For example, there has been an increasing number of empirical studies on tree mortality (e.g., Monserud and Sterba, 1999; Bigler and Bugmann, 2003, 2004; Wunder *et al.*, 2007; Wunder *et al.*, 2008; Gillner *et al.*, 2013; Holzwarth *et al.*, 2013) based on various data sources and different statistical methods. However, this empirical progress has been followed by little action regarding the implementation of more sophisticated mortality functions in forest gap models (but see Larocque *et al.*, 2011), and thus many models are still based on rather simplistic assumptions regarding tree mortality (Monserud, 2003).

Slow advances in enhancing the empirical foundation of forest gap models are unfortunate for two reasons in particular: First, although it is widely agreed that an increase of ecological realism in DVMs is needed by relying more on empirical data and mechanistic formulations (e.g., Prentice *et al.*, 2007; Fontes *et al.*, 2010; Galbraith *et al.*, 2010; Adams *et al.*, 2013), we know little about whether this is a suitable approach to increase the robustness of model projections. Second, current model versions are characterized by a high sensitivity to the choice of the formulation on the simulation of key processes such as tree mortality (Manusch *et al.*, 2012; Friend *et al.*, 2014), while forest dynamics remains a considerable source of uncertainty in simulations under climate change (Purves and Pacala, 2008).

In this thesis, I will therefore examine the potential and behavior of recently developed empirical mortality functions in DVMs (see chapters 1 and 2). In this work I will focus on a forest gap model, as this class of models provides the level of spatial resolution that is required to assess forest dynamics under climate change and different local conditions, i.e. to provide information that is useful in a forest management context in addition to providing fundamental ecological insights. I will rely on the forest gap model ForClim (Bugmann, 1996) that has been parameterized for all major tree species of Central Europe and was successfully tested for different forest types under a wide climatic gradient without requiring site-specific calibration (e.g., Bugmann and Solomon, 2000; Didion *et al.*, 2009b; Rasche *et al.*, 2011). The choice is also motivated by the fact that the recent implementation of a broad set of different sylvicultural techniques (Rasche *et al.*, 2011) provides the flexibility required to reflect Swiss forest management strategies in the simulations in an appropriate and realistic way.

Research aim and structure of the thesis

Two major objectives form the backbone of this thesis: In a first part (chapters 1 and 2), I aim to test and discuss the applicability of empirically derived mortality functions in dynamic vegetation models. Specifically, I want to

(1) implement empirical mortality functions of different origin into ForClim,
(2) compare their performance within this DVM framework, and
(3) evaluate their potential for applications that go beyond the empirical data sets.

In the second part (chapters 3 and 4), I will examine the sensitivity of typical Swiss forest stands to climate change, taking local stand conditions and common management strategies into account. To this end, I will

(4) develop a stratification of the Swiss forest area into typical forest stands, and
(5) run simulations for these forest stands under current climate and climate change scenarios using different versions of ForClim that were developed and evaluated in the first part of this thesis.

To this end, this thesis is structured into the following parts:

Chapter 1

Many DVMs still incorporate functions that reflect theoretical assumptions on tree mortality but have neither been derived from nor tested against empirical data. Thus, although suggested by various authors (e.g., Keane *et al.*, 2001), the applicability of empirically derived mortality functions in DVMs remains poorly understood. Concomitantly, the developers of empirical mortality functions rely on feedbacks from the DVM community to further derive sound, robust and accurate mortality models. To provide such recommendations, I replace the standard mortality function of ForClim by two empirically derived mortality functions that are based on inventory and tree-ring data, respectively. I compare the performance of these different model versions against long-term inventory data of two Norway spruce dominated forest stands under both managed and unmanaged conditions. Furthermore, I assess model behavior in long-term simulations to elucidate their sensitivity to climate change.

Chapter 2

Although empirical inventory data should provide reliable estimates of mortality rates, empirically estimated mortality parameters may not lead to optimal performance in a DVM due to issues with the data, structural errors in the model, or interactions with other model processes. Thus, a thorough understanding of the behavior of empirical mortality functions in a DVM framework is necessary. In this chapter, I address this issue by using Bayesian methods to inversely re-calibrate the parameters of an inventory-based mortality function (see chapter 1) in ForClim. Calibration and subsequent validation are based on 30 plots of the Swiss natural forest reserve network that include all major tree species of Central Europe. I use potential mismatches between empirically estimated and inversely calibrated mortality parameters to discuss the structural realism of ForClim. Furthermore, I assess parameter uncertainty and its consequences for model projections.

Chapter 3

The focus on a particular set of forest types for analyzing the impacts of climate change can be based, for instance, on expert judgment, statistical methods or specific interests (e.g., species conservation etc.). In this chapter, I test a largely objective, quantitative approach (i.e., stratification) that is based on the plot data of the Swiss National Forest Inventory (NFI). I identify those forest types that, regarding their stand structure and tree species composition, are most common and hence, typical for different eco-regions and elevation zones of Switzerland. Additionally, these forest stands are expected to form distinguishable units whose characteristics and future development can be reflected by ForClim.

Chapter 4

Switzerland is characterized by a high diversity of forest types, but the available studies on forest sensitivity to climate change often focus on extreme sites (e.g., dry sites where tree species already approach their physiological limits). Common (i.e., typical) forest stands are hardly considered although they build the backbone of current Swiss forestry, and hence their future development should be of high interest. I run simulations for 71 typical forest stands (see also chapter 3) using two versions of ForClim by including the most common Swiss forest management strategies and a variety of climate scenarios, assuming an A2 greenhouse gas emission scenario. I assess the sensitivity of these forest stands to climate change and discuss the effects of current management practices. Furthermore, I examine the impact of climate change on the forest ecosystem services that are most important for Switzerland.

References

Aber, J.D., Botkin, D.B., Melillo, J.M., 1979. Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. Can J Forest Res 9, 10-14.

Adams, H.D., Williams, A.P., Xu, C., Rauscher, S.A., Jiang, X., McDowell, N.G., 2013. Empirical and process-based approaches to climate-induced forest mortality models. Frontiers in Plant Science 4, 438.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

Badeck, F.-W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M., Mouillot, F., Schaber, J., Smith, B., 2001. Tree Species Composition in European Pristine Forests: Comparison of Stand Data to Model Predictions. Clim. Change 51, 307-347.

BAFU, 2009. Forschungsprogramm zu Auswirkungen des Klimawandels auf den Wald BAFU, Bern, http://www.bafu.admin.ch/wald/01198/09012/index.html?lang=de.

Bigler, C., Bräker, O., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots Pine stands of the Valais, Switzerland. Ecosystems 9, 330-343.

Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. Can. J. For. Res. 33, 210-221.

Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14, 902-914.

Bolliger, J., 2002. Schweizer Wälder und Klimaveränderungen: Vergleich von Simulationen quantitativer Vegetationsmodelle | Swiss forests and climate change: comparison of simulated quantitative vegetation models. Schweizerische Zeitschrift für Forstwesen 153, 167-175.

Bolliger, J., Kienast, F., Zimmermann, N.E., 2000. Risks of global warming on montane and subalpine forests in Switzerland – a modeling study. Reg Environ Change 1, 99-111.

Bonan, G.B., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320, 1444-1449.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972a. Rationale, limitations, and assumptions of a northeastern forest growth simulator. IBM Journal of Research and Development 16, 101-116.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972b. Some Ecological Consequences of a Computer Model of Forest Growth. J. Ecol. 60, 849-872.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B., 2007. Forecasting the effects of global warming on biodiversity. Bioscience 57, 227-236.

Brändli, U.-B., 2010. Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Bundesamt für Umwelt (BAFU), Birmensdorf, Bern.

Brang, P., Born, J., Augustin, S., Küchli, C., Thürig, E., Wermelinger, B., Wohlgemuth, T., Zimmermann, N.E., 2011. Forschungsprogramm Wald und Klimawandel. Synthese der ersten Programmphase 2009 - 2011. Birmensdorf: Eidg. Forschungsanstalt für WSL, Bern: Bundesamt für Umwelt.

Brang, P., Bugmann, H., Bürgi, A., Mühlethaler, U., Rigling, A., Schwitter, R., 2008. Klimawandel als waldbauliche Herausforderung. Schweizerische Zeitschrift für Forstwesen 159, 362-373.

Brzeziecki, B., Kienast, F., Wildi, O., 1995. Modeling potential impacts of climate-change on the spatial-distribution of zonal forest communities in Switzerland. J. Veg. Sci. 6, 257-268.

Bugmann, H., 1994. On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study. Ph.D. Thesis No. 10638, Swiss Federal Institute of Technology Zurich, Switzerland, 258 p.

Bugmann, H., 1997. Sensitivity of forests in the European Alps to future climatic change. Clim. Res. 8, 35-44.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259-305.

Bugmann, H., Brang, P., Elkin, C., Henne, P., Jakoby, O., Lévesque, M., Lischke, H., Psomas, A., Rigling, A., Wermelinger, B., Zimmermann, N.E., 2014. Climate change impacts on tree species, forest properties, and ecosystem services. In: CH2014-Impacts (2014) (Ed.), Toward Quantitative Scenarios of Climate Change Impacts in Switzerland. OCCR, FOEN, MeteoSwiss, C2SM, Agroscope, and ProClim, Bern, Switzerland, pp. 79-89.

Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055-2074.

Bugmann, H.K.M., Solomon, A.M., 2000. Explaining Forest Composition and Biomass across Multiple Biogeographical Regions. Ecol. Appl. 10, 95-114.

Busing, R.T., Mailly, D., 2004. Advances in spatial, individual-based modelling of forest dynamics. J. Veg. Sci. 15, 831-842.

CH2011, 2011. Swiss climate change scenarios CH2011. C2SM, MeteoSwiss, ETH, NCCR Climate and OcCC, Zurich, Switzerland, p. 88.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529-533.

Colombaroli, D., Tinner, W., 2013. Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. Holocene 23, 1625-1634.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., Young-Molling, C., 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. Global Change Biol. 7, 357-373.

Didion, M., Kupferschmid, A.D., Lexer, M.J., Rammer, W., Seidl, R., Bugmann, H., 2009a. Potentials and limitations of using large-scale forest inventory data for evaluating forest succession models. Ecol. Model. 220, 133-147.

Didion, M., Kupferschmid, A.D., Zingg, A., Fahse, L., Bugmann, H., 2009b. Gaining local accuracy while not losing generality - extending the range of gap model applications. Can J Forest Res 39, 1092-1107.

Elkin, C., Gutiérrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., Bugmann, H., 2013. A 2 °C warmer world is not safe for ecosystem services in the European Alps. Global Change Biol. 19, 1827-1840.

Feurdean, A., Tantau, I., Farcas, S., 2011. Holocene variability in the range distribution and abundance of Pinus, Picea abies, and Quercus in Romania; implications for their current status. Quat. Sci. Rev. 30, 3060-3075.

Fischlin, A., Gyalistras, D., 1997. Assessing impacts of climatic change on forests in the Alps. Global Ecol. Biogeogr. Lett. 6, 19-37.

Fontes, L., Bontemps, J.D., Bugmann, H., Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rotzer, T., Skovsgaard, J.P., 2010. Models for supporting forest management in a changing environment. For. Syst. 19, 8-29.

Frehner, M., Wasser, B., Schwitter, R., 2005. Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion, Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., Woodward, F.I., 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Acad. Sci. U.S.A. 111, 3280-3285.

Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecol. Model. 95, 249-287.

Fyfe, R.M., Woodbridge, J., Roberts, N., 2015. From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. Global Change Biol. 21, 1197-1212.

Galbraith, D., Levy, P.E., Sitch, S., Huntingford, C., Cox, P., Williams, M., Meir, P., 2010. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. New Phytol. 187, 647-665.

Gillner, S., Rüger, N., Roloff, A., Berger, U., 2013. Low relative growth rates predict future mortality of common beech (Fagus sylvatica L.). For. Ecol. Manage. 302, 372-378.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.J., Nabuurs, G.J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203-207.

Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O'Hara, R.B., Scheiter, S., Huth, A., 2012. Connecting dynamic vegetation models to data – an inverse perspective. J. Biogeogr. 39, 2240-2252.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kuhn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecol. Biogeogr. 21, 50-63.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. J. Ecol. 101, 220-230.

IPCC, 2007. Climate Change 2007; The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge, United Kingdom and New York, USA.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jeltsch, F., Moloney, K.A., Schurr, F.M., Kochy, M., Schwager, M., 2008. The state of plant population modelling in light of environmental change. Perspectives in Plant Ecology Evolution and Systematics 9, 171-189.

Jolly, W.M., Dobbertin, M., Zimmermann, N.E., Reichstein, M., 2005. Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. Geophys. Res. Lett. 32, L18409.

Keane, R., Austin, M., Field, C., Huth, A., Lexer, M., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree Mortality in Gap Models: Application to Climate Change. Clim. Change 51, 509-540.

Keane, R.E., Morgan, P., Running, S.W., 1996. FIRE-BGC - A mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. USDA Forest Service Intermountain Research Station Research Paper INT-RP-484, p. 142.

Kienast, F., 1991. Simulated effects of increasing atmospheric CO2 and changing climate on the successional characteristics of alpine forest ecosystems. Landscape Ecol. 5, 225-238.

Kienast, F., Brzeziecki, B., Wildi, O., 1996. Long-term adaptation potential of Central European mountain forests to climate change: A GIS-assisted sensitivity assessment. For. Ecol. Manage. 80, 133-153.

Kräuchi, N., Kienast, F., 1993. Modeling sub-alpine forest dynamics as inluenced by a changing environment. Water Air Soil Pollut. 68, 185-197.

Larocque, G.R., Archambault, L., Delisle, C., 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecol. Model. 199, 350-362.

Larocque, G.R., Archambault, L., Delisle, C., 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222, 2570-2583.

Leemans, R., Prentice, I.C., 1989. FORSKA-a general forest succession model. Meddelanden Från Växtbiologiska Institutionen.

Levesque, M., Rigling, A., Bugmann, H., Weber, P., Brang, P., 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric. For. Meteorol. 197, 1-12.

Lexer, M., Hönninger, K., 1998. Simulated effects of bark beetle infestations on stand dynamics in Picea abies stands: coupling a patch model and a stand risk model. In: Beniston, M., Innes, J. (Eds.), The Impacts of Climate Variability on Forests. Springer Berlin Heidelberg, pp. 289-308.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698-709.

Lindner, M., Sievänen, R., Pretzsch, H., 1997. Improving the simulation of stand structure in a forest gap model. For. Ecol. Manage. 95, 183-195.

Lischke, H., Zierl, B., 2002. Feedback between structured vegetation and soil water in a changing climate: A simulation study. In: Beniston, M. (Ed.), Climatic Change: Implications for the Hydrological Cycle and for Water Management. Springer Netherlands, pp. 349-377.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model. 90, 1-31.

Lopez-Merino, L., Sanchez, N.S., Kaal, J., Lopez-Saez, J.A., Cortizas, A.M., 2012. Post-disturbance vegetation dynamics during the Late Pleistocene and the Holocene: An example from NW Iberia. Global Planet. Change 92-93, 58-70.

Manusch, C., Bugmann, H., Heiri, C., Wolf, A., 2012. Tree mortality in dynamic vegetation models - A key feature for accurately simulating forest properties. Ecol. Model. 243, 101-111.

MEA, 2005. Millennium Ecosystem Assessment, Island Press, Washington, D.C.

Milad, M., Schaich, H., Burgi, M., Konold, W., 2011. Climate change and nature conservation in Central European forests: A review of consequences, concepts and challenges. For. Ecol. Manage. 261, 829-843.

Monserud, R.A., 2003. Evaluating forest models in a sustainable forest management context. Forest Biometry, Modelling and Information Sciences 1, 35-47.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109-123.

Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: The ecosystem demography model (ED). Ecol. Monogr. 71, 557-585.

Naudts, K., Ryder, J., J. McGrath, M., Otto, J., Chen, Y., Valade, A., Bellasen, V., Berhongaray, G., Bönisch, G., Campioli, M., Ghattas, J., De Groote, T., Haverd, V., Kattge, J., MacBean, N., Maignan, F., Merilä, P., Penuelas, J., Peylin, P., Pinty, B., Pretzsch, H., Schulze, E.D., Solyga, D., Vuichard, N., Yan, Y., Luyssaert, S., 2014. A vertically discretised canopy description for ORCHIDEE (SVN r2290) and the modifications to the energy, water and carbon fluxes. Geosci. Model Dev. Discuss. 7, 8565-8647.

OcCC, 2007. Klimaänderung und die Schweiz 2050. Erwartete Auswirkungen auf die Umwelt, Gesellschaft und Wirtschaft. OcCC and ProClim, Bern.

OcCC, 2008. Das Klima ändert - was nun? Der neue UN-Klimabericht (IPCC 2007) und die wichtigsten Ergebnisse aus Sicht der Schweiz. OcCC, Bern.

Pabst, R.J., Goslin, M.N., Garman, S.L., Spies, T.A., 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958-972.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. Ecol. Monogr. 66, 1-43.

Pacala, S.W., Canham, C.D., Silander Jr, J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980-1988.

Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S., Hickler, T., Lucht, W., Sitch, S., Smith, B., Sykes, M., 2007. Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell, J., Pataki, D., Pitelka, L. (Eds.), Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, pp. 175-192.

Purves, D., Pacala, S., 2008. Predictive models of forest dynamics. Science 320, 1452-1453.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2011. Getting a virtual forester fit for the challenge of climatic change. J. Appl. Ecol. 48, 1174-1186.

Reynolds, J.F., Bugmann, H., Pitelka, L.F., 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. Clim. Change 51, 541-557.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Global Change Biol. 19, 229-240.

Rigling, A., Brang, P., Bugmann, H., Kräuchi, N., Wohlgemuth, T., Zimmermann, N., 2008. Klimawandel als Prüfstein fur die Waldbewirtschaftung. Schweizerische Zeitschrift für Forstwesen 159, 316-325.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity - Global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Sato, H., Itoh, A., Kohyama, T., 2007. SEIB-DGVM: A new dynamic global vegetation model using a spatially explicit individual-based approach. Ecol. Model. 200, 279-307.

Schwörer, C., Henne, P.D., Tinner, W., 2014. A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. Global Change Biol. 20, 1512-1526.

Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (Ips typographus L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. For. Ecol. Manage. 256, 209-220.

Seidl, R., Rammer, W., Lexer, M.J., 2011. Climate change vulnerability of sustainable forest management in the Eastern Alps. Clim. Change 106, 225-254.

Shugart, H.H., 1984. A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. The Blackburn Press, New Jersey.

Shugart, H.H., Smith, T.M., 1996. A review of forest patch models and their application to global change research. Clim. Change 34, 131-153.

Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biol. 14, 2015-2039.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biol. 9, 161-185.

Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecol. Biogeogr. 10, 621-637.

Solomon, A.M., 1986. Transient response of forests to CO_2 induced climate change: simulation modeling experiments in eastern North America. Oecologia 68, 567-579.

Tinner, W., Theurillat, J.-P., 2003. Uppermost Limit, Extent, and Fluctuations of the Timberline and Treeline Ecocline in the Swiss Central Alps during the Past 11,500 Years. Arct. Antarct. Alp. Res. 35, 158-169.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. For. Ecol. Manage. 42, 95-110.

Watt, A.S., 1947. Pattern and Process in the Plant Community. J. Ecol. 35, 1-22.

Wehrli, A., Zingg, A., Bugmann, H., Huth, A., 2005. Using a forest patch model to predict the dynamics of stand structure in Swiss mountain forests. For. Ecol. Manage. 205, 149-167.

World Meteorological Organisation, 2014. WMO Greenhouse gas bulletin-the state of greenhouse gases in the atmosphere using global observations through 2013. WMO Geneva.

Wunder, J., Reineking, B., Bigler, C., Bugmann, H., 2008. Predicting tree mortality from growth data: how virtual ecologists can help real ecologists. J. Ecol. 96, 174-187.

Wunder, J., Reineking, B., Matter, J.-F., Bigler, C., Bugmann, H., 2007. Predicting tree death for Fagus sylvatica and Abies alba using permanent plot data. J. Veg. Sci. 18, 525-534.

Zimmermann, N.E., Bugmann, H., 2008. Die *Kastanie* im Engadin - oder was halten Baumarten von modellierten Potenzialgebieten? Schweizerische Zeitschrift für Forstwesen 159, 326-335.

1

The agony of choice: different empirical mortality models lead to sharply different future forest dynamics

Bircher, N., Cailleret, M., Bugmann, H., (2015)

Ecological Applications 25, 1303-1318

Abstract

Dynamic models are pivotal for projecting forest dynamics in a changing climate, from the local to the global scale. They encapsulate the processes of tree population dynamics with varying resolution. Yet, almost invariably tree mortality is modeled based on simple, theoretical assumptions that lack a physiological and/or empirical basis. Although this has been widely criticized and a growing number of empirically derived alternatives are available, they have not been tested systematically in models of forest dynamics.

We implemented an inventory-based and a tree-ring-based mortality routine in the forest gap model ForClim v3.0. We combined these routines with a stochastic and a deterministic approach for the determination of tree status (alive vs. dead). We tested the four new model versions for two Norway spruce forests in the Swiss Alps, one of which was managed (inventory time series spanning 72 years) and the other was unmanaged (41 years). Furthermore, we ran long-term simulations (~400 years) into the future under three climate scenarios to test model behavior under changing environmental conditions.

The tests against inventory data showed an excellent match of simulated basal area and stem numbers at the managed site and a fair agreement at the unmanaged site for three of the four empirical mortality models, thus rendering the choice of one particular model difficult. However, long-term simulations under current climate revealed very different behavior of the mortality models in terms of simulated changes of basal area and stem numbers, both in timing and magnitude, thus indicating high sensitivity of simulated forest dynamics to assumptions on tree mortality.

Our results underpin the potential of using empirical mortality routines in forest gap models. However, further tests are needed that span other climatic conditions and mixed forests. Short-term simulations to benchmark model behavior against empirical data are insufficient; long-term tests are needed that include both non-equilibrium and equilibrium conditions. Thus, there is the potential to greatly improve the robustness of future projections of forest dynamics via more reliable tree mortality submodels.

Keywords

Forest gap model; Mortality; Tree ring; Inventory data; Climate change; Forest succession; Modeling

Introduction

Climate-induced shifts of forest ecosystems in terms of tree species composition, productivity and dynamics have already been observed in recent decades and are expected to continue (Fischlin *et al.*, 2007). Since forests provide multiple services to humans such as wood production, protection from natural hazards, or recreation (MEA, 2005), assessing their future development is of high importance (Lindner *et al.*, 2010). To this end, reliable tools are needed (Lindner *et al.*, 1997). Forest gap models have a long history in forest dynamics research, including impact assessments of climate change. Gap models emphasize the longer-term development (Pabst *et al.*, 2008), including tree regeneration and natural mortality in multi-species stands. Thus, they are also suitable for forests with a complex composition and structure (Larocque *et al.*, 2011; Rasche *et al.*, 2011). Their parsimonious concept implies a minimum of required input data, parameters and algorithms, which allows for applications under a wide range of environmental conditions (Didion *et al.*, 2009b; Rasche *et al.*, 2012). However, these models may meet their limits when it comes to accurately reflecting specific processes of forest dynamics, such as tree mortality (cf. Bugmann, 2001).

Although it has long been recognized that the modeling of tree mortality is not based on robust concepts and sound empirical data (Keane *et al.*, 2001), dynamic vegetation models from the local (Bugmann, 2001) to the global scale (Friend *et al.*, 2014) are still lacking trustworthy mortality submodels. Many Growth-And-Yield models include empirically calibrated mortality equations based on logistic regression (e.g., SILVA, PrognAus; Hasenauer, 2006). However, they focus on the harvest potential of a forest stand within the time frame of one tree generation (i.e., one rotation). This focus does not permit the application of these models for assessing the influence of natural mortality on long-term forest dynamics in mixed forests and under changing environmental conditions, where mortality plays a crucial role. As a matter of fact, in the most recent Model Intercomparison Project (ISI-MIP), Friend et al. (2014) found that the discrepancy in simulated terrestrial carbon storage across different impact models is mostly due to uncertainties in carbon residence times (i.e., mortality rates) rather than differences in simulated net primary productivity. Similarly, using a Physio-Demo-Genetics model, Oddou-Muratorio and Davi (2014) have recently found that tree mortality was the main driver of evolutionary dynamics at the local scale.

Here, we focus on the case of forest gap models (Bugmann, 2001) to advance the issue. In these models, mortality is usually split into two parts: First, a stress-induced mortality formulation related to tree growth and, hence, to environmental conditions (light, soil properties, climate). If radial tree growth (i.e., basal area increment BAI, mm^2/year) falls below an absolute threshold or below a certain percentage of maximum growth at the respective tree size/age, the probability of tree mortality increases sharply (Solomon, 1986). The absolute threshold mainly kills small trees that experience high competition and those trees that suffer from adverse environmental conditions (i.e., climatic and soil conditions). The relative threshold mainly kills large trees whose productivity (BAI / total basal area) is reduced due to hydraulic constraints and/or carbon starvation (e.g., Sevanto *et al.*, 2014). Second, most gap models include an ‘intrinsic’ mortality rate that is independent of a tree’s vitality or of its environment, but is stochastic and mostly related to the particular species’ observed maximum age, assuming that small-scale disturbances can kill any tree at any moment (Bugmann, 2001). By doing so, a wide range of causes of individual tree death (such as pathogen attacks, lethal damage to small trees by falling boles, lightning strikes, etc.) is taken into account implicitly. Overall, these two components result in a U-shaped curve of mortality over tree age (or size), which is consistent with numerous empirical studies (Monserud and Sterba, 1999; Temesgen and Mitchell, 2005; Holzwarth *et al.*, 2013). Additionally, some models include an ‘exogenous’ mortality component that reflects large-scale disturbances, either generically without differentiation of the disturbance agents (Bugmann, 1996) or specifically such as wildfires (Miller and Urban, 1999), bark beetle infestations (Lexer and Hönninger, 1998) or windthrow (Pacala *et al.*, 1993).

The assumptions behind these approaches are highly simplistic (Monserud, 2003). Low growth rates per se do not necessarily result in high mortality (cf. Schulman, 1958; Loehle and LeBlanc, 1996; Cailleret *et al.*, 2013), whereas fast growing trees do not usually experience high longevity (Bigler and Veblen, 2009). Furthermore, the constant ‘intrinsic’ mortality cannot capture periods of low mortality rate (Holzwarth *et al.*, 2013), it should depend on tree size rather than age (Manusch et al. 2012), and should not differ between tree species as it is used to explain a wide set of mortality causes (Keane *et al.*, 2001). Thus, there is an urgent need to improve the mortality formulations in dynamic vegetation models by moving from theoretical to empirically-based approaches (Adams *et al.*, 2013).

Over the last 10+ years, a growing number of studies have derived tree mortality models based on empirical data, partly due to the increase of tree mortality phenomena in various regions of the world (Breshears *et al.*, 2005; Allen *et al.*, 2010; Peng *et al.*, 2011). Methodologically, the approaches differ significantly, using data sources such as tree rings (e.g., Bigler and Bugmann, 2004b; Gillner *et al.*, 2013) or forest inventories (e.g., Wunder *et al.*, 2008; Hurst *et al.*, 2011) and a variety of statistical modeling techniques, often logistic regression models, to determine the species-specific, growth-related predictors of tree mortality. While some studies focused on the impact of a single factor such as drought (Bigler *et al.*, 2006) or competition (Das *et al.*, 2011), others reflected general mortality without a differentiation of particular agents (Wyckoff and Clark, 2002), and yet others addressed different mortality modes (Holzwarth *et al.*, 2013). All these studies have greatly increased the empirical foundations for implementing more sophisticated process-based mortality formulations in models of long-term vegetation dynamics. However, even in those studies that were geared to design empirical mortality formulations for dynamic vegetation models (e.g., Bigler and Bugmann, 2004a) or that discussed their findings in this context (e.g., Senecal *et al.*, 2004; Lutz and Halpern, 2006; Das *et al.*, 2011), little progress has followed regarding their actual implementation and testing (e.g., Larocque *et al.*, 2011). Moving ahead in this field is urgent because (1) dynamic vegetation models are highly sensitive to the formulation of mortality (Manusch *et al.*, 2012); (2) tree mortality rates have already increased (e.g., van Mantgem and Stephenson, 2007) and are expected to increase further in the future due to climate change (e.g., Luo and Chen, 2013); and (3) empirical studies on tree mortality vary in many aspects such as in the resolution and time scale of the growth data, the tree species studied, and the input variables that were considered. For instance, some studies were restricted to a certain forest stand (e.g., Fridman and Stahl, 2001) or they included site-specific mortality factors (e.g., “site 1”, “site 2”, in Bravo-Oviedo *et al.*, 2006; Wunder *et al.*, 2008), such that their generalization is impossible. Additionally, some explanatory variables that were collected in the field, such as inter-tree distances (e.g., Schröder *et al.*, 2007; Taylor and MacLean, 2007) cannot be simulated in many dynamic vegetation models, as they are spatially implicit. Lastly, empirical mortality formulations were not usually tested for plausibility under environmental conditions differing from those of the original study.

Therefore, the main objective of the present study is to evaluate a range of empirically-based tree mortality models in a dynamic vegetation model, with the aim of deriving recommendations for the development of sound, robust, and accurate mortality models. Specifically, the mortality submodel of the ForClim model (Bugmann 1996) is replaced by two empirically derived mortality equations that are based on tree-ring and inventory data, respectively. We rigorously evaluate the performance of these equations against long-term empirical data from monospecific Norway spruce (*Picea abies*) stand dynamics under both managed and unmanaged conditions, and assess their behavior in the long-term, including their sensitivity to climate change.

Materials and methods

The ForClim model

ForClim is a cohort-based dynamic vegetation model that was developed to analyze successional pathways of various forest types in Central Europe (Bugmann, 1996) and other parts of the temperate zone (Bugmann and Solomon, 1995; Bugmann and Solomon, 2000; Shao *et al.*, 2001). Based on the theory of patch dynamics (Watt, 1947) tree development (growth), establishment and mortality are simulated with an annual time step on small areas ("patches") while the influence of climate and ecological processes is taken into consideration using a minimum of ecological assumptions. No interaction is assumed between trees of adjacent patches, i.e. the successional pattern at larger scales (forest stand to landscape) is obtained by averaging the simulation results from many patches (Bugmann, 2001).

The structure of ForClim is schematically visualized in Rasche *et al.* (2011). Basically, there are four submodels: The WEATHER and WATER submodels calculate bioclimatic inputs to the PLANT submodel (see below), such as minimum winter temperature, the annual degree-day sum, and soil moisture. A weather generator provides monthly temperature and precipitation data, where monthly means are sampled stochastically from long-term data assuming a normal distribution for temperature and a log-normal distribution for precipitation, respectively. These data are used by the WATER submodel together with the soil water holding capacity to calculate monthly drought indices based on a modified version of the soil water balance model by Thornthwaite and Mather (1957; Bugmann and Cramer, 1998). Tree establishment, growth and mortality are simulated in the PLANT submodel. Saplings are established with a predefined diameter at breast height (dbh) of 1.27 cm, provided that a range of biotic and abiotic factors are within species-specific thresholds (Bugmann 1996). Radial tree growth is modeled based on the carbon budget by Moore (1989), with several modifications (Rasche *et al.*, 2012). Species-specific optimal growth is reduced by several environmental factors including light availability, warmth (degree-day sum) and drought (soil moisture) during the growing season, and nutrient availability (plant-available nitrogen). Note that ForClim does not include any carbon or nutrient storage pools and thus is lacking temporal autocorrelation in simulated tree growth.

As explained above, the mortality probability for trees of cohort c and species s is modeled by two functions: A ‘background’ component that provides a constant, species-specific mortality rate that is derived from the putative maximum age of each species $(gPAge_c)$:

$$gPAge_c = \frac{kDeathP}{kAMax_s} \tag{1}$$

where $kDeathP$ is a mortality coefficient (4.605 by default) and $kAMax_s$ is the species-specific maximum age (e.g., 930 years for Norway spruce; Bugmann, 1994). This corresponds to the assumption that 1% of a tree population will survive to $kAMax_s$. Additionally, a stress-induced mortality $(gPStr_c)$ is included: if diameter increment falls below 10% of its maximum or below 3 mm (i.e., slow growth) for more than two consecutive years $(kSGrT = 2)$, the annual mortality probability is augmented by 0.368 $(kSlowGrP)$:

$$gPStr_c = \begin{cases} kSlowGrP & SGr_c > kSGrT \\ 0 & else \end{cases} \tag{2}$$

where SGr_c denotes the number of consecutive years a cohort has experienced slow growth. This corresponds to the assumption that slow growth leads to a 99% die-off within 10 years for all affected cohorts. The overall mortality probability $gPMort_c$ is calculated for each cohort using Monte Carlo techniques:

$$gPMort_c = gPAge_c + [1 - gPAge_c] * gPStr_c \tag{3}$$

While establishment and growth are modeled at the cohort level, mortality is applied to each single tree of a cohort. For all the trees within the cohort, a random number generator is used to determine whether a tree dies (i.e., a tree dies if a uniform random number [0…1] is below $gPMort_c$).

Finally, the current model version (ForClim v3.0) also includes a sophisticated MANAGEMENT submodel that embodies the most common sylvicultural practices of Central Europe (Rasche *et al.*, 2011).

Empirical mortality models

Inventory-based mortality function

The inventory-based mortality function (*IM*) was derived using single-tree data from plots of the Swiss National Forest Inventory (NFI) that had not experienced forest management for at least 50 years (J. Wunder and M. Abegg, *unpublished manuscript*). The callipering threshold was 12 cm (see Table 1), and the interval between inventories was 11 years.

Table 1: Summary characteristics of tree data used for the derivation of the tree-ring (TRM) and inventory-based (IM) mortality functions. The table shows the total number of tree species included in the studies, the proportion of the most frequent species, the total number of living and dead trees, and for diameter size, the minimum, median and maximum for living and dead trees (minimum/median/maximum).

	Tree data					
	Species		Stem numbers		Diameter size [cm]	
Mortality functions	Total number	Main species	Living	Dead	Living	Dead
TRM	1	Norway spruce (100%)	60 (16540*)	59 (59*)	12/33/87	11/33/81
IM	21	Norway spruce (36%) Fagus sylvatica (18%) Larix decidua (16%)	4055	226	12/27/116	12/19/77

* Number of (tree-ring) measurements with tree status "alive" respectively "dead"

IM was formulated as a logistic regression model where the survival probability depends on tree size, growth rate, shade tolerance and the degree-day sum:

$$\Pr\left(\mathrm{Y_{i,t}} = 1 \middle| \mathrm{X_{i,t}}\right) = \frac{1}{1 + \exp[\alpha_0 + \alpha_1 \times \mathrm{dbh_{i,t}} + \alpha_2 \times \mathrm{dbh^2_{i,t}} + \mathrm{relbai_{i,t,j}} + \alpha_3 \times DD_t + \mathrm{shadeTol}_{\mathrm{i}_k}]^{-1}} \quad (4)$$

where $\Pr\left(Y_{i,t} = 1 \middle| \boldsymbol{X}_{i,t}\right)$ is the probability of tree *i* at year *t* to be still alive in 11 years. DD is the logarithm of the annual degree-day sum (calculated with a threshold of mean monthly temperature of 5.5 °C). The estimate of the $relbai$ variable (relative basal area increment $= {}^{BAI}/_{BA}$) changes according to the class j of growth rates (four classes: "very low": relbai = 0%, "low": 0% < relbai ≤1.5 %, "fast": 1.5% < relbai ≤3% and "very fast": relbai >3%), whereas estimates of the *shadetol* variable change among the three classes k of species-specific shade tolerance ("high", "intermediate" and "low"; cf. Bugmann, 1994). An overview of all model coefficients is shown in Table 2.

Since ForClim has an annual time step, $\Pr(Y_{i,t} = 1 | \boldsymbol{X}_{i,t})$ was scaled to an annual survival probability:

$$gPSurv_{i,t} = 1 - (1 - \Pr(Y_{i,t} = 1 | X_{i,t}))^{1/11} \qquad (5)$$

Further details on the inventory-based mortality routine are in J. Wunder and M. Abegg (*unpublished manuscript*).

Tree-ring-based mortality function

The tree-ring-based mortality function (*TRM*) was taken from Bigler and Bugmann (2004b), who cored pairs of dead and living Norway spruce with a minimum dbh of 10 cm at three sites in the Swiss Alps (see Table 1). They used variable combinations of three different categories – absolute growth level, relative growth level, and growth trend – to fit logistic regression models of the annual probability of tree survival. For the present study, we used the model that showed the best goodness-of-fit in Bigler and Bugmann (2004b):

$$gPSurv_{i,t} = \frac{1}{1 + \exp[\beta_0 + \beta_1 \times \mathrm{locreg}_{5,\mathrm{i,t}} + \beta_2 \times \log(\mathrm{BAI}_{3,\mathrm{i,t}}) + \beta \times \log(\mathrm{relbai}_{\mathrm{i,t}})]^{-1}} \qquad (6)$$

where $locreg5$ denotes the slope of a local linear regression over 5 years of annual basal area increment, $\log(BAI_3)$ is the natural logarithm of the average basal area increment of the last 3 years, and $\log(relbai)$ is the natural logarithm of relative basal area increment of the last year (see also Table 2).

Table 2: Parameter coefficient values for the inventory-based (IM) and tree-ring-based (TRM) mortality function.

Parameters	**IM**	**TRM**
α_0	8.5900	–
α_1	0.0672	–
α_2	-0.0005	–
α_3	-1.0107	–
$\mathrm{relbai}_{\mathrm{i,t,1}}$ ("very low growth")	0 (base level)	–
$\mathrm{relbai}_{\mathrm{i,t,2}}$ ("low growth")	0.5810	–
$\mathrm{relbai}_{\mathrm{i,t,3}}$ ("fast growth")	1.1968	–
$\mathrm{relbai}_{\mathrm{i,t,4}}$ ("very fast growth")	2.0417	–
$\mathrm{shadeTol}_{\mathrm{i,1}}$ ("high")	0 (base level)	–
$\mathrm{shadeTol}_{\mathrm{i,2}}$ ("intermediate")	-0.8194	–
$\mathrm{shadeTol}_{\mathrm{i,3}}$ ("low")	-1.0075	–
β_0	–	14.668
β_1	–	0.577
β_2	–	0.319
β_3	–	1.769

Classification of tree status

Two approaches are widely used for tree status classification; deterministic (i.e., threshold) or stochastic (i.e., random number). In the present study, we compared the performance of both, as described below.

In the stochastic approach, which is commonly employed in dynamic vegetation models (Hawkes, 2000) such as in ForClim v3.0, a random number is drawn for each tree of a cohort to determine whether this tree dies or survives based on its survival probability (see explanations further above).

In the threshold approach, a tree is considered to be dead if its survival probability is lower than a given threshold. That is, no random processes are invoked at all. This method was used for tree status classification in the TRM model of Bigler and Bugmann (2004b). Due to the strong prevalence of measurements where tree status was “alive” (Table 1), they adjusted the threshold using classification accuracy criteria (true positive and true negative rate) and a prediction error (difference between the year of the last ring and the predicted year of death), reaching maximum model performance with a threshold of 0.975. We followed this procedure to derive a threshold for the IM model. However, only classification accuracy criteria were considered, as prediction error criteria would have required data with annual resolution, which were not available. Highest model performance was reached with a threshold of 0.9945 (for details see Appendix A).

In this latter approach, all trees of a cohort were uniformly classified as either alive or dead, since they all have the same mortality probability. To avoid the elimination of entire cohorts (rather than only a fraction of their trees), we modified the procedure, as follows. The number of trees of those cohorts with a survival probability below the threshold was reduced using a linear relationship between the number of trees in the cohort and the difference between their mortality probability and the threshold, i.e. the larger the difference between the threshold and the cohort’s mortality probability, the more trees died.

Table 3: Overview of tested ForClim versions, which are combinations of two mortality functions based on two different data sets (inventory / tree-ring) with two classification approaches (random number / threshold). Additionally, ForClim v3.0 was included whose mortality function is without an empirical background.

		Data set		
		Inventory	Tree Ring	None
Classification approach	Random number	*IM_randNr*	*TRM_randNr*	*ForClim v3.0*
	Threshold	*IM_threshold*	*TRM_threshold*	

Combining each mortality function (TRM; IM) with the two classification approaches (random number; threshold) resulted in four new ForClim versions in addition to the standard version, which is based on theoretical assumptions regarding mortality (ForClim v3.0; cf. Table 3). These mortality functions were applied to all trees in ForClim regardless of their size (i.e, down to newly established saplings with a dbh of 1.27 cm) even though the data for model calibration did not include trees with a dbh <10 cm (TRM) or <12 cm (IM).

Study sites

Two sites were used to conduct simulation studies, both located in the Central Alps of Switzerland (Table 4). Due to the restriction of the TRM function to Norway spruce, only mono-specific stands of that species were selected.

Table 4: The forest stands used in this study with information about their area, location, altitude, water holding capacity (bucket size), available nitrogen, the slope/aspect parameter, patch size in the model, number of patches in the initial patch set and simulation period with the number of inventories (n).

Site (area)	Location (°N / °E)	Altitude (m a.s.l.)	Climate (°C) / (mm)	Bucket size (cm)	Available Nitrogen (kg ha^{-1} yr^{-1})	Slope/ Aspect (–)	Patch size (m^2)	Patch number	Simulation period (n)
Sigriswil (1.5 ha)	46.4 / 7.5	1370	4.54 / 1625	10	80	0	500	30	1925-1997 (10)
Scatlè (3.47 ha)	46.5 / 9.3	1510	3.41 / 1570	10	80	-1	500	70	1965-2006 (4)

Site characteristics

Sigriswil is a site of the Growth-And-Yield research network of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). It consists of an uneven-aged selection forest where management was conducted on a regular basis (Wehrli *et al.*, 2005). Since 1925, harvest data (i.a., year of intervention, tree removal, and targeted species) including a follow-up inventory of the stand have been recorded ten times until 1997. The callipering threshold for the inventories was 7.5 cm.

Scatlè is a strictly protected forest reserve and one of the few relicts of primeval coniferous forests in Central Europe. There are no records or on-site evidence of human disturbance (i.e., management) for the last several centuries (Brang *et al.*, 2011). Data from four forest inventories were available between 1965 and 2006. Living and standing dead trees had been surveyed with a callipering threshold of 8 cm in the first inventory, and 4 cm thereafter.

Climate data and site parameters

Monthly mean temperature and precipitation sum for 1930–2010 were provided by the Land Use Dynamics Research Group at WSL. These data had been derived by a spatial interpolation of data from the MeteoSwiss network using DAYMET (Thornton *et al.*, 1997) to a grid with cell size of 1 hectare. For obtaining long-term temperature and precipitation means, we followed the approach of Rasche et al. (2011), i.e. we used the data series of the cell covering the center of the forest stand and its eight closest neighbors. Averages, standard deviations and cross-correlations of monthly temperature and precipitation were derived by aggregating the daily climate data from the different cells and averaging the resulting data series. Further site parameters including nitrogen availability [$kg \cdot ha^{-1} \cdot yr^{-1}$], maximum soil water holding capacity [cm] and slope/aspect were estimated from site descriptions. No other site parameters were adjusted.

Simulation set-up

Simulations were run for two time periods: “short-term simulations” under current climate for a comparison against the historical time series (inventory data), and “long-term simulations” into the future including climate change scenarios. Only Norway spruce was allowed to establish, and no other tree species were initialized.

For the short-term simulations, the models were initialized with the single-tree data (species, dbh) of the first inventory conducted at the study sites (years 1925 and 1965 in Sigriswil and Scatlè, respectively). Trees from the first inventory were randomly and evenly allocated to the initial set of patches (cf. Wehrli *et al.*, 2005). The initial set (i.e., number) of patches was given by the rounded ratio of total stand area to patch size (500 m^2). To reduce stochastic noise in the results while keeping simulation time reasonably low, simulations were performed for 200 patches. Hence, if the initial set of patches was below 200, they were replicated (cf. Didion *et al.*, 2009b), and the ‘surplus’ patches were randomly sampled without replacement from all initial patches. In contrast to Scatlè, where no management was applied, we implemented an uneven-aged (‘plentering’) regime at Sigriswil. For this harvesting technique, a residual basal area (i.e., basal area that remains after the intervention) serves as initial value for a “plenter equilibrium function” to determine the optimal number of stems in each dbh class. The trees in each dbh class that exceed this optimal number are considered to be “surplus ingrowth”. Additionally, a target diameter (target dbh) is defined for harvesting trees in the higher dbh classes. In user-defined intervals, the number of trees in each diameter class is checked, and trees are removed if they are above the optimal number or the target diameter (cf. Appendix S1 in Rasche *et al.*, 2011). To define intervention years and derive suitable values for the residual basal area and the target dbh (see Appendix B), we followed the “specific management” approach of Rasche et al. (2011).

Simulations into the future were run for the natural forest reserve of Scatlè only. The models were initialized with the single-tree data of the last inventory (2006) and run until the year 2400. Climate change was assumed to take place between 2010 and 2085, employing a linear trend between the current and future climate while the climate was assumed to be stable afterwards. We applied the delta change method on the current climate using delta values from the CH2011 report (Fischer *et al.*, 2015, Appendix 3) for the Northeastern region of Switzerland (CHNE) (Table 5). Simulations were run for an RCP3PD scenario, which is based on the assumption of a global average temperature increase of about 2 °C (“2°-scenario”), and for an A1B scenario. As a baseline, a simulation was also run for the period 2006-2400 using current climatic conditions.

Table 5: Parameter settings for the climate change scenarios (RCP3PD and A1B) for North-Eastern region of Switzerland according to CH2011 report. Upper estimates (i.e., the 97.5th percentile) for temperature and lower estimates (i.e., the 2.5th percentile) for precipitation were used. Compared to the reference climate, absolute changes (differences) are given for temperatures while changes in precipitation are relative (factors). Standard deviations and the cross-correlations between monthly temperature and precipitation values were assumed to stay constant during climate change.

	RCP3PD		A1B	
Season	Temp (°C)	Prec (%)	Temp (°C)	Prec (%)
Spring	+1.67	*0.935	+3.69	*0.936
Summer	+2.2	*0.853	+4.84	*0.713
Fall	+1.89	*0.863	+4.29	*0.824
Winter	+2.15	*0.896	+4.22	*0.891

Results

Short-term simulations: Sigriswil

In Sigriswil, simulated basal area and stem numbers of all model versions matched measured data very well (Figure 1a and 1b, respectively; Appendix H). One exception was *IM_threshold,* which considerably underestimated tree numbers although this had only a slight impact on basal area (cf. Appendix H: relative bias for stem numbers was ~-40.6% while only -4.2% for BA), indicating that the underestimation was mainly due to the lower dbh classes. In fact, 73% of all trees with dbh ≤16 cm were killed after the first simulation year when using *IM_threshold*. Between the first four inventories (1925-1943), *TRM_randNr* and *TRM_threshold* showed a slightly higher stand-level basal area increment (BAI) than the other models because they did not simulate any natural tree death during this period (higher stem number in Figure 1b). After 1950, the development of basal area was very similar for all model versions, but BAI was underestimated compared to the empirical data. Stem numbers were consistently underestimated as well after this point (1950), which is possibly related to the initialization data. In the empirical data, trees with a dbh <7.5 cm were not included due to the callipering threshold, and hence the trees that were initially present in the lower size classes in reality were not simulated in the model.

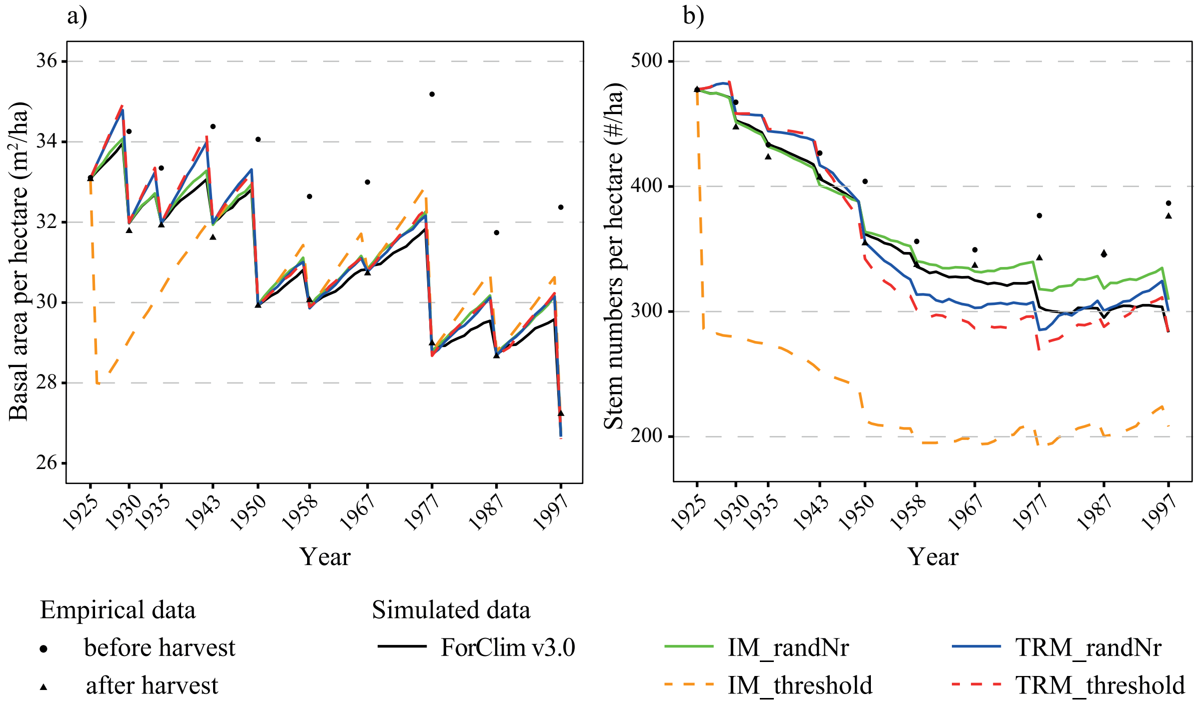


Figure 1: Observed and simulated mean basal area a) and stem numbers b) for Sigriswil. Years on the x-axis indicate time points when management and inventories were conducted. For better visualization, standard deviations of simulated basal area is not shown in the figure but listed separately in Appendix D.

Short-term simulations: Scatlè

For the period of 1965 to 1977, simulated basal area and stem numbers were in the same range as the observed data (Figure 2). On average, basal area was underestimated by -9.6% (-6.6% to -12.1% depending on the model) and stem numbers by -8.6% (-0.5% to -29.1%) compared to observations. Particularly *IM_threshold* was not able to cope with the initialization data, as it killed nearly 80% of all trees with a dbh ≤24 cm just after the beginning of the simulation whereas stem number remained nearly constant afterwards. Simulation results of *TRM_threshold* (basal area: -6.6%, stem numbers: -0.5%) and *TRM_randNr* (basal area: -8.5%, stem numbers: -2.2%) matched the observed data closely.

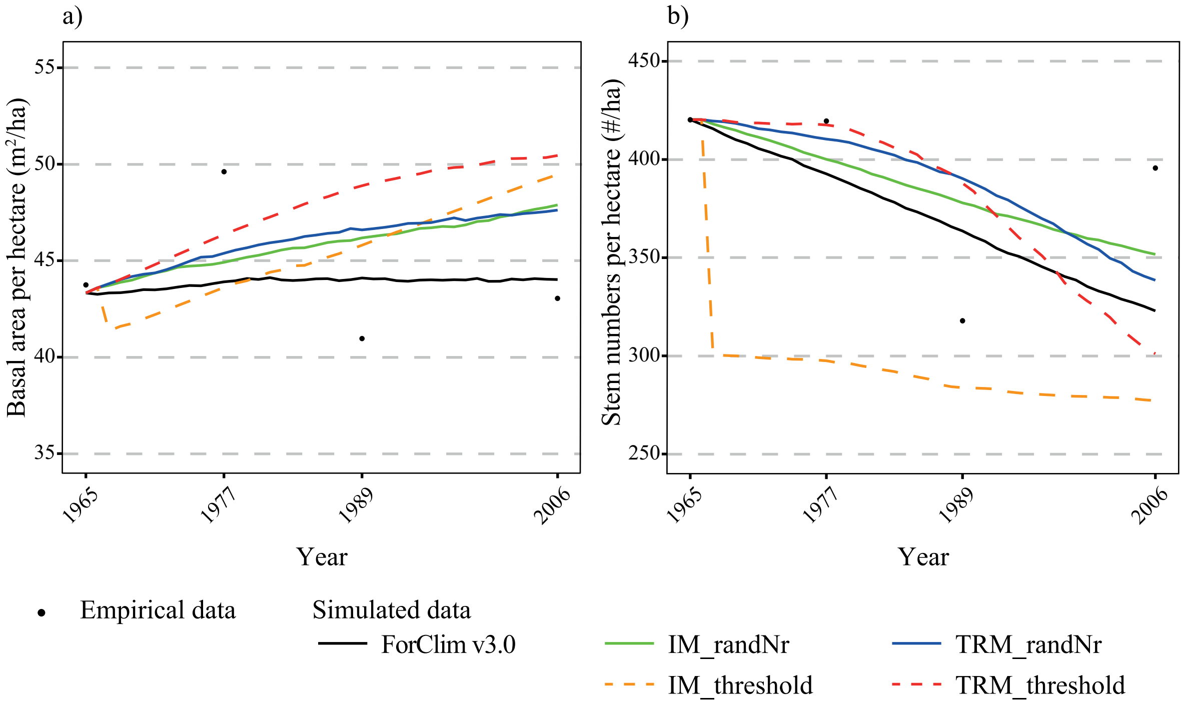


Figure 2: Observed and simulated mean basal area a) and stem numbers b) for Scatlè. Years on the x-axis indicate time points when inventories were conducted. For better visualization, standard deviations of simulated basal area is not shown in the figure but listed separately in Appendix E.

From 1977 to 1989, a sharp decline in basal area and stem numbers occurred in the empirical data (Figure 2a and 2b, respectively), mainly due to avalanche-induced mortality in winter 1984 (Brang *et al.*, 2011). The avalanches impacted mainly trees with a dbh between 18 and 38 cm (cf. lower left panel of Figure 3). In the empirical data, the number of snags increased strongly in these classes compared to the previous inventory, whereas the number of living trees dropped. As natural disturbances are not considered in ForClim, these effects could not be reproduced in the simulation. Instead, a steady decrease in stem numbers was simulated in all versions while basal area increased slightly or was constant (Figure 2a and 2b, respectively). This resulted in an average overestimation by +13.1 ±4.2% of basal area and +13.5 ±13.9% for stem numbers, respectively.

For the period 1989 to 2006, forest dynamics in Scatlè were characterized by an enhanced phase of regeneration, visible from the strong increase in stem numbers of trees with a dbh ≤16 cm in the empirical data (Figure 3), and a slight increase of basal area (Figure 2a), both of which most likely are indirect consequences of the avalanches. *TRM_randNr* and *TRM_threshold* showed a small decrease in BAI while it was nearly constant in *IM_randNr* and *IM_threshold*. *ForClim 3.0* did not show any increase of basal area at all (Figure 2a). The decrease in stem numbers was stronger for *TRM_threshold*, whose behavior was quite similar to the one of *IM_threshold* (Figure 3). Average differences between simulated and observed basal area were somewhat less pronounced (+11.3 ±5.7% depending on the model) due to the recovery of basal area in the observed data. Again, stem numbers were underestimated (-19.6 ±7.5%), especially in the lowest dbh classes (≤16 cm; Figure 3, lower right panel).

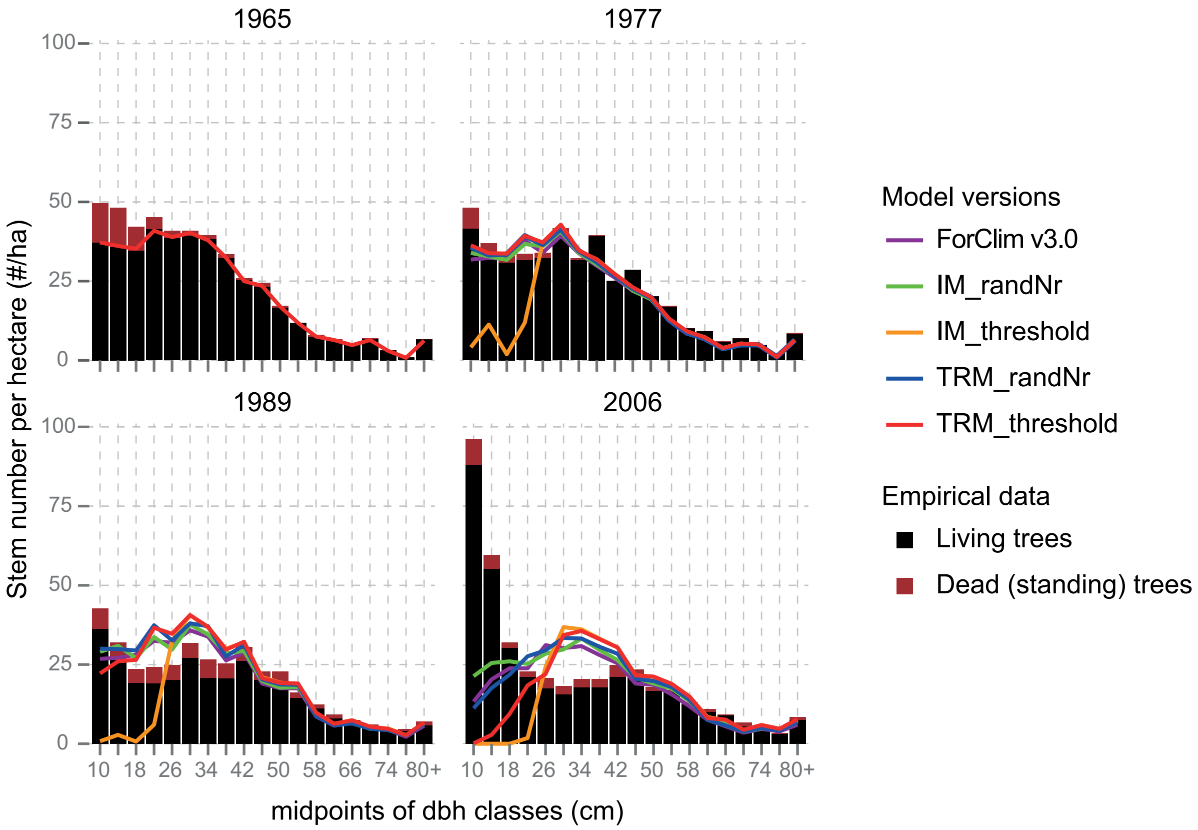


Figure 3: Observed and simulated dbh distribution for Scatlè. The years 1965, 1977, 1989 and 2006, when inventories were conducted, are displayed. The callipering threshold in Scatlè was 8 cm in 1965, consequently, the model initialization did not include any tree data below. It has to be noticed that this threshold was lowered to 4 cm for the inventories in 1977, 1989 and 2006. Still, for comparison reasons, results for trees smaller than 8 cm are not displayed.

Throughout the simulations, the number of large trees was quite similar between all model versions and in good agreement with observed data (Figure 3, cf. Appendix H for relative bias in BA). However, in the low dbh classes (<30 cm), *IM_threshold* failed to accurately reproduce observed stem numbers (cf. Appendix H: relative bias for stem numbers < -24%). Constant stem numbers after the heavy killing of trees at the beginning of the simulation combined with a strong increase of basal area indicate that basal area increment was mainly due to the growth of the largest trees, whose numbers remained almost constant. The other four model versions produced very similar simulation results except in 2006 when *TRM_threshold* featured fewer small trees than *ForClim v3.0*, *IM_randNr*, and *TRM_randNr*.

Long-term simulations: Current climate

In contrast to the short-term simulations, simulations over 400 years under current climatic conditions revealed distinct differences between the five model versions (see black lines in Figure 4). *ForClim v3.0* showed a weak increase of basal area up to a maximum of 44.6 m^2 in 2046, followed by a slow but steady decrease until the end of the simulation period. Similarly, the other model versions also predicted an initial increase in basal area, but with different maximum values (52.6. 69.0, 47.8, and 54.9 m^2) at different points in time (years 2167, 2303, 2066, and 2118) for *IM_randNR, IM_threshold, TRM_randNr,* and *TRM_threshold,* respectively.

In terms of stem numbers, all model versions predicted a decline at the beginning of the simulation, but it differed in duration and magnitude. *ForClim v3.0* reached the lowest value of stem numbers rather early, i.e. in the year 2051 (466 stems/ha), while it was reached in 2091 (381 stems/ha), 2118 (407 stems/ha), and 2151 (153 stems/ha) for the *TRM_randNr, IM_randNr* and *TRM_threshold* models, respectively. After an initial sharp decline, *IM_threshold* kept stem numbers at a very low level, reaching a minimum (164 stems/ha) in the year 2346. Afterwards, the increase in stem numbers was very small for this model version, whereas it was much larger for the other versions.

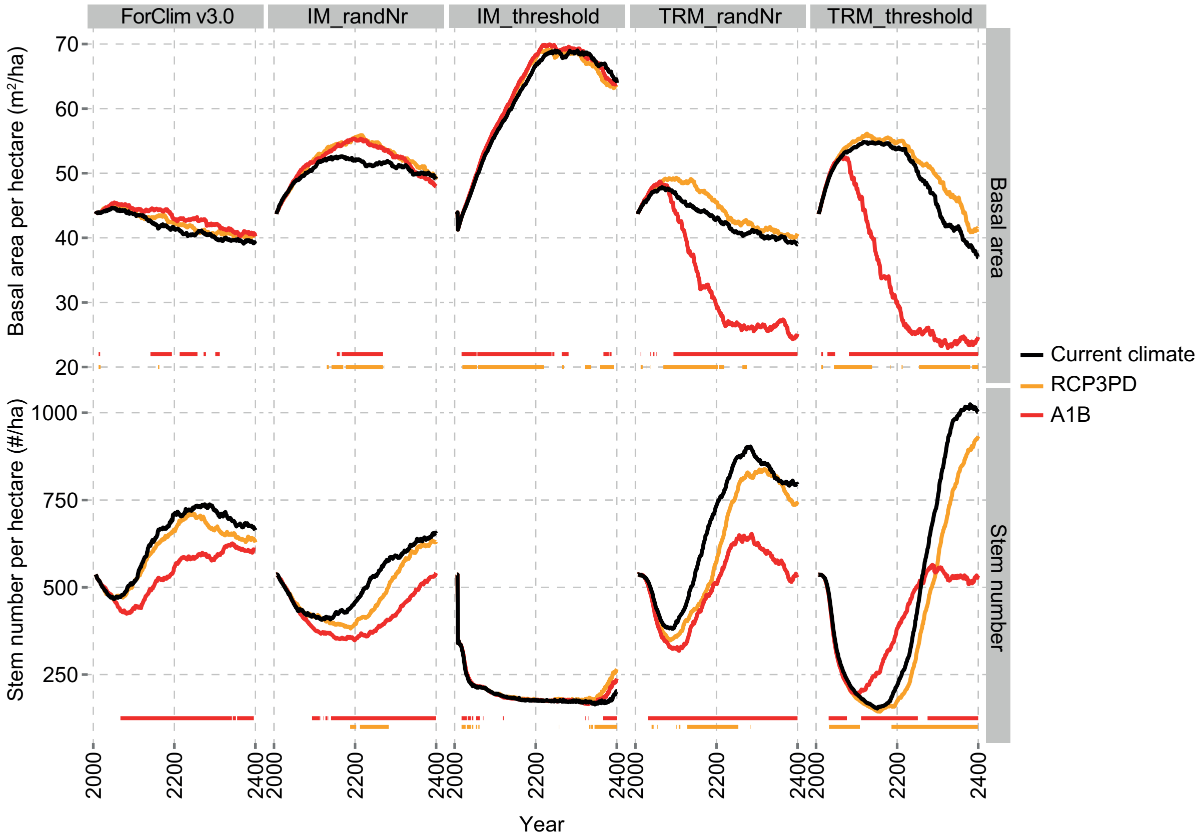


Figure 4: Simulated basal area (upper panels) and stem numbers (lower panels) for the period of 2006-2400 for Scatlè under current climate (black lines) and two climate change scenarios (RCP3PD scenario (“moderate”): orange lines; A1B scenario (“strong”): red lines). Only Norway spruce was considered in the simulations. Horizontal lines indicate significant differences (paired *t* test; $P < 0.05$) between yearly simulation results of the current climate and the RCP3PD scenario (orange) respectively the A1B scenario (red).

Long-term simulations: climate Change

In ForClim, two growth-limiting factors are directly affected by climatic change: the degree-day and the soil moisture growth factors; they were affected quite differently by climate change, as explained below.

Under moderate climate change (scenario RCP3PD), the degree-day growth factor increased by 40%, whereas the soil moisture growth factor was marginally reduced (<1%; Appendix G), essentially leading to better growth of Norway spruce compared to the growth simulated under current climate. However, changes in basal area were hardly significant for ForClim v3.0 (paired *t* test; p>0.05; cf. Figure 4). For the other model versions, the differences were partly significant, but amounted to a few square meters per hectare only. In accordance with simulated higher basal area, stem numbers were generally below current levels up to 210 stems/ha in the *TRM_threshold* model.

Under stronger climate change (A1B), simulated growing conditions for Norway spruce were improved as well. Compared to current climate, the degree-day growth factor increased by 70% while the growth reduction due to drier conditions (i.e., reduced soil moisture) amounted to 5% (Appendix G). Still, compared to the RCP3PD scenario, *ForClim v3.0, IM_randNr*, and *IM_threshold* did not show notable differences in basal area. Establishment of Norway spruce was constrained because of increased minimum winter temperatures (Appendix G), which explains the significantly lower stem numbers, but not the short-term reduction in basal area, as the latter is determined mainly by the trees with a large diameter. Thus, the patterns of stem numbers and in particular of basal area predicted by *TRM_randNr* and *TRM_threshold* were in stark contrast to those of the other model versions. Basal area dropped from 49 $m^2 \cdot ha^{-1}$ and 53 $m^2 \cdot ha^{-1}$ to around 26 $m^2 \cdot ha^{-1}$ and 25 $m^2 \cdot ha^{-1}$ (in 2220 and 2240) for *TRM_randNr* and *TRM_threshold,* respectively.

Discussion

We tested the performance of the gap model ForClim when using empirical mortality models as compared to the theoretical formulation incorporated in ForClim (v3.0). With the exception of *IM_threshold*, all mortality models produced accurate results as compared against short-term forest inventory data under both unmanaged and managed conditions. Long-term simulation results, however, differed distinctively between model versions, underlining the strong influence of the mortality function on future forest development.

Test at a managed site: Sigriswil

Predicted basal area and stem numbers agreed well with observed data. This was expected, as harvests regularly removed surplus ingrowth and thus eliminated the differences that developed between observed and simulated data as well as between the different model versions. We recognize the potential weakness of evaluating mortality models in intensively managed forests (cf. Didion *et al.*, 2009a) where natural mortality plays a subordinate role (Harkonen *et al.*, 2010) – most of the trees, especially slow-growing ones, are removed by harvesting. Nevertheless, this setup still constitutes a major challenge for forest models that deal with management (Pretzsch *et al.*, 2008) as it requires an adequate representation of several processes including tree growth, mortality, and harvesting. Other studies found highly exaggerated simulated tree mortality (e.g., Pabst *et al.*, 2008) or were forced to switch off natural mortality entirely to avoid awkward results (e.g., Lafond *et al.*, 2014). In this sense, the application of the model at Sigriswil demonstrated that the simultaneous use of natural mortality and a management regime is possible in ForClim; this is in stark contrast with earlier experiences (cf. Rasche *et al.*, 2011). However, tests at Sigriswil also revealed that measured BAI after harvesting was typically much higher than simulated by ForClim (Figure 1). Considering that basal area and the number of trees to be harvested using the plentering technique was not fixed but depended on surplus ingrowth, this suggests that tree growth is underestimated and/or mortality rates are overestimated (cf. Wunder *et al.*, 2006; see Appendix F).This is an area of ongoing research, to improve the relationships between light availability and growth in the model, so as to solve this issue. Additionally, the feedbacks between growth, mortality and management need further consideration, but the present application clearly underlines the value of managed stands for testing the balanced representation of ecological processes in models of vegetation dynamics.

Test at an unmanaged site: Scatlè

An underestimation of BAI was also evident in the simulation between the inventories of 1965 and 1977 at Scatlè (the avalanche event precludes such an analysis after 1984). However, most of the predicted values of total stem numbers and dbh distribution agreed well with observations. All ForClim versions accurately predicted tree numbers in the higher dbh classes (Figure 3). Even though these trees are a small minority in terms of stem numbers, their correct prediction is crucial as they strongly contribute to stand basal area.

In contrast, small trees show generally higher turnover rates, as they are more subject to asymmetrical competition for light and water (e.g., Holzwarth *et al.*, 2013). The relatively high callipering limit of the empirical data hindered the evaluation of mortality rates of the small size classes. Additional model tests for young Norway spruce stands would extend our understanding regarding the effects of the mortality submodel for very small trees and tree establishment. However, data on the population dynamics of these tree size classes are exceedingly rare, and thus our analysis should still be meaningful. The very high simulated mortality rates in the small dbh classes reported for some model versions confirm earlier results (cf. Wehrli *et al.*, 2005). This was especially distinct in *IM_threshold,* which showed a clearly awkward behavior, and to a lesser extent in *TRM_threshold*. The overall results from the other model versions in the short-term simulations did not allow for a clear discrimination of their performance (cf. performance values in Appendix H).

Long-term simulations

Long-term simulations (>200 years), even under current climate, can reveal significant differences in terms of the plausibility of model behavior compared to shorter simulation periods of 50 to 60 years (Bugmann *et al.*, 2001; Didion *et al.*, 2009b). Indeed, our simulation results for a 400-year period highlighted that in the long run the mortality models behave very differently even under constant climate conditions. This confirms earlier conjectures that were based on a range of theoretical mortality models (Bugmann *et al.*, 2001). In contrast to the other ForClim versions, *ForClim v3.0* showed only a small increase of basal area at the beginning of the simulation due to its constant background mortality. After a substantial increase in basal area in the other model versions, low light availability caused a reverse trend that was faster for the *TRM* models than for the *IM* models. Indeed, the *TRM* function solely includes variables related to growth ($locreg_5$, BAI_3, *relbai*) and thus is highly sensitive to this process, while only the *relbai* variable is included in the IM whose effect is further mitigated by the variable's factorial character (i.e., small changes in relbai do not cause a mortality response unless relbai then falls into another class). Furthermore, the *IM* function led to rather low mortality rates for trees that were beyond the juvenile phase, even if they showed very low growth. Hence, no decline of basal area was visible in *IM_randNr*.

Under a moderate climate change scenario (RCP3PD), all ForClim versions reacted in a similar manner relative to their behavior under the current climate. They simulated slightly higher basal area due to the higher degree-day sum that fostered growth while the slight increase in drought conditions had a negligible effect. These patterns are consistent on the one hand with historical growth changes of Norway spruce in Europe, resulting from nitrogen deposition and an increase of temperature (e.g., Hasenauer *et al.*, 1999; Charru *et al.*, 2013), and on the other hand with projections of Norway spruce productivity under climate change (Briceño-Elizondo *et al.*, 2006; Matala *et al.*, 2006; Kapeller *et al.*, 2012). Lower stem numbers were also simulated due to enhanced competition for light, which reduced tree regeneration rates.

Similar projections were obtained under the A1B scenario except for the *TRM* models, where BA strongly decreased after the end of the 21st century in spite of better growing conditions. This paradox is caused by the calculation of the overall growth reduction, where growth equals zero when only one environmental requirement is not fulfilled (Bugmann, 1996). Under the A1B scenario, drought indices were beyond the threshold for Norway spruce - which implies zero growth - on 50% of the simulated forest patches each year, compared to only 5% under current climate (Appendix G). In contrast to the mortality algorithm in *ForClim 3.0* and the *IM* function, the *TRM* function is highly sensitive to strong annual changes in tree growth, due to the high importance of the *relbai* variable in the prediction of tree mortality (which explained 66% of the mortality events in the empirical data; Appendix C). This effect was enhanced when the TRM function was implemented in ForClim (93% to 94%; Appendix C). The effects of the mean growth rate of the last three years (BAI_3) and of the trend variable $locreg_5$ were negligible as medium-frequency variation in radial growth was not accurately simulated due to the lack of autocorrelation in successive ring-widths. This highlights the need for a more realistic simulation of growth in ForClim under prolonged periods of stress, and to evaluate the realism of single years for which growth is simulated to be zero (i.e., missing tree rings; cf. Wunder *et al.*, 2006). For future model development, such unrealistic annual declines in tree growth could be mitigated e.g. by implementing (i) thresholds for maximum changes in annual diameter increment derived from tree-ring data, or (ii) pools of surplus carbohydrates that can be used in subsequent years (Misson *et al.*, 2004).

Tree-ring vs. inventory-based mortality functions

The *TRM* function was specifically calibrated for Norway spruce and has not shown marked differences in performance when validated for two other Norway spruce stands (Bigler and Bugmann, 2004b); thus a better performance of this function in mono-specific spruce forests was expected relative to the more general *IM* function. This was not confirmed by the simulation results, however. The fact that 36% of the trees used for the calibration of the *IM* function were Norway spruce (J. Wunder and M. Abegg, *unpublished manuscript*) may have contributed to the good performance of the *IM* function.

Still, the question arises whether the performance of these functions would be similar in multi-specific forests; the prediction of species composition is a crucial feature of forest succession models. Particularly if climate change pushes some tree species towards or beyond their physiological limits, this may be reflected very differently in the two types of mortality functions. For example, reduced growth due to drought may instantaneously lead to increased mortality rates in the *TRM* function, while it will be dampened in the *IM* function (one growth variable with factorial character). Thus, model behavior is likely to differ by tree species and its growth dynamics, which may lead to strongly different simulated tree species composition. Hence, applying these mortality functions to more diverse forest ecosystems is a crucial next step.

In this context, however, we face the problem that *TRM* functions are usually developed for one to a few species at best, for a few sites and often using site-specific methodologies, which strongly limits their use in succession models that feature dozens of species. One approach might be to develop species-specific mortality functions for plant functional types rather than species. We feel, however, that a better way to address this problem would be to derive one general mortality algorithm using meta-analysis approaches. In either case, data scarcity linked with the high effort required to expand the database beyond individual sites constitute the main constraints to such an endeavor.

In contrast, forest inventories usually cover a wide range of tree species and large areas (e.g., Holzwarth *et al.*, 2013), thus making the development of *IM* models more straightforward although not without problems, either. First, inventory data almost always lack an annual resolution of tree-ring data (but cf. van Mantgem and Stephenson, 2007). For the application in a dynamic vegetation model, growth and mortality need to be converted to an annual (or even finer) resolution, thus smoothing out any inter-annual variation that is likely to contain important ecological information (Biondi, 1999). Second, spatially extensive inventory data usually cover a few decades at most, which is a short time window in view of most trees' life expectancy. Thus, reactions to extreme site conditions caused by events with rare occurrence and short duration (e.g., drought) may remain unreflected in growth-mortality relationships. In contrast, tree-ring data normally cover a much longer time span (i.e., a tree's entire life), such that they are more likely to capture the full processes and environmental conditions experienced by the trees, and thus to reflect stand dynamics more accurately. Third, inventory data usually neglect small tree size classes (typically, data are measured for dbh >10 cm only); however, also many tree-ring data miss a part of early tree life. Yet, it has to be recognized that using sophisticated recent methods (e.g., Lichstein *et al.*, 2009; Lichstein *et al.*, 2010; Lichstein *et al.*, 2014), it is possible to develop accurate tree mortality models, particularly if large-scale inventory data such as the FIA in the US are available.

The 'thinning' stage: high mortality but low data availability

Excluding the smallest trees from model calibration can lead to considerable uncertainties in the simulation of stand dynamics, because during this "thinning" phase mortality is high and future stand dynamics are shaped strongly. First, empirical mortality functions may not realistically reflect the relationship between growth and mortality of small trees that experience particularly low light availability. Our simulations for Scatlè indicate that considerable differences in the smallest dbh classes can be observed within a few decades, which may significantly affect tree species composition in the long term. Second, the selection of the threshold value is typically based on the same data that had been used for calibration (e.g., Bigler and Bugmann, 2004b, this study). This results in a strong dependence on the sampled data set and in a potential bias due to the strong prevalence of "living" events (Manel *et al.*, 2001; Lawson *et al.*, 2013). If data for the smallest dbh classes are not considered, an overestimation of the threshold value and thus the mortality of small trees may occur, as shown by the *IM_threshold* and *TRM_threshold* models. There, the random approach allowed for a mitigation of these effects, which led to very different simulation results even with the same mortality routine. These findings support the argument of Zhou and Buongiorno (2004) that including stochasticity contributes to a more accurate and flexible reflection of natural processes in forests (cf. also Fortin and Langevin, 2012). Third, even if the mortality functions work perfectly well, problems may arise from other submodels (e.g., establishment, or growth), as these may be lacking a commensurate empirical foundation and resolution (cf. Wyckoff and Clark, 2002; Wunder *et al.*, 2006).

Research needs

Loehle and LeBlanc (1996) suggested that running simulations at single sites under current climate constitutes an insufficient test for model realism; our findings strongly support this point. Instead, tests under conditions of climate change tend to be much more telling. Furthermore, a comparison of different model versions is highly suitable for detecting structural inconsistencies (cf. Bugmann *et al.*, 2001). Bigler and Bugmann (2004a) found that the predicted numbers of living and dead trees may diverge strongly between different empirical mortality functions. However, they evaluated these functions outside of a dynamic modeling framework, where the interactions with other model processes can be expected to balance the different effects of the mortality functions.

Our results show that in long-term simulations, predictions of forest dynamics vary considerably depending on the choice of the mortality function. This is consistent with findings by Friend *et al.* (2014) where the choice of the (theoretical) mortality function had a strong effect on future vegetation predictions and their uncertainty. However, not only stress-induced but also disturbance-related tree mortality plays a crucial role in long-term forest dynamics (Turner, 2010). While the death of single trees due to endemic pests or other small disturbance agents is implicitly considered in the ‘age-related’ mortality (Rasche *et al.*, 2013) or in the intercept of the empirical mortality functions (this study), larger disturbances are rarely represented in forest gap models. Model development in this field primarily requires a better empirical understanding of disturbance events (i.e., predisposing factors, interaction among disturbance agents) and practical solutions to integrate spatially explicit disturbance processes into models that lack an explicit consideration of space (Seidl *et al.*, 2011). For stress-induced mortality, empirically based process formulations are expected to be a clear improvement compared to theoretical designs (Keane *et al.*, 2001). Theoretical concepts can have high predictive power provided that the underlying theory regarding how the processes are modelled is correct and the model is parameterized “well”. However, in reality these processes are not usually measured or are not measurable, and thus parameter values remain highly uncertain. In contrast, empirical formulations are directly derived from measured data and hence, their structure and parameter values are not subject to speculation. Although empirical formulations depend on the data source used for calibration and may have limited predictive power beyond this data set, they have already proven to be superior to theoretical approaches in the context of tree mortality (Bigler and Bugmann, 2004a; Wunder *et al.*, 2006). Our results encourage empirical functions as a valid alternative to theoretical concepts. However, uncertainty of model predictions obviously still prevails. Consequently, further research is needed to assess the sensitivity of dynamic vegetation models to the structure and parameterization of empirical mortality functions (cf. McDowell *et al.*, 2013). In addition, so far little consideration has been given to the issue whether a direct implementation of an empirical function into a forest dynamics model allows for a full exploitation of the function’s potential, or whether a re-calibration within the framework of the forest model is required to maximize its performance. Inverse modeling techniques (cf. Hartig *et al.*, 2012) are highly promising to better consider interactions between sub-models and to assess the uncertainty in model parameterization and predictions.

Conclusions

We implemented several empirical mortality functions in a dynamic vegetation model and applied it to both managed and unmanaged forest sites, which is, to the best of our knowledge, a novel approach in forest dynamics modeling. We demonstrated that empirical mortality formulations are valuable to replace the current simple mortality algorithms in dynamic vegetation models. When applied to mono-specific stands, fairly accurate results are achieved in both managed and unmanaged forests. However, simulation tests are not conclusive if conducted against inventory data that span a few decades only. Instead, long-term simulations and climate change scenarios have high power to identify differences between the mortality functions, although they do not necessarily allow for the discrimination of "good" vs. "inappropriate" functions.

Simulation results from models of long-term vegetation dynamics critically depend on the mortality algorithm that is used. The implementation of empirically derived algorithms – rather than mortality models that are based on theoretical considerations alone – contributes strongly to the detection of structural model errors and, hence, to model improvement.

We highlighted the advantages and disadvantages of inventory- and tree-ring-based mortality functions. Further research is required to determine which approach serves best for a given modeling objective. Such tests should include the application in mixed-species forests and changing climatic conditions that push tree species towards their physiological limits. In the derivation of empirical mortality functions, more attention should be paid to the smallest dbh classes, as small trees are subject to high mortality rates whose magnitude and cause should be captured realistically if we are to accurately simulate forest dynamics.

Acknowledgments

This research was funded by the Swiss Federal Office for the Environment FOEN in the context of the program "Forests and Climate Change". We would like to thank Jan Wunder and Christof Bigler for helpful discussions, Dominic Michel for IT assistance, and Andreas Zingg for providing inventory data of the Growth-And-Yield research network. We gratefully acknowledge the comments of two anonymous reviewers and of the editor that contributed to the quality of this paper.

References

Adams, H.D., Williams, A.P., Xu, C., Rauscher, S.A., Jiang, X., McDowell, N.G., 2013. Empirical and process-based approaches to climate-induced forest mortality models. Frontiers in Plant Science 4, 438.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330-343.

Bigler, C., Bugmann, H., 2004a. Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. Ecol. Model. 174, 225-239.

Bigler, C., Bugmann, H., 2004b. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14, 902-914.

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130-1138.

Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol. Appl. 9, 216-227.

Brang, P., Bugmann, H., Heiri, C., 2011. Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Birmensdorf, Eidg. Forschungsanstalt WSL; Zürich, ETH Zürich. Bern, Stuttgart, Wien, Haupt.

Bravo-Oviedo, A., Sterba, H., del Río, M., Bravo, F., 2006. Competition-induced mortality for Mediterranean Pinus pinaster Ait. and P. sylvestris L. For. Ecol. Manage. 222, 88-98.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. 102, 15144-15148.

Briceño-Elizondo, E., Garcia-Gonzalo, J., Peltola, H., Matala, J., Kellomäki, S., 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. For. Ecol. Manage. 232, 152-167.

Bugmann, H., 1994. On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study. Ph.D. Thesis No. 10638, Swiss Federal Institute of Technology Zurich, Switzerland, 258 p.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259-305.

Bugmann, H., Cramer, W., 1998. Improving the behaviour of forest gap models along drought gradients. For. Ecol. Manage. 103, 247-263.

Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055-2074.

Bugmann, H.K.M., Solomon, A.M., 1995. The use of a European forest model in North America: A study of ecosystem response to climate gradients. J. Biogeogr. 22, 477-484.

Bugmann, H.K.M., Solomon, A.M., 2000. Explaining Forest Composition and Biomass across Multiple Biogeographical Regions. Ecol. Appl. 10, 95-114.

Bugmann, H.K.M., Wullschleger, S.D., Price, D.T., Ogle, K., Clark, D.F., Solomon, A.M., 2001. Comparing the performance of forest gap models in North America. Clim. Change 51, 349-388.

Cailleret, M., Nourtier, M., Amm, A., Durand-Gillmann, M., Davi, H., 2013. Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann. For. Sci. 71, 643-657.

Charru, M., Seynave, I., Hervé, J.-C., Bontemps, J.-D., 2013. Spatial patterns of historical growth changes in Norway spruce across western European mountains and the key effect of climate warming. Trees 28, 205-221.

Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manage. 261, 1203-1213.

Didion, M., Kupferschmid, A.D., Lexer, M.J., Rammer, W., Seidl, R., Bugmann, H., 2009a. Potentials and limitations of using large-scale forest inventory data for evaluating forest succession models. Ecol. Model. 220, 133-147.

Didion, M., Kupferschmid, A.D., Zingg, A., Fahse, L., Bugmann, H., 2009b. Gaining local accuracy while not losing generality - extending the range of gap model applications. Can J Forest Res 39, 1092-1107.

Fischer, A.M., Liniger, M.A., Appenzeller, C., 2015. Climate scenarios of seasonal means: inter-variable and inter-seasonal correlations of change estimates. CH2011 Extension Series No. 3. MeteoSwiss and Center for Climate Systems Modeling, Zurich, Switzerland.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J., A.A., V., 2007. Ecosystems, their properties, goods, and services. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), IPCC Fourth Assessment Report (AR4). Cambridge University Press, Cambridge, pp. 211-272.

Fortin, M., Langevin, L., 2012. Stochastic or deterministic single-tree models: is there any difference in growth predictions? Ann. For. Sci. 69, 271-282.

Fridman, J., Stahl, G., 2001. A three-step approach for modelling tree mortality in Swedish forests. Scand. J. For. Res. 16, 455-466.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., Woodward, F.I., 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Acad. Sci. U.S.A. 111, 3280-3285.

Gillner, S., Rüger, N., Roloff, A., Berger, U., 2013. Low relative growth rates predict future mortality of common beech (Fagus sylvatica L.). For. Ecol. Manage. 302, 372-378.

Harkonen, S., Makinen, A., Tokola, T., Rasinmaki, J., Kalliovirta, J., 2010. Evaluation of forest growth simulators with NFI permanent sample plot data from Finland. For. Ecol. Manage. 259, 573-582.

Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O'Hara, R.B., Scheiter, S., Huth, A., 2012. Connecting dynamic vegetation models to data – an inverse perspective. J. Biogeogr. 39, 2240-2252.

Hasenauer, H., 2006. Sustainable forest management: growth models for Europe. Springer, Berlin.

Hasenauer, H., Nemani, R.R., Schadauer, K., Running, S.W., 1999. Forest growth response to changing climate between 1961 and 1990 in Austria. For. Ecol. Manage. 122, 209-219.

Hawkes, C., 2000. Woody plant mortality algorithms: description, problems and progress. Ecol. Model. 126, 225-248.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. J. Ecol. 101, 220-230.

Hurst, J.M., Allen, R.B., Coomes, D.A., Duncan, R.P., 2011. Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane Nothofagus forest. Plos One 6.

Kapeller, S., Lexer, M.J., Geburek, T., Hiebl, J., Schueler, S., 2012. Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate. For. Ecol. Manage. 271, 46-57.

Keane, R., Austin, M., Field, C., Huth, A., Lexer, M., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree Mortality in Gap Models: Application to Climate Change. Clim. Change 51, 509-540.

Lafond, V., Lagarrigues, G., Cordonnier, T., Courbaud, B., 2014. Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. Ann. For. Sci. 71, 173-186.

Larocque, G.R., Archambault, L., Delisle, C., 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222, 2570-2583.

Lawson, C.R., Hodgson, J.A., Wilson, R.J., Richards, S.A., 2013. Prevalence, thresholds and the performance of presence–absence models. Methods in Ecology and Evolution 5, 54-64.

Lexer, M., Hönninger, K., 1998. Simulated effects of bark beetle infestations on stand dynamics in Picea abies stands: coupling a patch model and a stand risk model. In: Beniston, M., Innes, J. (Eds.), The Impacts of Climate Variability on Forests. Springer Berlin Heidelberg, pp. 289-308.

Lichstein, J.W., Dushoff, J., Ogle, K., Chen, A.P., Purves, D.W., Caspersen, J.P., Pacala, S.W., 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. Ecol. Appl. 20, 684-699.

Lichstein, J.W., Golaz, N.Z., Malyshev, S., Shevliakova, E., Zhang, T., Sheffield, J., Birdsey, R.A., Sarmiento, J.L., Pacala, S.W., 2014. Confronting terrestrial biosphere models with forest inventory data. Ecol. Appl. 24, 699-715.

Lichstein, J.W., Wirth, C., Horn, H.S., Pacala, S.W., 2009. Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), Old-Growth Forests: Function, Fate and Value. Springer, 233 Spring Street, New York, Ny 10013, United States, pp. 301-341.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698-709.

Lindner, M., Sievänen, R., Pretzsch, H., 1997. Improving the simulation of stand structure in a forest gap model. For. Ecol. Manage. 95, 183-195.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model. 90, 1-31.

Luo, Y., Chen, H.Y.H., 2013. Observations from old forests underestimate climate change effects on tree mortality. Nat Commun 4, 1655.

Lutz, J.A., Halpern, C.B., 2006. Tree Mortality during Early Forest Development: A Long-Term Study of Rates, Causes, and Consequences. Ecol. Monogr. 76, 257-275.

Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921-931.

Manusch, C., Bugmann, H., Heiri, C., Wolf, A., 2012. Tree mortality in dynamic vegetation models - A key feature for accurately simulating forest properties. Ecol. Model. 243, 101-111.

Matala, J., Ojansuu, R., Peltola, H., Raitio, H., Kellomaki, S., 2006. Modelling the response of tree growth to temperature and CO2 elevation as related to the fertility and current temperature sum of a site. Ecol. Model. 199, 39-52.

McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Holtta, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Martinez-Vilalta, J., Mencuccini, M., Plaut, J.A., Ogee, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yepez, E.A., Pockman, W.T., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytol. 200, 304-321.

MEA, 2005. Millennium Ecosystem Assessment, Island Press, Washington, D.C.

Miller, C., Urban, D.L., 1999. A model of surface fire, climate and forest pattern in the Sierra Nevada, California. Ecol. Model. 114, 113-135.

Misson, L., Rathgeber, C., Guiot, J., 2004. Dendroecological analysis of climatic effects on Quercus petraea and Pinus halepensis radial growth using the process-based MAIDEN model. Can. J. For. Res. 34, 888-898.

Monserud, R.A., 2003. Evaluating forest models in a sustainable forest management context. Forest Biometry, Modelling and Information Sciences 1, 35-47.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109-123.

Moore, A.D., 1989. On the maximum growth equation used in forest gap simulation-models. Ecol. Model. 45, 63-67.

Oddou-Muratorio, S., Davi, H., 2014. Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evolutionary Applications 7, 453-467.

Pabst, R.J., Goslin, M.N., Garman, S.L., Spies, T.A., 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. For. Ecol. Manage. 256, 958-972.

Pacala, S.W., Canham, C.D., Silander Jr, J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980-1988.

Peng, C.H., Ma, Z.H., Lei, X.D., Zhu, Q., Chen, H., Wang, W.F., Liu, S.R., Li, W.Z., Fang, X.Q., Zhou, X.L., 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat. Clim. Chang. 1, 467-471.

Pretzsch, H., Grote, R., Reineking, B., Rotzer, T., Seifert, S., 2008. Models for forest ecosystem management: A European perspective. Ann. Bot. 101, 1065-1087.

Rasche, L., Fahse, L., Bugmann, H., 2013. Key factors affecting the future provision of tree-based forest ecosystem goods and services. Clim. Change 118, 579-593.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2011. Getting a virtual forester fit for the challenge of climatic change. J. Appl. Ecol. 48, 1174-1186.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2012. Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. Ecol. Model. 232, 133-143.

Schröder, J., Röhle, H., Gerold, D., Münder, K., 2007. Modeling individual-tree growth in stands under forest conversion in East Germany. European Journal of Forest Research 126, 459-472.

Schulman, E., 1958. Bristlecone pine, oldest known living thing. National Geographic 113, 355-372.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpaci, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., Mohren, F., 2011. Modelling natural disturbances in forest ecosystems: a review. Ecol. Model. 222, 903-924.

Senecal, D., Kneeshaw, D., Messier, C., 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. 34, 396-404.

Sevanto, S., McDowell, N.G., Dickman, L.T., Pangle, R., Pockman, W.T., 2014. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. Plant Cell Environ. 37, 153-161.

Shao, G.F., Bugmann, H., Yan, X.D., 2001. A comparative analysis of the structure and behavior of three gap models at sites in northeastern China. Clim. Change 51, 389-413.

Solomon, A.M., 1986. Transient response of forests to CO_2 induced climate change: simulation modeling experiments in eastern North America. Oecologia 68, 567-579.

Taylor, S.L., MacLean, D.A., 2007. Spatiotemporal patterns of mortality in declining balsam fir and spruce stands. For. Ecol. Manage. 253, 188-201.

Temesgen, H., Mitchell, S.J., 2005. An Individual-Tree Mortality Model for Complex Stands of Southeastern British Columbia. Western Journal of Applied Forestry 20, 101-109.

Thornthwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology, Drexel Institute of Technology, Centerton, New Jersey 10, 185-311.

Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. Journal of Hydrology 190, 214-251.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833-2849.

van Mantgem, P.J., Stephenson, N.L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecol. Lett. 10, 909-916.

Watt, A.S., 1947. Pattern and Process in the Plant Community. J. Ecol. 35, 1-22.

Wehrli, A., Zingg, A., Bugmann, H., Huth, A., 2005. Using a forest patch model to predict the dynamics of stand structure in Swiss mountain forests. For. Ecol. Manage. 205, 149-167.

Wunder, J., Bigler, C., Reineking, B., Fahse, L., Bugmann, H., 2006. Optimisation of tree mortality models based on growth patterns. Ecol. Model. 197, 196-206.

Wunder, J., Brzeziecki, B., Żybura, H., Reineking, B., Bigler, C., Bugmann, H., 2008. Growth–mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. Oikos 117, 815-828.

Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. J. Ecol. 90, 604-615.

Zhou, M., Buongiorno, J., 2004. Nonlinearity and noise interaction in a model of forest growth. Ecol. Model. 180, 291-304.

Supplemental Material

APPENDIX A: Derivation of IM classification threshold

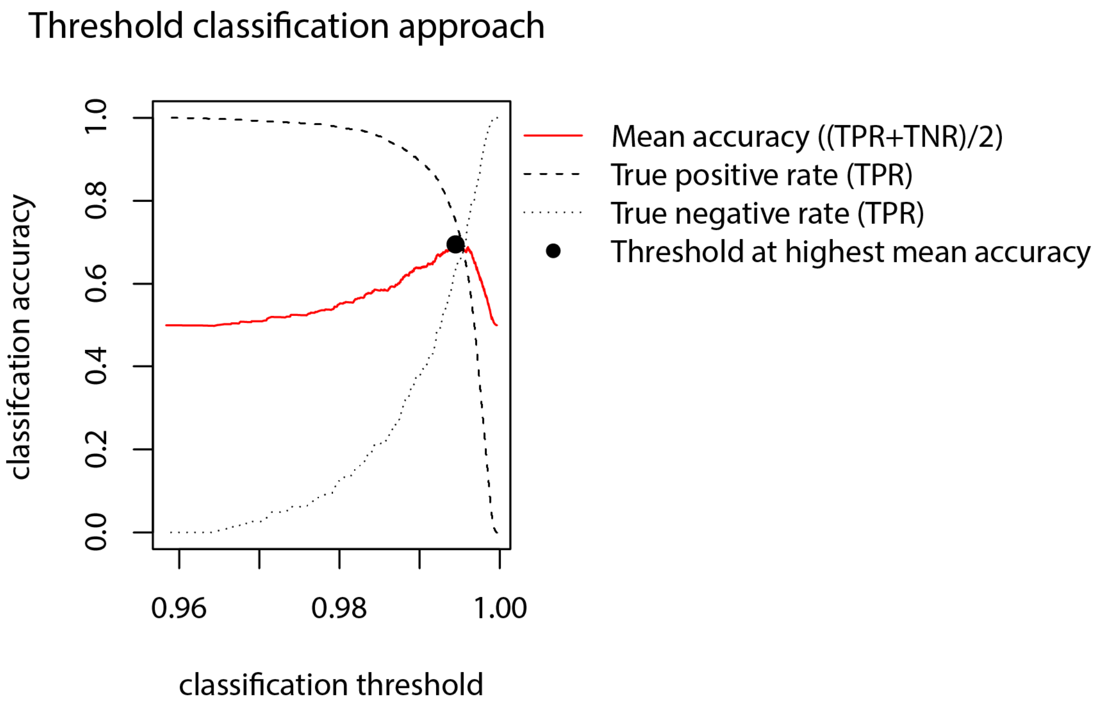


Figure A1: True positive and negative rate of IM function (black lines) applied to its calibration data set (see also Table 1), its averaged sum (red line) and the classification threshold (0.9945) that holds the highest mean classification accuracy (black point).

APPENDIX B: Parameter settings for management regime in Sigriswil

Table B1: Parameter settings for management regime in Sigriswil for each year where management was conducted according to inventory data. kResBA [m^2] denotes residual basal area, i.e. the basal area that should remain after management event took place. kTargetDBH [cm] denotes the target diameter. Trees that exceed target diameter are cut first to reach residual basal area.

Year	1930	1935	1943	1950	1958	1967	1977	1987	1997
kResBA [m^2]	32	32	32	30	30	31	29	29	27
kTargetDBH [cm]	80	80	80	80	80	80	80	80	80

APPENDIX C: Variance decomposition analysis for the variables of the TRM function

Table C1: Variance decomposition analysis for the TRM function. The proportions (%) of variance explained by the variables of the TRM function are listed for the dataset used by Bigler and Bugmann (2004) at Davos (observed) and for simulation results by the ForClim version *TRM_randNr* (simulated) for the three climate scenarios at Scatlè.

	observed	simulated (current climate)	simulated (RCP3PD)	simulated (A1B)
relbai	66.3 (%)	93.0 (%)	93.4 (%)	94.5 (%)
BAI_3	22.9 (%)	6.7 (%)	6.4 (%)	5.1 (%)
$locreg_5$	10.8 (%)	0.3 (%)	0.2 (%)	0.4 (%)

LITERATURE CITED

Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14, 902-914.

APPENDIX D: Simulated basal area and stem numbers at Sigriswil

Table D1: Means and [standard deviations] for simulated basal area and stem numbers at Sigriswil for each year of inventory after harvest was conducted.

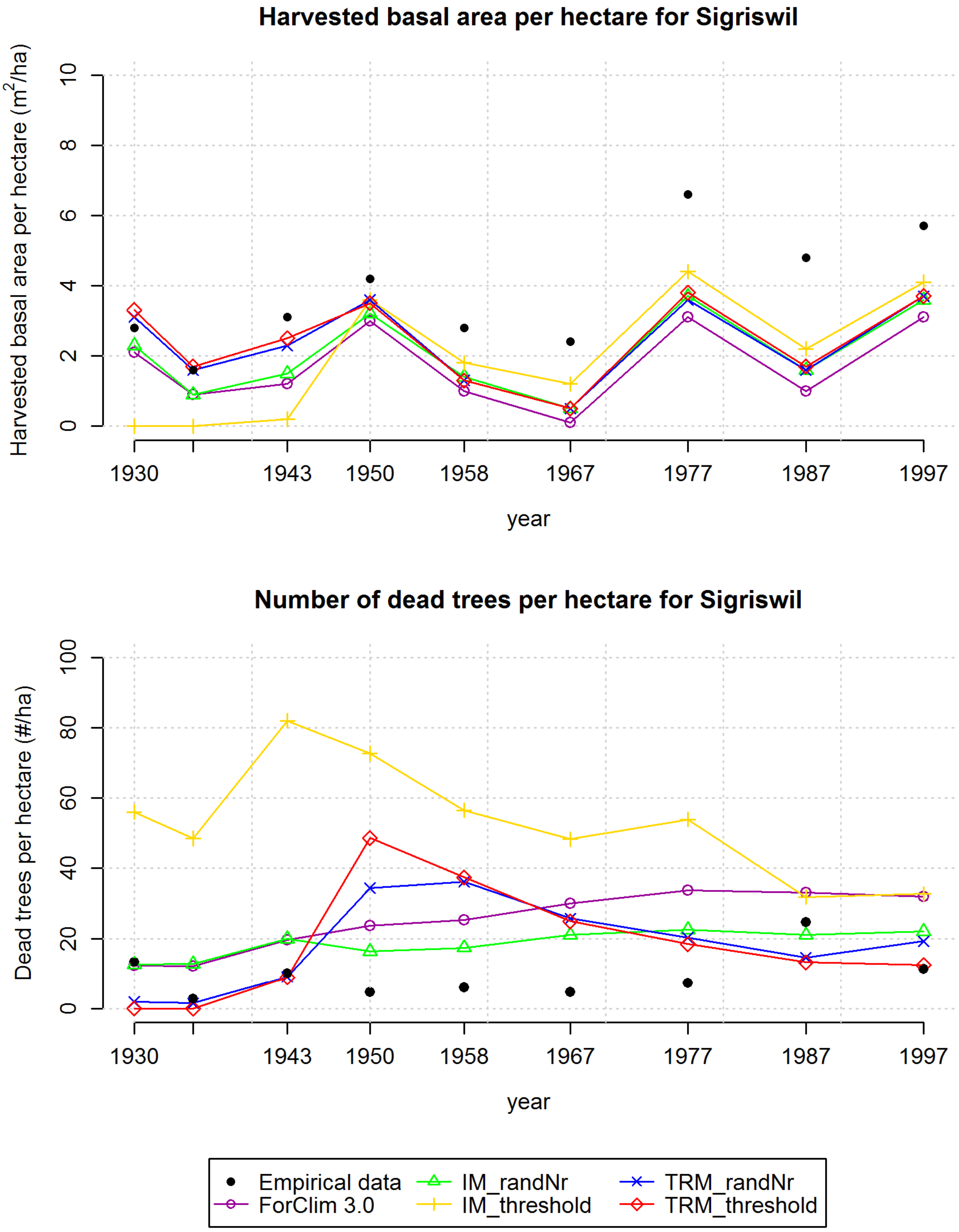
	ForClim v3.0	**IM randNr**	**IM threshold**	**TRM randNr**	**TRM threshold**	**ForClim v3.0**	**IM randNr**	**IM threshold**	**TRM randNr**	**TRM threshold**
			Basal area					Stem numbers		
1925	33.1	33.1	33.1	33.1	33.1	477.7	477.7	477.7	477.7	477.7
	[5.4]	[5.4]	[5.4]	[5.4]	[5.4]	[14.3]	[14.3]	[14.3]	[14.3]	[14.3]
1930	32.0	32.0	29.1	32.0	32.0	452.8	451.6	279.9	458.3	458.2
	[8.8]	[8.8]	[5.4]	[9.6]	[9.6]	[60.5]	[62.6]	[63.2]	[71.6]	[73.9]
1935	32.0	32.0	30.3	32.0	32.0	433.9	431.8	273.1	444.3	445.8
	[9.7]	[9.8]	[5.6]	[11.2]	[11.1]	[68.8]	[71.3]	[51.5]	[82.8]	[86.4]
1943	32.0	31.9	32.0	32.0	32.0	406.0	400.8	252.7	416.9	417.1
	[10.8]	[11.3]	[6.3]	[13.2]	[13.4]	[80.8]	[81.0]	[43.5]	[94.6]	[99.8]
1950	29.9	30.0	29.9	29.9	30.0	361.9	363.6	212.8	355.2	342.1
	[12.9]	[13.5]	[11.8]	[15.3]	[15.4]	[98.2]	[99.6]	[76.4]	[100.3]	[94.4]
1958	29.9	29.9	29.9	29.9	29.9	335.9	340.2	195.0	313.5	301.5
	[13.5]	[14.6]	[13.8]	[15.8]	[15.7]	[94.9]	[102.2]	[84.8]	[88.7]	[82.2]
1967	30.8	30.8	30.8	30.8	30.8	324.9	332.0	192.1	302.9	286.6
	[13.4]	[14.8]	[15.5]	[15.7]	[15.4]	[96.7]	[95.3]	[86.1]	[95.2]	[86.3]
1977	28.8	28.8	28.8	28.7	28.7	303.6	317.9	188.6	285.3	267.7
	[14.7]	[16.4]	[18.6]	[16.9]	[17.0]	[109.7]	[108.2]	[103.5]	[136.3]	[115.6]
1987	28.7	28.7	28.8	28.7	28.7	295.1	318.4	200.3	300.6	287.8
	[14.8]	[17.0]	[19.9]	[17.0]	[17.3]	[118.3]	[125.7]	[118.9]	[165.9]	[163.1]
1997	26.7	26.7	26.8	26.7	26.6	283.4	309.4	208.1	300.1	281.1
	[15.9]	[17.7]	[21.3]	[17.7]	[18.3]	[133.0]	[149.4]	[149.7]	[196.8]	[205.5]

APPENDIX E: Simulated basal area and stem numbers at Scatlè

Table E1: Means and [standard deviations] for simulated basal area and stem numbers at Scatlè for each year of inventory.

	ForClim v3.0	**IM randNr**	**IM threshold**	**TRM randNr**	**TRM threshold**	**ForClim v3.0**	**IM randNr**	**IM threshold**	**TRM randNr**	**TRM threshold**
			Basal area					Stem numbers		
1965	43.3	43.3	43.3	43.3	43.3	420.3	420.3	420.3	420.3	420.3
	[10.6]	[10.6]	[10.6]	[10.6]	[10.6]	[7.9]	[7.9]	[7.9]	[7.9]	[7.9]
1977	43.9	44.9	43.6	45.4	46.4	392.7	400.1	297.5	410.4	417.6
	[10.5]	[10.3]	[10.7]	[9.3]	[10.2]	[23.3]	[23.3]	[38.1]	[19.2]	[16.2]
1989	44.1	46.2	45.8	46.6	48.9	363.6	377.9	283.8	390.3	387.9
	[10.1]	[10.1]	[10.9]	[8.2]	[9.5]	[32.3]	[30.6]	[40.7]	[30.5]	[37.6]
2006	44.0	47.9	49.5	47.6	50.5	322.9	351.7	277.2	338.5	301.1
	[9.8]	[9.9]	[10.7]	[7.4]	[8.8]	[38.2]	[34.6]	[42.7]	[31.3]	[27.3]

APPENDIX F: Harvested basal area and dead trees in Sigriswil


Harvested basal area per hectare for Sigriswil

Number of dead trees per hectare for Sigriswil

Figure F1: Observed and simulated harvest of basal area (m^2/ha) in Sigriswil for each year of inventory (upper panel) and number of dead trees per hectare and inventory (lower panel).

APPENDIX G: Climate factors in ForClim long-term simulations

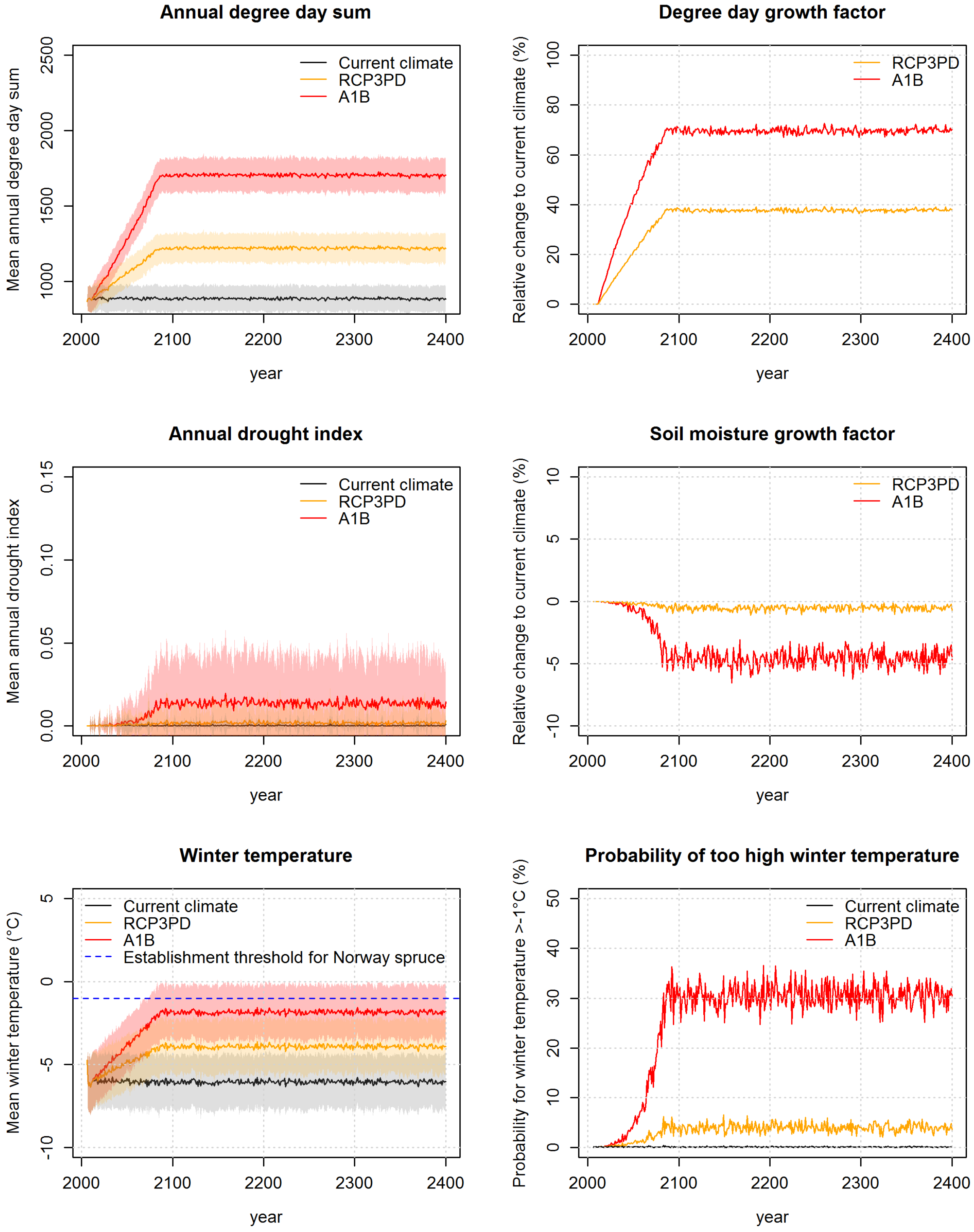


Figure G1: Climatic factors in ForClim long-term simulations for different climate scenarios (current climate, RCP3PD, A1B). Included are the annual averages of degree day sum, drought index and winter temperatures (left panels). For the degree day and soil moisture growth factors, changes in percent compared to the current climate are shown. Additionally, the probability to reach an average winter temperature above -1°C (establishment threshold for Norway spruce) for the three applied climate scenarios is shown (lower right panel).

APPENDIX H: Performance values for the different model versions at Sigriswil and Scatlè

Table H1: Performance values for the sites Sigriswil and Scatlè for the different model versions. Log-likelihoods were calculated using a linear regression between simulated and observed basal area and stem numbers respectively while (n) denotes the number of sampling points (i.e., number of inventories) available. For Sigriswil, basal area and stem numbers before and after harvest was taken into account. For calculating corrected AIC values (AICc), delta AIC (ΔAIC), and Akaike weights (ω), the number of parameters included in the different mortality functions (npar) was considered. AIC values were calculated only for Sigriswil as sampling size was too small at Scatlè. Relative bias and relative root mean squared error were calculate for both sites, but, again, note small sampling size at Scatlè. Highest performance for basal area and stem numbers at both sites are highlighted in grey.

			basal area						**stem numbers**					
Site (n)	model version	npar	log-likelihood	AICc	ΔAIC	ω	bias %	RMSE%	log-likelihood	AICc	ΔAIC	ω	bias%	RMSE%
Sigriswil (18)	ForClim.3.0	2	-31.88	68.56	1.80	0.20	-2.81	12.25	-90.88	186.55	0.16	0.48	-5.72	24.96
	IM_randNr	6	-28.48	76.59	9.84	0.00	-2.30	10.04	-83.38	186.39	0.00	0.51	-3.57	15.57
	IM_threshold	6	-37.78	95.19	28.44	0.00	-4.22	18.43	-116.51	252.66	66.27	0.00	-40.63	177.35
	TRM_randNr	4	-28.36	67.79	1.04	0.30	-2.01	8.77	-91.54	194.16	7.77	0.01	-5.86	25.58
	TRM_threshold	4	-27.84	66.75	0.00	0.50	-1.88	8.22	-95.83	202.74	16.34	0.00	-8.13	35.50
Scatlè (3)	ForClim.3.0	2	-8.27	–	–	–	-1.19	2.52	-16.11	–	–	–	-4.76	10.10
	IM_randNr	6	-9.04	–	–	–	4.02	8.53	-15.64	–	–	–	-0.30	0.64
	IM_threshold	6	-9.53	–	–	–	3.94	8.35	-18.08	–	–	–	-24.24	51.42
	TRM_randNr	4	-9.00	–	–	–	4.48	9.51	-16.20	–	–	–	0.54	1.13
	TRM_threshold	4	-9.89	–	–	–	9.04	19.17	-16.91	–	–	–	-2.34	4.97

2

Bayesian statistics provide new insights on structural realism of a dynamic vegetation model

Bircher, N., Hartig, F., Hülsmann, L., Heiri, C., Bugmann, H., Cailleret, M.

Manuscript; submitted to Ecological Applications

Abstract

Dynamic vegetation models (DVMs) are important tools to understand and predict the functioning and dynamics of terrestrial ecosystems under changing environmental conditions. A persisting problem for these models is uncertainty due to the choice of parameter values and sensitivity to process formulations that are insufficiently constrained by empirical evidence. Better inclusion of empirical data has been advocated, with the idea that key processes should be estimated from empirical data independently of the DVM, and only then be incorporated in a DVM. However, due to the wide range of processes and interactions within a DVM, it is unclear whether such independently estimated formulations would lead to enhanced overall model performance.

We compare the performance of the DVM ForClim that contains (1) a theoretical mortality function (ForClim v3.3); (2) an empirical mortality function whose parameters were estimated independently of the DVM, and (3) the same empirical mortality function with parameters estimated using Bayesian calibration (BC) of the DVM. For the BC and the subsequent validation, we used inventory data from 9 and 21 ecologically distinct Swiss natural forest reserves, respectively, which include the main tree species of Central Europe.

The values of the calibrated mortality parameters were similar to most of those that had been fitted empirically, suggesting that the general structure of ForClim is realistic. Some discrepancies were found for the relationship between mortality and shade tolerance, suggesting a possible need for partially refining the model structure. The BC led to the best model fit compared to the other model versions, on both the calibration and the validation data. Parametric uncertainty mostly influenced stem numbers in the low dbh classes, suggesting that general stand structure can be predicted accurately, but recruitment and hence the development of tree species composition is more challenging to predict.

We conclude that BC is a strong asset to discuss ecological functions in a DVM framework even when direct estimates of a process are available – in our case, it (1) allowed determining parameter values that resulted in lower predictive error, (2) identified potential structural problems in the model, and (3) provided better estimates of predictive uncertainty. Thus, we recommend BC not only as a tool for the improvement of short-term model predictions, but even more so for assessing the structural realism of DVMs.

Key words

Forest gap model, Bayesian calibration, tree mortality, inventory data

Introduction

The response of terrestrial ecosystems to environmental change is a key issue in ecology with wide-ranging consequences for stakeholders and policy makers. Many scientific analyses on this topic rely on process-based dynamic vegetation models (DVMs), which encapsulate the demographic changes of plant communities over time based on abiotic and biotic conditions (e.g., Foley *et al.*, 1998; Bonan *et al.*, 2003; Hartig *et al.*, 2012). Even though most DVMs are fairly consistent in the projection of qualitative ecosystem properties in response to altered climatic conditions (e.g., Pereira *et al.*, 2010), they often disagree on the magnitude of change (Moorcroft, 2006) and reveal high sensitivity to physiological and particularly demographic processes (e.g., Galbraith *et al.*, 2010; Friend *et al.*, 2014; Rowland *et al.*, 2014). To improve the robustness of model projections, many authors have suggested to reconsider DVMs designs, with a specific focus on the mechanistic description of key processes such as tree mortality that had so far been treated in a rather simplistic manner (e.g., Bugmann, 2001; Prentice *et al.*, 2007; Sitch *et al.*, 2008; Galbraith *et al.*, 2010; Adams *et al.*, 2013).

Including more detailed process formulations in DVMs raises the question of a closer connection to empirical data. Traditionally, model parameters in DVMs were determined independently of the model, i.e. based on observations. The outcome of this direct parameterization in terms of model behavior was then tested against reference data (cf. Bossel, 1992; Pacala *et al.*, 1996). However, such a direct parameterization of all parameters in a DVM requires a large set of specialized observations (cf. Le Roux *et al.*, 2001) that are typically hard to achieve or not available at all (Hartig *et al.*, 2012). Consequently, many parameters in current DVMs are weakly constrained or originate from theoretical conjectures that are not verified empirically (cf. Mäkelä *et al.*, 2000).

A solution to this problem that has become increasingly popular in recent years is to generate parameter estimates by an inverse modeling approach, also called inverse calibration, i.e. to infer parameter values based on the match between empirical data and model outputs (van Oijen *et al.*, 2005). Inverse modeling approaches, such as Bayesian methods, allow for harnessing data sources that would not be suited for direct parameter estimation, and therefore open up novel opportunities to constrain parameter-rich process-based models (Hartig *et al.*, 2012). Moreover, in the framework of Bayesian statistics, it is possible to combine direct parameter estimates (via the “prior distribution”) with estimates that are generated inversely (via the “likelihood”). The result of a Bayesian calibration (BC) is a probability distribution function (the “posterior”) that represents the combination of all direct and inverse information on the respective parameter, and can be used for ecological interpretation and prediction.

To date, BC of statistical and process-based models has been applied mainly to calibrate processes for which ecological knowledge was scarce and parameter uncertainty was large (e.g., O'Hara *et al.*, 2002; van Oijen *et al.*, 2005; Larssen *et al.*, 2006; Reinds *et al.*, 2008; Hartig *et al.*, 2014), and/or for model intercomparison (e.g., van Oijen *et al.*, 2011; van Oijen *et al.*, 2013). However, as pointed out by Hartig *et al.* (2012), if reliable information on model parameters is directly available, an interesting additional possibility of the approach is to compare direct (prior) and inverse (posterior) parameter estimates. A mismatch between direct and inverse parameter estimate would point at either (1) a structural problem in the model, (2) a systematic bias in the data, or (3) a discrepancy between the nature of the parameter in the model and the parameter that is measured in the field (e.g., Ramin and Arhonditsis, 2013). Hence, in addition to better parameter estimates, a calibration with direct and inverse information can lead to an improved understanding of how ecological processes are interacting and represented in the model.

An example of a DVM for which direct and inverse data are available is ForClim, a forest gap model that projects the long-term dynamics of temperate forests by simulating establishment, growth and mortality of individual trees based on site- and species-specific environmental constraints (Bugmann, 2001). In a recent study, Bircher *et al.* (2015) used ForClim to examine whether better empirical descriptions of tree mortality would reduce uncertainties in model projections, a point that has been suggested by various authors (cf. Bugmann, 2001; Keane *et al.*, 2001; Hasenauer, 2006; Heiri, 2009; Friend *et al.*, 2014). This effort highlighted that the choice of mortality function strongly influences simulation results at decadal time scales. A better understanding of each mortality function and its interactions with other ecological processes in the model (e.g., tree growth) was identified as a key priority.

Here, we address this issue by using Bayesian statistics to inversely re-calibrate the parameters of an inventory-based (i.e., directly estimated) mortality function that was included in ForClim by Bircher *et al.* (2015). This effort was based on inventory data from 9 and 21 plots of the Swiss natural forest reserve network for calibration and validation, respectively, which cover a wide variety of forest types and include all major tree species of Central Europe. We aimed to (1) determine if the inversely calibrated mortality parameters match with empirical estimates; (2) identify causes of potential mismatches, for example errors in model structure, interactions between different model processes (e.g., growth – mortality), or quality of the empirical data; (3) assess if the inverse calibration leads to an improvement of model performance in terms of key forest characteristics (e.g., total basal area, stem numbers); and (4) assess if the posterior uncertainty in inversely estimated mortality parameters translates into significant uncertainties in model projections.

Materials and methods

The ForClim model

ForClim is an individual-based forest gap model developed to simulate the dynamics of temperate forests in Central Europe (Bugmann, 1996) and on other continents (Bugmann and Solomon, 1995; Bugmann and Solomon, 2000; Shao *et al.*, 2001). Tree growth, establishment, and mortality are simulated on independent patches (≈800 m^2) in annual steps, using a parsimonious number of ecological assumptions regarding the influence of climate and ecological processes on tree demography. Averaging the results across all simulated patches allows for obtaining mean successional dynamics at the forest stand scale (Bugmann, 2001).

The structure of ForClim v3.3 (Mina *et al.*, submitted) consists of four sub-models: The PLANT sub-model simulates tree establishment, growth and mortality. Annual growth is calculated using the carbon budget model by Moore (1989), subject to several subsequent modifications (Rasche *et al.*, 2012). Tree growth is reduced if light availability, degree-day sum, soil moisture during the growing season, nutrient availability and crown length are below optimum (Bugmann, 1996; Didion *et al.*, 2009b). Tree recruitment, modeled as the species-specific rate of establishment of saplings with a diameter at breast height (dbh) of 1.27 cm, is also reduced when environmental conditions are unfavorable. Tree mortality is modeled as a combination of a constant “background” mortality related to species-specific maximum age, and a stress-induced mortality that is activated if the annual diameter increment of a tree falls below an absolute or relative threshold for more than two consecutive years. In contrast to establishment and growth, which are operating on the cohort level, mortality is applied to each tree of a cohort individually, assuming a binomial model with the prescribed mortality probability. A more detailed description of the mortality function is provided in Bircher *et al.* (2015). Required bioclimatic inputs include minimum winter temperature, the annual degree-day sum, and soil moisture; they are provided by the WEATHER and WATER submodels based on long-term temperature and precipitation data, and on site-specific soil water holding capacity. Finally, the MANAGEMENT submodel allows for applying the most common planting and harvesting techniques of Central Europe (Rasche *et al.*, 2011).

Empirical mortality function

In a previous study, direct estimates of an inventory-based tree mortality model had been derived using data from the Swiss National Forest Inventory (NFI; J. Wunder and M. Abegg, *unpublished manuscript*). Only single-tree data from plots where no forest management had taken place for at least 50 years were considered. The callipering threshold on these plots was 12 cm and the mean interval between two inventories was 11 years. Fitted with a logistic regression, this “independent regression” (IR) expresses the probability of tree i to be still alive at year t, i.e. $Pr\ (Y_{i,t}=1)$, according to tree *dbh*, relative basal area increment (*relbai* = $BAI/_{BA}$), shade tolerance (*shadeTol*), and to the local annual degree-day sum (*DD*; calculated with a threshold of mean monthly temperature of 5.5 °C):

$$\Pr\left(\mathrm{Y_{i,t}} = 1 \middle| \mathrm{dbh_{i,t}}, \mathrm{relbai_{i,t,j}}, DD_t, \mathrm{shadeTol_{i_k}}\right) = \frac{1}{1 + \exp[\alpha_0 + \alpha_1 \times \mathrm{dbh_{i,t}} + \alpha_2 \times \mathrm{dbh^2_{i,t}} + \mathrm{relbai_{i,t_j}} + \alpha_3 \times DD_t + \mathrm{shadeTol_{i_k}}]^{-1}} \qquad (1)$$

The estimate of the $relbai$ variable changes according to the class j of growth rates (four classes: “very low”: relbai = 0%, “low”: 0% < relbai ≤1.5 %, “fast”: 1.5% < relbai ≤3% and “very fast”: relbai >3%). The variable $shadeTol$ expresses species-specific shade tolerance (high, intermediate, and low; cf. Bugmann, 1994). Its estimates change among three classes k with class 1 (*“shadeHigh”*) being the reference class to estimates for class 2 (*“shadeIntm”*) and class 3 (*“shadeLow”*). For the implementation in ForClim, $\Pr\left(Y_{i,t} = 1 \middle| X_{i,t}\right)$ was rescaled to an annual survival probability $gPSurv_{i,t} = 1 - \left(1 - \Pr\left(Y_{i,t} = 1 \middle| X_{i,t}\right)\right)^{1/11}$ (Bircher *et al.*, 2015). Below, we refer to the ForClim version containing this independent regression with its original structure and coefficient values as “ForClim_IR”.

Data for Bayesian calibration and validation

The aim of the BC was to recalibrate the empirical mortality submodel of ForClim_IR by comparing ForClim outputs to inventory data alone, thus pretending ignorance of the directly fitted parameter estimates of the mortality submodel. The inventory data used for the BC and the subsequent validation of the alternative mortality function were selected from the 306 permanent plots of the Swiss forest reserve network (Brang *et al.*, 2011). Forest management had been excluded from these reserves at least since their foundation (cf. inventory period in Table 1 and 2). All reserves contain one or more so-called permanent plots where each tree with a dbh ≥4 cm is individually tagged and repeatedly measured in predefined intervals.

Table 1: Site descriptions of the permanent plots used for calibration including some information on location, area size, elevation, climate (mean annual temperature and precipitation sum), and dominating tree species. The number of species with a 10%-proportion on stand basal area is given by the stand diversity. Stand dynamic refers to the inter-annual rate of change in stem numbers. The slope/aspect parameter is an input of ForClim, defined as (0 = flat terrain, 1 = steep slope (10-30°), 2 = very steep slope (>30°); the sign denotes south-facing (+) respectively north-facing (-) slopes). The inventory period is the time between the first and the last inventory used for calibration, with n indicating the number of inventories.

Site	**Location (°N / °E)**	**Area (ha)**	**Elevation (m a.s.l.)**	**Climate (°C) / (mm)**	**Main species**	**Stand diversity**	**Stand dynamic**	**Slope / Aspect**	**Inventory period (n)**
Adenberg_03	47.6, 8.6	0.45	~505	9.0 / 1020	*F. sylvatica, Q. robur*	2	0.026	0	1970-2012 (5)
Bois de Chênes_02	46.4, 6.2	0.49	~570	9.5 / 1094	*Q. robur, F. sylvatica*	3	0.013	+1	1970-2007 (4)
Fuerstenhalde_01	47.6, 8.5	0.53	~460	9.2 / 1065	*F. sylvatica*	2	0.019	0	1971-2012 (4)
Girstel_04	47.3, 8.5	0.22	~675	7.9 / 1297	*P. sylvestris, F. sylvatica, P. abies*	5	0.016	-1	1964-2006 (5)
Leihubelwald_02	46.9, 8.1	0.25	~1240	6.1 / 1770	*A. alba, F. sylvatica, P. abies*	3	0.007	-1	1973-2011 (4)
Nationalpark_07	46.7, 10.2	0.56	~1860	2.3 / 915	*P. abies, P. cembra*	2	0.006	0	1977-2012 (3)
St.Jean_01	47.1, 7.0	0.28	~1375	4.7 / 1520	*A. pseudoplatanus, P. abies*	2	0.011	0	1961-2006 (5)
Vorm Stein_02	47.6, 8.5	0.24	~540	9.2 / 1067	*Q. robur, F. sylvatica, P. sylvestris, P. abies*	4	0.011	+2	1972-2012 (4)
Tariche Haute Côte_04	47.3, 7.2	0.56	~740	7.9 / 1250	*A. alba, F. sylvatica*	3	0.016	+1	1974-2012 (4)

Table 2: Site descriptions of the permanent plots used for validation including some information on location, area size, elevation, climate (mean annual temperature and precipitation sum), and dominating tree species. The number of species with a 10%-proportion on stand basal area is given by the stand diversity. Stand dynamic refers to the inter-annual rate of change in stem numbers. The slope/aspect parameter is an input of ForClim, defined as (0 = flat terrain, 1 = steep slope (10-30°), 2 = very steep slope (>30°); the sign denotes south-facing (+) respectively north-facing (-) slopes). The inventory period is the time between the first and the last inventory used for calibration, with n indicating the number of inventories. The names of validation sites that belong to a natural forest reserve where also a calibration site was located are marked in bold.

Site	**Location (°N / °E)**	**Area (ha)**	**Elevation (m a.s.l.)**	**Climate (°C) / (mm)**	**Main species**	**Stand diversity**	**Stand dynamic**	**Slope / Aspect (–)**	**Inventory period (n)**
Adenberg_01	47.6 / 8.6	0.45	~520	9.0 / 1017	*F. sylvatica, Q. robur*	2	0.023	+1	1970-2012 (5)
Adenberg_02	47.6 / 8.6	0.45	~500	9.0 / 1017	*F. sylvatica, Q .robur*	3	0.020	0	1970-2012 (5)
Adenberg_04	47.6 / 8.6	0.45	~520	9.1 / 1006	*F. sylvatica, Q.robur*	2	0.025	+1	1970-2012 (5)
Bois de Chênes_01	46.4 / 6.2	0.49	~550	9.6 / 1075	*F. sylvatica*	1	0.004	0	1970-2007 (4)
Bonfol_03	47.5 / 7.2	0.53	~440	9.5 / 1003	*Q. robur*	2	0.009	0	1962-2001 (5)
Fuerstenhalde_02	47.6 / 8.5	0.53	~470	9.2 / 1076	*F. sylvatica*	1	0.018	0	1971-2012 (4)
Girstel_11	47.3 / 8.5	0.14	~720	8.1 / 1270	*A. pseudoplatanus, F. sylvatica*	3	0.018	+1	1972-2007 (4)
Leihubelwald_03	46.9 / 8.1	0.24	~1140	6.6 / 1690	*A. alba, F. sylvatica*	2	0.023	+1	1973-2011 (4)
Leihubelwald_04	46.9 / 8.1	0.25	~1100	6.7 / 1668	*P. abies, A. alba*	2	0.008	0	1973-2011 (4)
Nationalpark_05	46.7 / 10.2	0.61	~1985	1.2 / 981	*L. decidua, P. cembra*	3	0.006	0	1978-2013 (3)
Pfynwald_01	46.3 / 7.6	0.19	~575	10 / 670	*P. sylvestris*	2	0.010	+1	1956-2003 (6)
Scatlè_01	46.8 / 9.0	3.47	~1650	3.7 / 1582	*P. abies*	1	0.014	+1	1965-2006 (4)
St.Jean_02	47.1 / 7.0	0.44	~1370	4.8 / 1510	*P. abies*	1	0.007	0	1961-2006 (5)
Tariche Haute Côte_03	47.3 / 7.2	0.91	~735	8.1 / 1228	*F. sylvatica, A. alba*	2	0.009	-1	1974-2012 (4)
Tariche Haute Côte_06	47.3 / 7.2	0.54	~720	8.1 / 1228	*F. sylvatica, A. alba*	2	0.011	0	1976-2012 (4)
Tutschgenhalden_13	47.5 / 8.8	0.25	~600	9.1 / 1151	*F. sylvatica, A. alba*	2	0.012	0	1971-2013 (4)
Tutschgenhalden_14	47.5 / 8.8	0.58	~580	9.1 / 1151	*F. sylvatica, P. abies*	2	0.008	0	1971-2013 (4)
Vorm Stein_01	47.5 / 8.5	0.25	~545	8.9 / 1144	*F. sylvatica P. abies, Q. robur*	3	0.018	+2	1972-2012 (4)
Weidwald_02	47.4 / 8.0	0.76	~635	8.7 / 1163	*F. sylvatica*	2	0.010	0	1976-2011 (4)
Weidwald_03	47.4 / 8.0	0.25	~660	8.6 / 1180	*F. sylvatica*	1	0.013	0	1976-2011 (4)
Weidwald_04	47.4 / 8.0	0.53	~640	8.6 / 1180	*F. sylvatica, Q. robur*	4	0.014	+1	1976-2011 (4)

A subset of plots was selected for model calibration according to the following criteria: (1) plots were excluded that showed evidence of recent natural disturbances (e.g., wind storms) as these are not considered in the model; (2) plots had to have a minimum size of 0.2 ha to guarantee that forest structure and composition is representative of the site; (3) plots had to have a minimum record period of 35 years to allow for an adequate consideration of forest dynamics; (4) only one plot was chosen per forest reserve to avoid pseudo-replication within the calibration data; (5) an adequate representation of all main tree species of Central Europe and a variety of forest types was sought in the calibration data set. The plot with the highest number of species was selected first (Girstel_04; Table 1). In a next step, we included those plots with the highest proportion of one main tree species in Switzerland such as European beech *Fagus sylvatica* (Adenberg_03), silver fir *Abies alba* (Leihubelwald_02), Norway spruce *Picea abies* (Nationalpark_07), Norway maple *Acer pseudoplatanus* (St.Jean_01), Scots pine *Pinus sylvestris* (VormStein_02), Swiss stone pine *Pinus cembra* (Nationalpark_07), European larch *Larix decidua* (Nationalpark_07), and oak species *Quercus robur / petraea* (Bois de Chênes_02). This set of calibration plots was complemented by two permanent plots with comparatively high stand dynamics, i.e., with a high inter-decadal rate of change in stem numbers: Fürstenhalde_01 and Tariche Haute Côte_04. Thus, in total nine permanent plots were selected for calibration (Figure 1; Table 1).

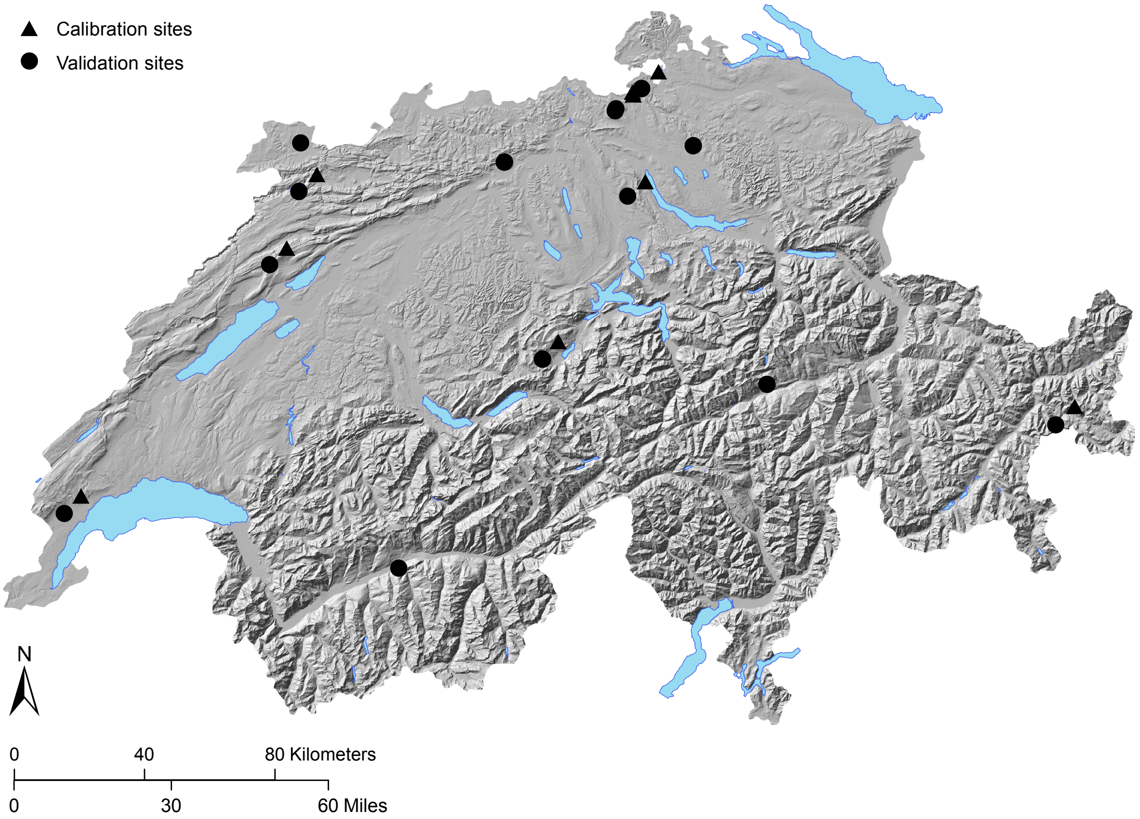


Figure 1: Location of the nine calibration and 21 validation sites in Switzerland.

For the validation, we selected data from the remaining permanent plots with a minimum record period of 35 years and at least two inventories. The minimum area requirement was reduced to 0.1 ha to allow for sites with ‘extreme’ climatic conditions (e.g., warm-dry in

Pfynwald). Again, permanent plots with records or apparent effects of recent disturbances were not considered. Twenty-one sites were selected for validation (Figure 1; Table 2).

Bayesian calibration

BC focused on all parameters of the empirical mortality function except for the annual degree-day sum estimate, as this variable was not directly related to the growth-mortality relationship of the model but rather to site conditions. In addition to the parameters of the mortality function, we included the growth parameter $kGRateD$ in the calibration to test for possible trade-offs of the annual diameter increment of a cohort ($GRateD$ in cm/yr) with the mortality parameters. When using stand demography as calibration criterion, trade-offs between growth and mortality are likely to occur because a joint increase of both processes may lead to similar stand demography (cf. Hartig *et al.*, 2014).

For the BC, we changed $relbai$ from a factorial to a continuous variable to increase the sensitivity of the mortality function to changes in relative growth rate. Furthermore, the parameter of the low shade-tolerance class (*shadeLow*) was redefined as the difference to the intermediate shade-tolerance class (*shadeIntm*) rather than to the original reference class (*shadeHigh*). All empirically derived parameters were updated accordingly. These adjustments reduce correlations between the parameters of the shade tolerance classes and therefore improve the convergence of the Markov Chain Monte Carlo (MCMC) algorithm in the BC. For the same reason, the variables dbh, $dbh^2,$ and $relbai$ were centered to reduce correlations with the $intercept$ of the mortality function.

BC requires expressing prior knowledge about the parameter values in the prior distribution $P(\theta)$, where θ denotes the parameter vector of the model (Table 3). Although the estimate and confidence interval of each parameter of the mortality function had been determined by logistic regression, we deliberately set wide (i.e., non-informative) priors to obtain a picture of the parameter estimates that would result from the inverse calibration only. Truncated normal distributions were assigned for *relbai* and *GrowthRateD* (minimum=0), and uniform prior distributions were assigned to the other parameters.

It has often been found useful to consider more than one data type for model calibration (cf. Grimm and Railsback, 2012), and thus we constructed a likelihood function consisting of two components: the first part specifies the likelihood for basal area increment, defined by the probability$P(D_{BAInc}|\theta)$ of obtaining the observed basal areal increment given the model with parameters θ and a normally-distributed error model with a relative standard deviation of 0.3 (cf. van Oijen *et al.*, 2005). The second part specifies the likelihood for the stem number distribution, defined as the probability ($P(D_{Stem}|\theta)$) of obtaining the observed stem numbers in 4 cm dbh classes for each year an inventory was conducted, given the model parameters and a poisson error model per dbh class. The lowest dbh class (i.e., (0, 4] cm) was not considered, as it was not available in the observed data. The partial likelihood for stem numbers is strongly influenced by the very abundant trees in the low dbh classes, whereas medium- and large-sized trees have a stronger influence on basal area increment. Mixing both data types in one likelihood function should therefore create a balanced description of forest dynamics (cf. Grimm and Railsback, 2012).

Both likelihoods were expressed as logarithmic values (log-likelihood), which means that the joint (total) likelihood $P(D|\theta)$ can simply be written as their sum. We finally included a weighting factor of 0.025 on the joint likelihood:

$$P(D|\theta) = 0.025 * (P_{BAInc}(D|\theta) + P_{Stem}(D|\theta)) \qquad (2)$$

The weighting factor essentially decreases relative likelihood differences, making deviations from the observed data more probable. If the likelihood consisted of the normal term based on BAI only, we could have achieved the same effect by increasing the standard deviation of the normal distribution. Hence, the weighting of 0.025 essentially expresses a likelihood with a wider error model than in the two partial likelihood elements alone, accounting for the fact that a lot of variation is likely to exist between sites as well as time steps that cannot be explained by ForClim, and that was not yet included in the basic partial likelihood that were constructed to account for the variability at one site and for one point in time.

Bayes' theorem states that the support given to a certain parameter combination, i.e. the posterior probability $P(\theta|D)$, is proportional to the product of the prior and the joint likelihood:

$$P(\theta|D) \propto P(\theta) * P(D|\theta) \qquad (3)$$

We used a MCMC algorithm to estimate the posterior parameter distributions (Metropolis *et al.*, 1953). An adaptive MCMC element was included that calculated the covariance of all parameters after a predefined number of iteration steps (set to 1000). Subsequently, the proposal covariance matrix was adjusted following Gelman et al. (1996; see also Rosenthal, 2011):

$$\textstyle\sum_p = \left[\frac{(2.38)^2}{n}\right] \sum_n) \qquad (4)$$

where $\sum_p$ is the proposal covariance matrix based on the number of tested parameters n and the empirical covariance matrix $\sum_n$ of the parameters $X_0, \ldots X_n$.

The convergence of the MCMC was examined by visual inspection of the trace plots and by calculating the Gelman-Rubin scale-reduction factors. We considered parameters with scale-reduction factors smaller than 1.05 as having converged (Gelman and Rubin, 1992).

Simulation set-up

The model was initialized with single-tree data (species, dbh) from the first inventory conducted on the permanent plots. Since there was no spatial information about tree position on the plot, trees were allocated randomly and evenly to an initial set of patches, each with a size of 800 m^2 (cf. Wehrli *et al.*, 2005). Depending on the ratio of the permanent plot area and patch size (Table 1 and 2), this resulted in the direct initialization of 2 to 44 patches. This initial set of patches was then replicated to allow for averaging out stochasticity across simulation runs. The final patch number was set to 200 for the validation sites but was reduced to 100 for the calibration sites, as simulation time on a dedicated cluster with 96 nodes still presented a major constraint to the BC. A few tree species that are not parameterized in ForClim but are present in some forest reserves, albeit with very minor abundance, were not considered in the simulations.

Model evaluation

The result of BC is generally the full posterior probability distribution for each parameter. Still, we found it helpful to derive one best estimate from this distribution to allow for an easier comparison with the simulations using the IR parameters. For this purpose, we used maximum a posteriori value (i.e., the mode of the joint posterior estimated from the MCMC samples), hereafter called “BC-MAP”.

We compared the outputs of ForClim using the BC-MAP parameters to the empirically derived ForClim_IR and ForClim v3.3. We first ran all three model versions for the calibration and the validation sites, and calculated the likelihood values as described above. Second, we also calculated the total and shade-tolerance class-specific (i.e., summing up the values for all species of a certain shade tolerance class) basal area and stem numbers at the end of the simulation (cf. Didion *et al.*, 2009a; Rasche *et al.*, 2012), which had not been targeted in the calibration and therefore can be viewed as a second level of model validation. Third, to assess the posterior predictive uncertainty of the BC, we ran 1000 simulations per validation site with different parameter combinations drawn from the posterior distribution.

Results

Calibration

Direct (empirical) fitting vs. indirect fitting

The maximum *a posteriori* estimates (BC-MAP) for the coefficients of the parameters *kIntercept*, *kDBH,* and *kRelbai* were very close to the empirical estimates (IR), while those for *kDBH*^{2}, *kGRateD*, and shade tolerance (*kShadeLow ,kShadeIntm, kShadeHigh*) differed (Table 3, Figure 2). These differences between IR and BC-MAP estimates are presented and evaluated in more detail below.

Table 3: Prior and posterior probability distributions for the 7 re-calibrated parameters. For the prior distribution, minimum and maximum values are listed. The distributions of the priors were truncated normal (minimum=0) for the parameters of relbai and GrowhtRateD, but uniform for the other parameters. Posterior distributions are characterized by the median and the 2.5 respectively 97.5% quantile. Additionally, the values of maximum posterior estimates (MAP) are indicated. Correlations (Corr.) between parameters are listed if >0.3, negative correlations are indicated by a minus sign (-).

Parameter vector Θ [Θ(1)… Θ(7)]				Prior prob. distribution		Posterior prob. distribution				
Name	Θ(i)	Unit	Original value	Min	Max	2.5%	Median	97.5%	MAP	Corr. [Θ(i)]
kIntercept	1		8.59	-5.0	25.0	8.1664	8.7617	9.7707	8.2194	[-3, -7]
kDBH	2	cm	0.0672	-0.2	0.2	0.0206	0.0663	0.1199	0.0603	[-7]
kDBH^2	3	cm^2	-0.0005	-0.02	0.001	-0.0009	0.0005	0.0010	0.0006	[-1]
kRelbai	4	%	42.11	0.0003	144.8	9.1824	43.7314	82.7687	43.1083	
kShadeLow	5	–	-0.1881	-5.0	5.0	-3.6617	-0.1212	4.4868	0.7078	[-6]
kShadeIntm	6	–	-1.0075	-5.0	5.0	0.1360	1.8736	4.8001	0.8832	[-5, -7]
kGRateD	7	cm	1.0	0.09	2.0	0.6076	0.7351	0.8824	0.8583	[-1, -2, -6]

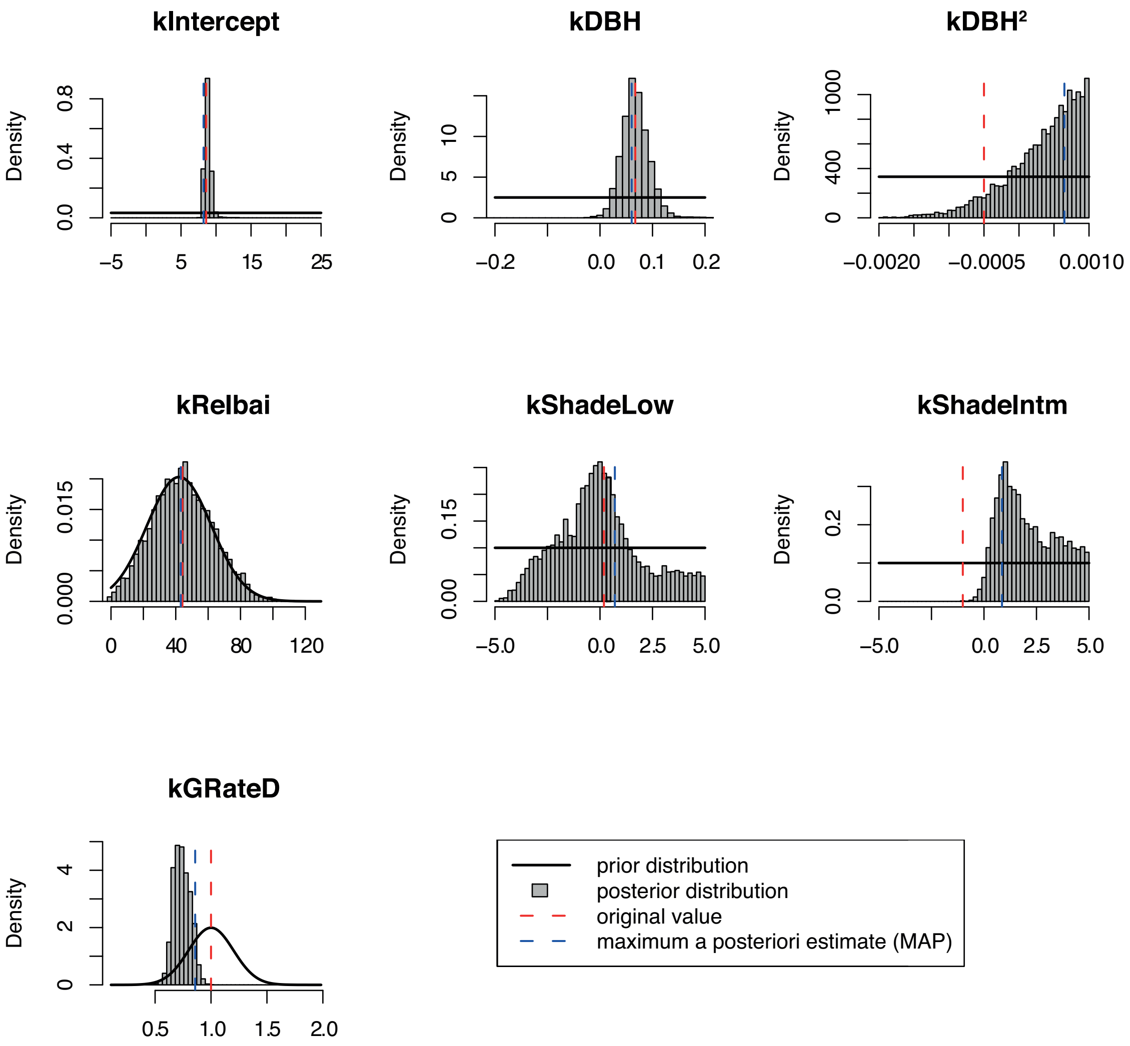


Figure 2: Prior and posterior distributions of the seven re-calibrated parameters. The original mean values of the empirical function and the maximum a posterior estimates are plotted as well.

Estimates for *kShadeIntm* moved from a negative (-1.01) to a positive value (median: 1.87; MAP: 0.88), indicating that – everything else being equal – intermediately shade-tolerant species do not have a lower survival probability than the high shade tolerance class species, in contrast to the IR estimate. The BC median for *kShadeLow* (-0.12) was close to the empirical value (-0.19), but as we redefined it relative to *ShadeIntm*, the shift observed for *kShadeIntm* implies that also *kShadeLow* shifted relatively to the reference class *kShadeHigh*. In fact, the MAP of *kShadeLow* (0.71) implies that the survival probability of shade-intolerant species is higher compared to the reference shade tolerance class than for species with intermediate shade tolerance.

The BC further resulted in a change in the *dbh*^{2} parameter from a negative to a positive value (empirical fit: -0.0005; BC median: 0.0005; MAP: 0.0006). As the linear *dbh* term continues to have a positive parameter estimate, this means that the BC fits a simple quadratic increase of mortality with dbh. The left-skewed posterior distribution in the *dbh*^{2} estimate suggests that values outside the prior distribution may yield even higher likelihood values.

The posterior distribution of the overall diameter increment parameter *GRateD* was rather narrow (95% credibility interval: 0.61 - 0.88), revealing low uncertainty about this parameter, whereas the BC median and MAP (0.74 and 0.86, respectively) were slightly lower than the original value (1.0). *GRateD* showed a strong correlation with *kIntercept* (-0.76), whereas all other parameter correlations were below 0.5.

Likelihood of model predictions

As one would expect, the BC-MAP model version showed the highest performance on the calibration data (Table 4). BC-MAP yielded the highest average total likelihood (-26.4), followed by ForClim_IR (-30.1) and ForClim v3.3 (-34.4), and the best performance of all models at four out of nine sites. Compared to ForClim v3.3 or ForClim_IR separately, BC-MAP was even superior at 6 out of 9 sites (see Supplemental Material Appendix A). The independent analysis of the two likelihood components revealed a better average performance of BC-MAP for basal area increment (BAI), while for stem numbers, its performance was similar to that of ForClim_IR, and it performed better than ForClim v3.3 (-18.5 vs. -20.7).

Table 4: Performance comparison at calibration and validation sites for three ForClim model versions – the current ForClim version 3.3, the model version hosting the empirical mortality function with the original parameter values (ForClim_IR) and the calibrated model versions that yielded the maximum likelihood (BC-MAP). The table shows the average values for the individual log likelihood components (stem numbers and basal area increment) and the total log likelihood, the average rank of the model for each likelihood component and the number of sites where a model version performed best (# best performance).

		Stem numbers			Basal area increment			**Total likelihood**		
		ForClim v3.3	ForClim_IR	BC-MAP	ForClim v3.3	ForClim_IR	BC-MAP	**ForClim v3.3**	**ForClim_IR**	**BC-MAP**
Average LL	Calibration	-20.7	-18.5	-18.5	-13.7	-11.7	-8.0	**-34.4**	**-30.1**	**-26.4**
	Validation	-33.7	-22.1	-21.5	-23.1	-41.9	-26.4	**-56.7**	**-63.9**	**-47.8**
Average rank	Calibration	2.7	1.6	1.4	2.2	2.0	1.6	**2.3**	**1.9**	**1.6**
	Validation	2.4	1.5	2.0	1.7	2.3	1.9	**2.2**	**2.1**	**1.6**
# best performance	Calibration	1	4[a]	5[a]	3[a]	3	4[a]	**3**	**3**	**4**
	Validation	5	10	6	12	4	5	**7**	**6**	**8**

[a]For one site, two model versions showed best performance.

Validation

Likelihood of model predictions

BC-MAP showed the best overall performance on the independent validation data, as revealed by the likelihood values calculated based on both BAI and stem size distributions (Table 4). BC-MAP had the highest average total likelihood (-47.8), while ForClim_IR (-63.9) performed notably worse than ForClim v3.3 (-56.7). This was mainly due to the predictions of BAI, for which ForClim v3.3 performed distinctly better (mean likelihood: -23.1; highest performance at 12 sites) than BC-MAP (-26.4; 5 sites) and ForClim_IR (-41.9; 4 sites). In contrast, ForClim v3.3 did not predict stem numbers well (-33.7; 5 sites) compared to BC-MAP (-21.5; 6 sites) and ForClim_IR (-22.1; 10 sites). Total likelihood of BC-MAP was highest at 8 out of 21 sites (ForClim v3.3: 7, ForClim_IR: 6). In a direct comparison with ForClim_IR only, it was higher at 14 sites (see Supplemental Material Appendix A).

Performance of the predictions in basal area and stem numbers at the end of the simulation

At the end of the simulation period, ForClim v3.3, which showed highest likelihood in terms of BAI, underestimated total basal area somewhat at the validation sites (median: -1.8 m^2/ha), while BC-MAP and ForClim_IR strongly overestimated basal area (median: 4.4 m^2/ha 7.5 m^2/ha, respectively; cf. Figure 3 and Figure 5a). Regarding the average absolute differences between observed and simulated total basal area, ForClim v3.3 also performed best, but differences between the models were smaller (4.7 m^2/ha for ForClim v3.3 vs. 5.3 m^2/ha and 7.5 m^2/ha for BC-MAP and ForClim_IR, respectively). For basal area in the high shade tolerance class, the median difference was zero for both ForClim v3.3 and BC-MAP, in contrast to ForClim_IR (4.8 m^2/ha). For the intermediate shade tolerance class, results across model versions were quite similar and generally in good agreement with observed data (median absolute differences <0.8 m^2/ha). Basal area in the low shade tolerance classes was generally overestimated by all model versions, most pronounced in BC-MAP (median difference: 2.7 m^2/ha; mean absolute difference: 2.7 m^2/ha).

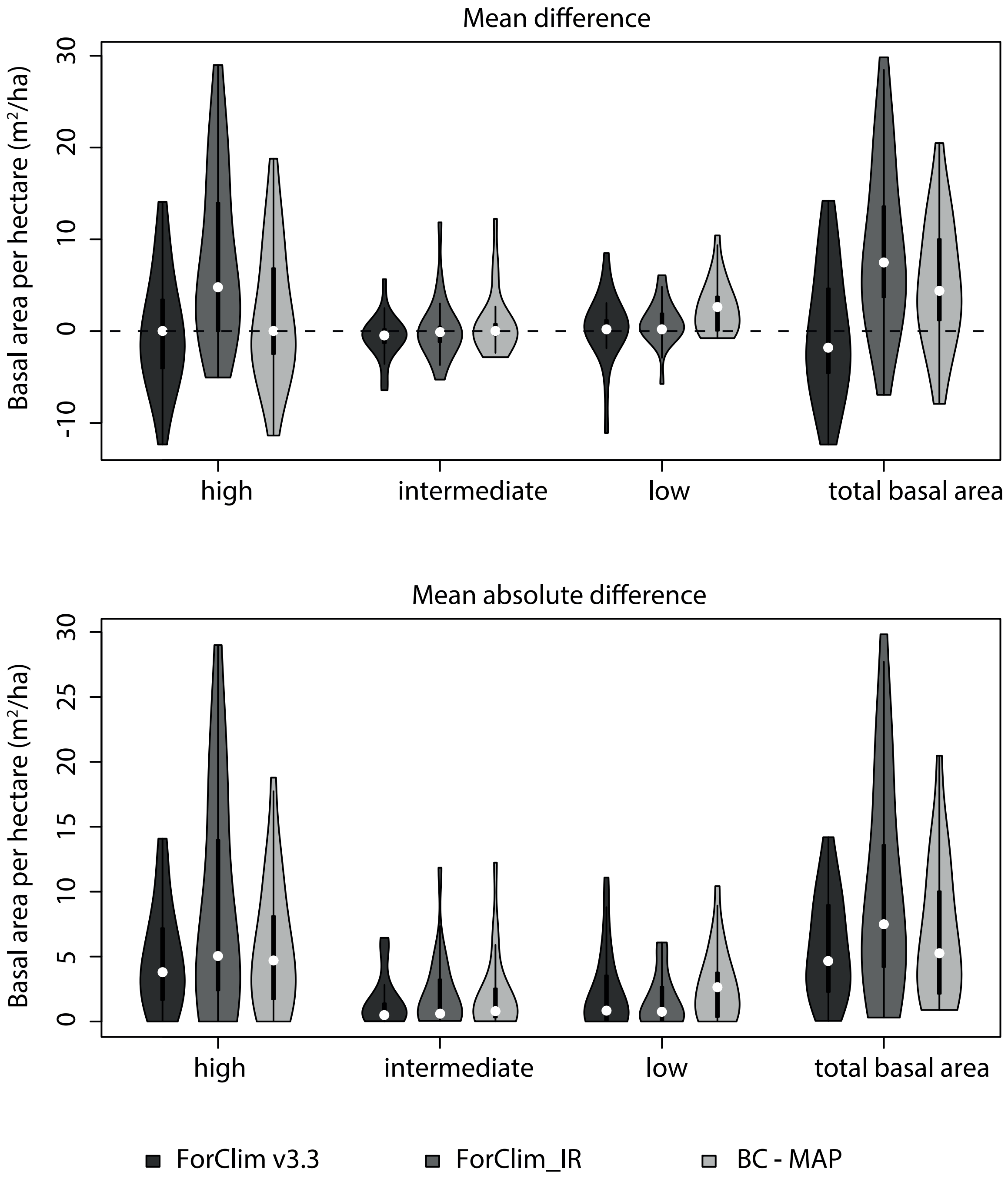


Figure 3: Violin plots of actual (upper panel) and absolute (lower panel) differences in observed and simulated basal area for different shade tolerance classes (high, intermediate and low) and total basal for different model versions. Differences were calculated regarding simulation and observation data for the last inventory respectively last year of simulation at all validation sites (n=21). Note absolute reference values (2.5%-percentile /median/ 97.5% percentile) for total basal area (27.5/45.3/68.4 m^2/ha), high (0.0/30.7/53.4 m^2/ha), intermediate (0.7/3.3/43.9 m^2/ha), and low shade tolerant species (0.0/2.8/30.4 m^2/ha).

Simulation results differed more strongly in the prediction of stem numbers. In the high shade tolerance class, BC-MAP and ForClim_IR were generally overestimating stem numbers in the dbh classes from 4 to 12 cm (mean difference: 20.1 stems/ha for BC-MAP and 27.1 stems/ha for ForClim_IR, respectively), whereas ForClim v3.3 was underestimating (-30.9 stems/ha) (Figure 4). On average, BC-MAP was closer to observations than ForClim v3.3 in these dbh classes. All model versions generally overestimated tree numbers for diameters between 12 and 28 cm, whereas predicted stem numbers with a dbh >28 cm were very close to observations (see also Appendix F: average absolute difference was <9 stems/ha for trees >28 cm). The pattern was similar for the intermediate shade tolerance class, for which BC-MAP predicted, on average, stem numbers most accurately in the dbh classes from 4 to 12 cm (mean difference: -0.7 stems/ha). For trees >12 cm, average differences were small for all model versions (see Appendix F). Lastly, for species in the low shade tolerance class, BC-MAP slightly overestimated stem numbers for trees from 4 to 8 cm (mean difference: 2.3 stems/ha), but was substantially closer to observations than ForClim v3.3 (-41.9 stems/ha) and ForClim_IR (-25.4 stems). A similar trend was found for the 8-12 cm dbh class. For trees >12 cm, model behavior was extremely similar and in good agreement with observed data (mean absolute differences <11.0 stems/ha, see Appendix F).

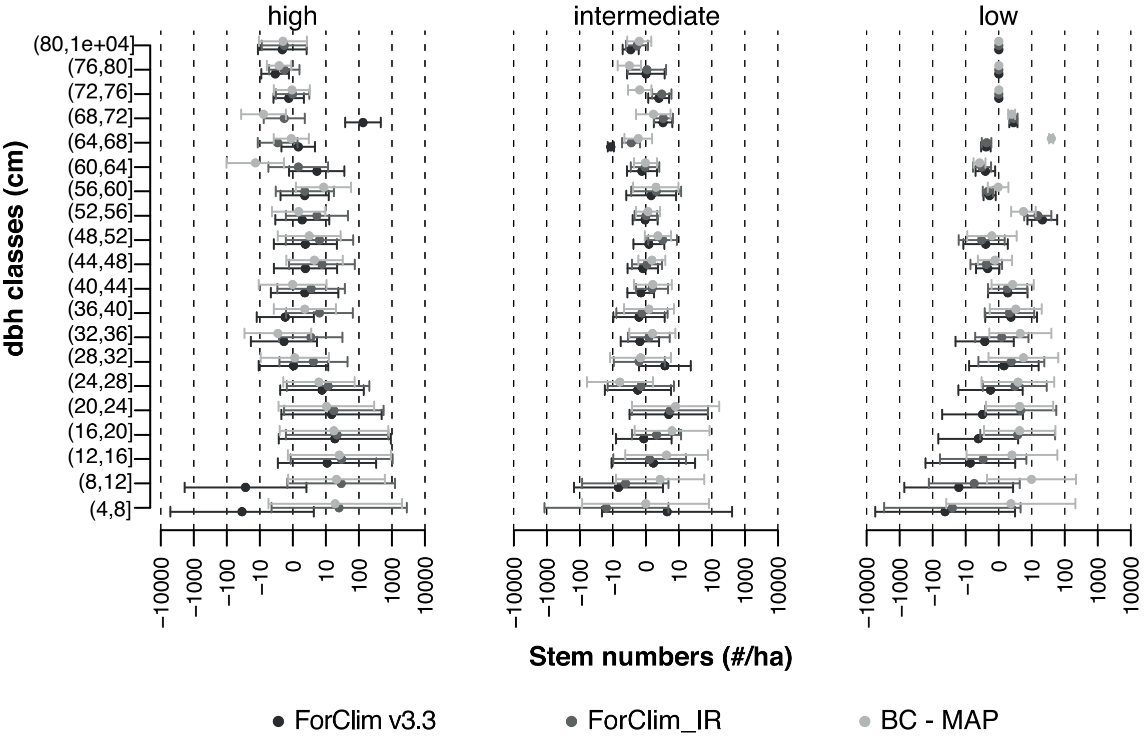


Figure 4: Differences between observed and simulated stem numbers for different model versions (ForClim v3.3, ForClim_IR, and BC-MAP): Means and standard deviations across all validation sites were calculated for each dbh class and for the three shade tolerance classes (high, intermediate and low). Note log-scale of stem numbers.

ForClim sensitivity to parameter estimates

As shown above and revealed by the posterior distributions (Figure 2), some parameters showed considerable posterior uncertainty. When forwarding this uncertainty to the outputs of ForClim, however, we found that parameter uncertainty led to moderate predictive uncertainty only, with slight differences between the different model outputs.

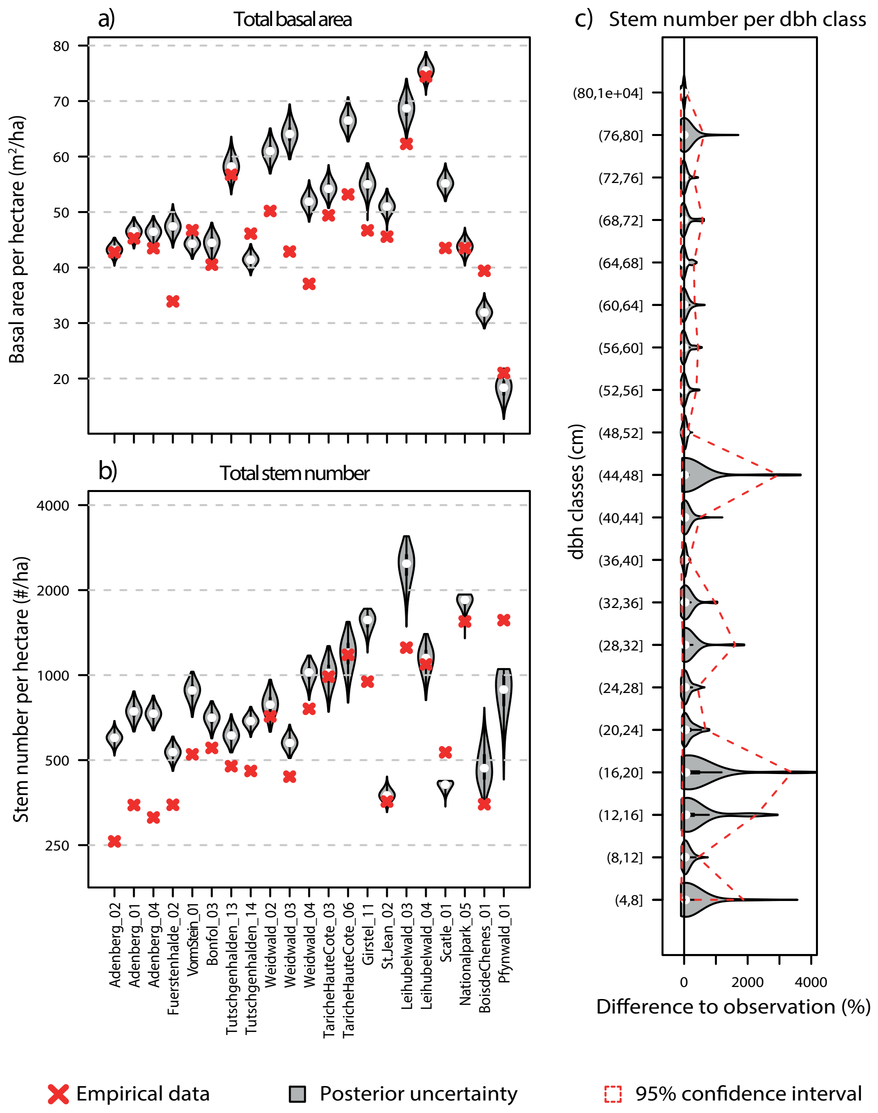


Figure 5: Posterior model output uncertainty and empirical observations for a) total basal area (upper left panel) and b) stem numbers (lower left panel). The violin plots are drawn from outputs of 1000 ForClim simulations per validation site with parameters drawn from the posterior distribution. Validation sites are ordered according to their latitude (north to south). c) Relative posterior uncertainty for stem numbers per dbh classes. Uncertainty is expressed by the relative difference between simulated and observed stem numbers in percent (%). Each violinplot includes 1000 values per validation site (n=21’000). The dashed red line indicates the 95% confidence interval.

Specifically, the width of the site-specific posterior 95% credibility intervals for total basal area ranged from 3.1 to 6.6 m^2/ha, with a median of 4.3 m^2/ha (upper left panel in Figure 5) and from 46.7 to 1095 stems/ha with a median of 224 stems/ha for total stem numbers (lower left panel in Figure 5). The distance of the upper border of the 95% credibility interval from the median was on average 4.7 ±1.9% and 5.1 ± 3.3% for the lower border, respectively. For total stem numbers, the distance of the upper and lower border of the 95% credibility interval from the median was 12.4 ±6.5% and 14.2 ±6.9%, respectively. We additionally assessed the average predictive error based on the entire distribution (as opposed to only using the MAP as above) by calculating posterior 95% intervals of absolute difference between observed and simulated data. The 95% confidence interval was between 0.2 and 21.0 m^2/ha for total basal area with a median of 5.0 m^2/ha and between 11.1 and 1217.6 stems/ha for total stem number with a median of 198.3 stems/ha, respectively.

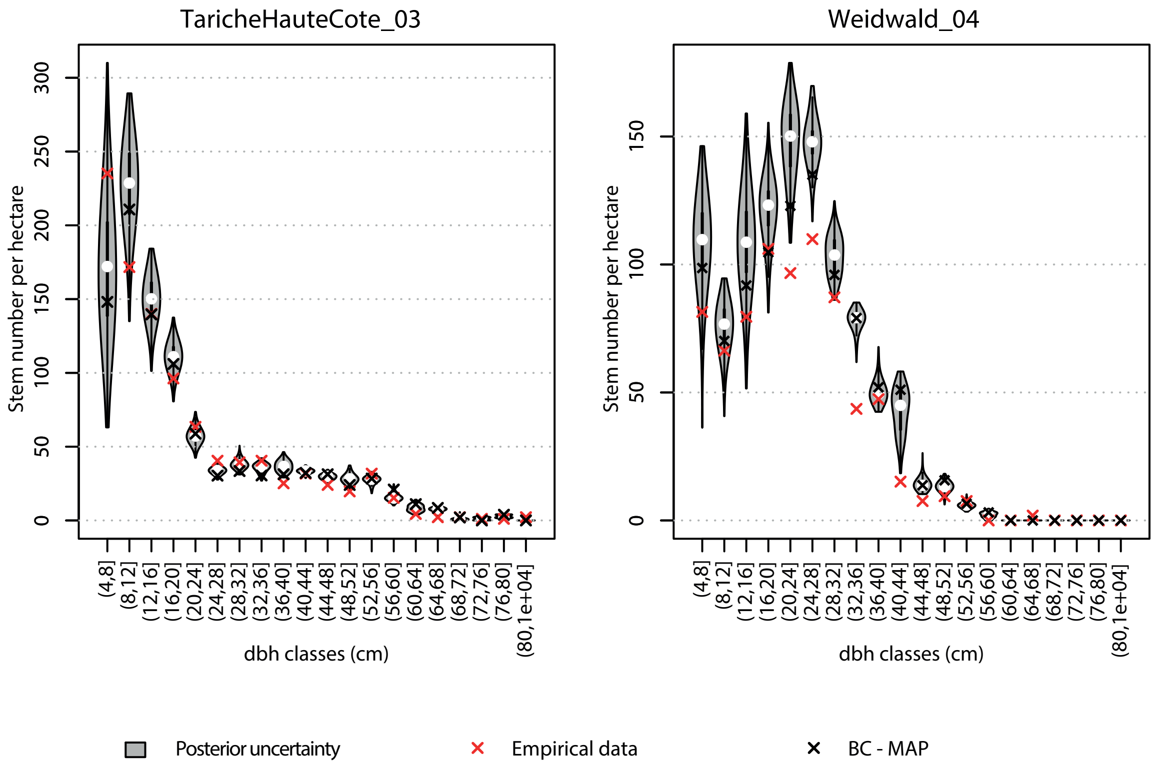


Figure 6: DBH distribution of two selected permanent plots (Tariche Haute Côte 03 and Weidwald 04). Violin plots show posterior model uncertainty expressed by total stem numbers outputs of 1000 ForClim simulations per validation site with different mortality parameter combinations drawn from the posterior distribution. Empirical observations and simulation results with BC-MAP are shown as well.

Model sensitivity to the parametric uncertainty expressed by the Bayesian posterior distribution was more pronounced for the lower dbh classes than for the higher ones (right panel in Figure 5c; see also the large posterior uncertainty for absolute stem numbers in the smallest dbh classes for the site Tariche Haute Côte 03: Figure 6, left panel). With increasing tree size, the width of the relative posterior uncertainty generally decreased (right panel in Figure 5c; Appendix B). This was particularly pronounced for permanent plots that showed a rather natural (i.e., negative exponentially-shaped) dbh distribution (e.g., Tariche Haute Côte 03). When dbh classes other than the smallest ones were dominating the stand, such as in Weidwald 04 (right panel in Figure 6), these dbh classes were subject to increased uncertainty as well.

Discussion

Model fit

Science and management require DVMs that provide reliable projections of forest dynamics. A necessary condition for having confidence in such projections is that the models accurately predict past vegetation dynamics, but also that process representations with empirically-based parameters are used (e.g., Adams *et al.*, 2013). When including empirically-based submodels in DVMs, one needs to carefully test the behavior and accuracy of the overall model, especially when the parameters of the submodels are derived independently of the DVM. We tested whether the parameter estimates of a rather detailed, environmentally driven mortality function that were derived from independent fits to inventory data would be matched when incorporating that function in a DVM and estimating its parameters using BC. Our results generally show a good agreement for the parameters of the *intercept*, *dbh*, and *relbai*; the latter two having a positive impact on tree survival. However, the inverse BC strongly modified the parameter estimates for dbh^2, shade tolerance (*ShadeLow, ShadeIntm*), and *GRateD*.

In the BC, the effect of dbh^2 on tree survival was estimated to be positive, while it was weakly negative in the independent regression. Combined with the positive linear effect of *dbh,* the negative effect of dbh^2 usually reflects the increased mortality rates of large trees (e.g., Lorimer and Frelich, 1984; Monserud and Sterba, 1999; Temesgen and Mitchell, 2005; Holzwarth *et al.*, 2013). This change in the estimate for dbh^2 likely reflects our decision to modify *relbai* from a factorial variable with only four classes in the IR version (i.e., the bin width of a class was rather large in the empirical parameterization) to a continuous variable for the BC. The relative basal area increment, *relbai*, is an important predictor of mortality probability (Bigler and Bugmann, 2004; Macalady and Bugmann, 2014), as it reflects that trees with low productivity are usually more prone to die than those that are highly productive (e.g., Monserud, 1976; Wyckoff and Clark, 2002). Since simulated values of *relbai* quickly drop to very low levels for trees with a large dbh (cf. Appendix E), this reduced the survival probability of large trees in a similar way as dbh^2 would have done.

Based on the parameterization with the NFI dataset (ForClim_IR), species of low and intermediate shade tolerance had a lower survival probability than shade-tolerant trees, in accordance with the theory on life-history strategies of pioneer vs. late-successional species (Grime, 1977). Yet, the opposite trend was found in the BC. This can be explained by the decrease in stem numbers over dbh and time in the calibration data, which differed strongly among the three shade-tolerance classes. In the calibration dataset, the decline was stronger for shade-tolerant species than for shade-intolerant species (lower panel in Appendix E). Therefore, it seems likely that parameter estimates were obtained that estimated higher mortality rates for shade-tolerant than pioneer species. The independent regression would not show the same result, as trees with a dbh <12 cm are not included in the NFI dataset. Moreover, we observed a relatively high uncertainty as well as a divergence of the median and MAP values of *ShadeLow* (cf. Figure 2). This may originate from interactions with other parameters, but potentially also from the fact that a variety of species was included in each shade tolerance class, each of which may feature very different strategies to face multiple abiotic stress. Within a single shade tolerance class, for example, species may exhibit strongly different growth-mortality relationships (Kane and Kolb, 2014). In addition, these relationships may change with tree age (Bigler and Veblen, 2009) and especially with increasing size, due to the parallel change of the abiotic environment and the species response (e.g., Valladares and Niinemets, 2008). It may therefore be difficult to obtain stable estimates for these broad classes, and more detailed, possibly species-specific parameters would need to be fitted.

Performance of the three model versions

For the calibration sites, the BC brought a clear improvement of model performance when using our likelihood function as the criterion of fit, both for the joint likelihood and the two individual likelihood components (basal area vs. tree numbers). This shows that the calibration succeeded in improving the fit through varying model parameters.

The fact that the better performance of BC-MAP in terms of likelihood was also evident from the validation sites suggests that the model was not overfitted by the BC procedure, at least not at the decadal time scale. Best performance at most of the validation sites (cf. Appendix A) is a strong indicator that the risk of a large model deficiency (i.e., prediction being far off the observations) at a specific site was mitigated during BC. In contrast, ForClim v3.3 performed best for predicting basal area increment between the inventories and basal area at the end of the simulation (Figure 3), but clearly underestimated stem numbers on average and at the site scale especially for small (4-12 cm) trees in the low and high shade-tolerant classes. For the larger dbh classes, agreement between observed and simulated stem numbers was high. ForClim_IR was as performant as BC-MAP in terms of stem numbers; however this was offset by the strong overestimation of BAI of shade-tolerant species.

Several factors may explain why the BC-MAP parameter estimates performed best. First, the calibration data for BC-MAP included data on small trees (dbh >4 cm), while the ForClim_IR calibration had used an NFI dataset that included only data of trees with dbh > 12 cm. Second, the overestimation of basal area for highly shade-tolerant species that was observed for ForClim_IR was most likely due to the relatively low mortality rates of this shade tolerance class in the NFI dataset (Wunder, *pers. comm.*). Such an overestimation was not observed for BC-MAP owing to (1) the reduction in the parameter annual growth rate *GRateD* and (2) the increase in the parameters $kShadeLow$ and $kShadeIntm$ with the BC approach. Thus, we conjecture that the observed parameter shifts are attempts of the BC to find an adequate balance between predicted growth and mortality rates in the model to match the calibration data in terms of basal area increment and stem numbers. The relatively high negative correlation between *gRateD* and the *intercept* of the mortality function (i.e., increase of the growth parameter leads to a reduced survival probability) supports this assumption as well.

Our results suggest that the balance between the representation of growth vs. mortality processes in the model could be further improved: The performance of ForClim v3.3 and ForClim_IR, whose growth function remained unchanged, was very heterogeneous across dbh and shade tolerance classes. Furthermore, the uncertainty in the posterior distributions of the shade tolerance parameters was large. We interpret this as an indication that a species- and size-differentiated growth-mortality relationship would be useful to improve model performance (cf. Wunder *et al.*, 2008; Bigler and Veblen, 2009; Ireland *et al.*, 2014). For instance, the parameter $kGRateD$ could be calibrated separately for each shade tolerance class, or even for each tree species using a hierarchical Bayesian approach (e.g., Rüger *et al.*, 2009).

Posterior uncertainty and model sensitivity

Running simulations of a DVM using one thousand parameter combinations that were stochastically sampled based on their posterior distribution presents a considerable advantage of Bayesian methods over standard simulation techniques, as it allows us to quantify the predictive uncertainty (Hartig *et al.*, 2012). This approach is often used to compare predictive uncertainty before and after calibration (i.e., prior and posterior predictive uncertainty; van Oijen *et al.*, 2005). As we deliberately used wide priors, we only calculated posterior predictive uncertainty for different model outputs as caused by the uncertainty in parameter estimates.

Predictive uncertainty was high particularly for stem numbers (cf. Lagarrigues *et al.*, 2015). The smallest dbh classes were the main source of this uncertainty, as revealed by the high predictive uncertainty at validation sites with particularly high numbers of small trees (e.g., Leihubelwald 03, Bois de Chênes 01, and Pfynwald 01). In contrast, relative differences between simulated and observed stem numbers (cf. Figure 5c) were comparatively low in higher dbh classes, indicating a lower sensitivity to parameter changes. These findings are also supported by the relatively low predictive uncertainty for total basal area, which is influenced mostly by the large trees.

Unfortunately, one cannot infer model sensitivity to changes in mortality parameters directly from the predictive uncertainty of model outputs. Mortality is a key process in DVMs (Manusch *et al.*, 2012), for which they normally show high sensitivity (e.g., Friend *et al.*, 2014; Bircher *et al.*, 2015). However, large uncertainty in a particular output primarily suggests that the data used for calibration in combination with the likelihood that we applied had relatively low power to constrain this particular model output, but not necessarily that the respective model output is particularly sensitive to parameter changes.

The calibration and validation process included inventory data with an average length of 40 years (maximum: 47 years), which limits the assessment of model robustness. Although we think that the large variety of sites used for the calibration and validation support the model's capability of providing accurate predictions beyond this time horizon, caveats remain. We identified comparatively high model uncertainty concerning the survival of small trees, which would determine long-term tree species composition. This requires further tests to assess how parametric uncertainty affects model outputs in long-term simulations, such as for simulating potential natural vegetation (PNV).

Direct vs. inverse parameter estimates

Our study highlights that parameter estimates from BC may differ considerably from those derived from an independent empirical fit. The parameters from BC resulted in better model performance on independent validation data, but this does not necessarily mean that these would be the most appropriate parameters to use. Rather, it needs to be addressed why these differences occur.

One reason may arise from the differences between the data sets used for the calibration (NFI vs. forest reserves). The sampling plots included in the two datasets cover a large array of forest types from vastly different site conditions and climates, and they were affected only marginally by external disturbances. However, the inventory series were longer in the reserve data set (>35 yrs compared to only 20 years in the NFI), and the callipering threshold was lower in the permanent plots used for the BC (4 cm) than in the NFI (12 cm). However, considerably more trees with a dbh >12 cm were included in the NFI dataset.

A second reason is obviously that the calibration may compensate for structural errors in the processes formulations that are incorporated in the model (Hartig *et al.*, 2012; Hartig and Dormann, in review).

A third reason may be that the directly measured parameters are not those that lead to best model performance. This may sound counterintuitive, as one would expect that estimates derived from an independent regression must be most appropriate as they directly relate to the actual mortality process, without being subject to the interactions of the (possibly flawed) structure of the DVM. However, models are necessary abstractions of reality (e.g., Bugmann, 2001). In complicated ecological models, nonlinear processes give rise to higher-level dynamics and patterns (idea of emergence, e.g., Levin, 1992), and often existing variability is averaged over such nonlinear processes (e.g. intraspecific variability; Chesson, 1998). In such a situation, it is possible that directly and inversely fitted parameters are not matching, and one would prefer the inverse estimation, as it leads to more accurate higher-level dynamics (Hartig and Dormann, in review).

The comparison of direct and inverse parameter estimates may serve as the basis for a debate whether original or calibrated values should be used for model application. A single case study like ours, however, cannot provide an unambiguous answer. We argue that, on short temporal scales, calibrated parameters may lead to more accurate predictions, and may therefore be preferable in the context of a specific project with a defined simulation period. However, if one wants to predict on longer time scales, the use of calibrated parameters that do not agree with directly measured parameters should be questioned, as uncertainties in the model structure may heavily affect model extrapolations (cf. Refsgaard *et al.*, 2006). This is particularly true when only a handful of parameters are calibrated, as in the present study. In such cases, the calibration procedure may lead to parameter values that compensate for suboptimal parameter choices elsewehere, or for flaws in the model structure. Thus, when context-independent parameter estimates are sought that are suitable for extrapolation, discrepancies between direct and inverse parameter estimates need to be examined and resolved. This will lead to an increase of structural realism in ecological models and, in the long term, will improve the quality and transferability of model predictions (cf. benefits of structural realism: understanding and prediction; Hartig & Dormann, in review).

The latter point highlights an important message of this study: the prevailing parameterization paradigm in vegetation modeling is to statistically derive submodels or functions based on independent, high-quality datasets and to implement them into DVMs in a “one-by-one” fashion. Alternatively, recent studies have used Bayesian statistics to replace direct by inverse parameter estimates, typically with wide priors, expressing no or vague information on the parameters (e.g., van Oijen *et al.*, 2005; Minunno *et al.*, 2013; Vrugt and Sadegh, 2013; Bagnara *et al.*, in press). In our study, we demonstrated how Bayesian statistics can be used for exploring the agreement of direct and inverse parameter estimates and thus, analyzing the structural functionality and interaction of a recently modified process representation in a DVM (cf. Wang *et al.*, 2009). Such an analysis of structural realism in DVMs is not implicitly bound to the implementation of new functions (cf. van Oijen *et al.*, 2011). Theoretically, it could be pursued systematically to examine processes of various ecological models by an established set of functions and data sets, analogously to the proposal of Prentice *et al.* (2007) regarding the benchmarking of DVMs, thus providing an implicit and simultaneous estimate of parameter uncertainty and structural error (and its location via the parameters that disagree).

Conclusions

We compared the performance of the ForClim forest gap model using (1) the original version with a generic mortality function, and a new, inventory-based mortality function whose parameters were (2) derived from field data or (3) calibrated using an inverse modeling approach.

The values of most of the calibrated mortality parameters were similar to the parameters that had been fitted independently of ForClim using forest inventory data. This suggests that the general structure of ForClim is appropriate. Small but ecologically important differences between the parameterizations, in particular regarding the relationship between species' shade tolerance and life history traits such as growth and mortality and their interaction require further examination and may lead to refinements of specific process interactions in the model.

We found that model performance was improved after BC for the joint likelihood and better balanced regarding standard model outputs across a wide range of validation sites compared to the other model versions. Model sensitivity related to parameter uncertainty was very high for dbh classes with high stem numbers (i.e., small trees) but rather low for larger trees and for standard model outputs such as basal area. Thus, overall forest stand structure seems to be less affected by parameter uncertainties. Still, high model sensitivity for small trees may translate into significant predictive uncertainties regarding tree species composition in longer-term simulations, which requires further testing.

Our results indicate that DVMs can be improved by calibration even when empirical parameter estimates of very good quality are available. Since unsatisfactory performance originates most likely from structural errors in the model, the use of (Bayesian) calibrated parameter values should not end with an unquestioned application of those parameters in the DVM. Rather, it should primarily support the identification of possible structural uncertainties, thus leading to an increase of structural realism in the model and, eventually, to improved and more reliable model applications.

Acknowledgments

This research was funded by the Swiss Federal Office for the Environment FOEN in the context of the program “Forests and Climate Change” and by the Swiss National Science Foundation project No. 140968. We like to thank Dominic Michel for high-quality programming support.

References

Adams, H.D., Williams, A.P., Xu, C., Rauscher, S.A., Jiang, X., McDowell, N.G., 2013. Empirical and process-based approaches to climate-induced forest mortality models. Frontiers in Plant Science 4, 438.

Bagnara, M., Sottocornola, M., Cescatti, A., Minerbi, S., Montagnani, L., Gianelle, D., Magnani, F., in press. Bayesian optimization of a light use efficiency model for the estimation of daily gross primary productivity in a range of Italian forest ecosystems. Ecol. Model.

Bigler, C., Bugmann, H., 2004. Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. Ecol. Model. 174, 225-239.

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130-1138.

Bircher, N., Cailleret, M., Bugmann, H., 2015. The agony of choice: different empirical mortality models lead to sharply different future forest dynamics. Ecol. Appl. 25, 1303-1318.

Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M., Oleson, K.W., 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. Global Change Biol. 9, 1543-1566.

Bossel, H., 1992. Real-structure process description as the basis of understanding ecosystems and their development. Ecol. Model. 63, 261-276.

Brang, P., Bugmann, H., Heiri, C., 2011. Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Birmensdorf, Eidg. Forschungsanstalt WSL; Zürich, ETH Zürich. Bern, Stuttgart, Wien, Haupt.

Bugmann, H., 1994. On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study. Ph.D. Thesis No. 10638, Swiss Federal Institute of Technology Zurich, Switzerland, 258 p.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259-305.

Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055-2074.

Bugmann, H.K.M., Solomon, A.M., 1995. The use of a European forest model in North America: A study of ecosystem response to climate gradients. J. Biogeogr. 22, 477-484.

Bugmann, H.K.M., Solomon, A.M., 2000. Explaining Forest Composition and Biomass across Multiple Biogeographical Regions. Ecol. Appl. 10, 95-114.

Chesson, P., 1998. Making sense of spatial models in ecology. Modeling Spatiotemporal Dynamics in Ecology, 151-166.

Didion, M., Kupferschmid, A.D., Lexer, M.J., Rammer, W., Seidl, R., Bugmann, H., 2009a. Potentials and limitations of using large-scale forest inventory data for evaluating forest succession models. Ecol. Model. 220, 133-147.

Didion, M., Kupferschmid, A.D., Zingg, A., Fahse, L., Bugmann, H., 2009b. Gaining local accuracy while not losing generality - extending the range of gap model applications. Can J Forest Res 39, 1092-1107.

Foley, J.A., Levis, S., Prentice, I.C., Pollard, D., Thompson, S.L., 1998. Coupling dynamic models of climate and vegetation. Global Change Biol. 4, 561-579.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., Woodward, F.I., 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Acad. Sci. U.S.A. 111, 3280-3285.

Galbraith, D., Levy, P.E., Sitch, S., Huntingford, C., Cox, P., Williams, M., Meir, P., 2010. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. New Phytol. 187, 647-665.

Gelman, A., Roberts, G., Gilks, W., 1996. Efficient metropolis jumping hules. Bayesian statistics 5, 599-608.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Statistical science, 457-472.

Grime, J.P., 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. The American Naturalist 111, 1169-1194.

Grimm, V., Railsback, S.F., 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. Philosophical Transactions of the Royal Society B-Biological Sciences 367, 298-310.

Hartig, F., Dislich, C., Wiegand, T., Huth, A., 2014. Technical Note: Approximate Bayesian parameterization of a process-based tropical forest model. Biogeosciences 11, 1261-1272.

Hartig, F., Dormann, C.F., in review. Structural realism of ecological theories and its consequences for understanding, predictions and stable inference. Ecol. Model.

Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O’Hara, R.B., Scheiter, S., Huth, A., 2012. Connecting dynamic vegetation models to data – an inverse perspective. J. Biogeogr. 39, 2240-2252.

Hasenauer, H., 2006. Sustainable forest management: growth models for Europe. Springer, Berlin.

Heiri, C., 2009. Stand dynamics in Swiss forest reserves: an analysis based on long-term forest reserve data and dynamic modeling. Ph.D. Thesis No. 18388, Swiss Federal Institute of Technology Zurich, Switzerland, 155 p.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. J. Ecol. 101, 220-230.

Ireland, K.B., Moore, M.M., Fule, P.Z., Zegler, T.J., Keane, R.E., 2014. Slow lifelong growth predisposes Populus tremuloides trees to mortality. Oecologia 175, 847-859.

Kane, J.M., Kolb, T.E., 2014. Short- and long-term growth characteristics associated with tree mortality in southwestern mixed-conifer forests. Can. J. For. Res. 44, 1227-1235.

Keane, R., Austin, M., Field, C., Huth, A., Lexer, M., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree Mortality in Gap Models: Application to Climate Change. Clim. Change 51, 509-540.

Lagarrigues, G., Jabot, F., Lafond, V., Courbaud, B., 2015. Approximate Bayesian computation to recalibrate individual-based models with population data: Illustration with a forest simulation model. Ecol. Model., in press.

Larssen, T., Huseby, R.B., Cosby, B.J., Host, G., Hogasen, T., Aldrin, M., 2006. Forecasting acidification effects using a Bayesian calibration and uncertainty propagation approach. Environ. Sci. Technol. 40, 7841-7847.

Le Roux, X., Lacointe, A., Escobar-Gutierrez, A., Le Dizes, S., 2001. Carbon-based models of individual tree growth: A critical appraisal. Ann. For. Sci. 58, 469-506.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Lorimer, C.G., Frelich, L.E., 1984. A simulation of equilibrium diameter distributions of sugar maple (Acer saccharum). Bulletin of the Torrey Botanical Club 111, 193-199.

Macalady, A.K., Bugmann, H., 2014. Growth-Mortality Relationships in Pinon Pine (Pinus edulis) during Severe Droughts of the Past Century: Shifting Processes in Space and Time. Plos One 9, 17.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Agren, G.I., Oliver, C.D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20, 289-298.

Manusch, C., Bugmann, H., Heiri, C., Wolf, A., 2012. Tree mortality in dynamic vegetation models - A key feature for accurately simulating forest properties. Ecol. Model. 243, 101-111.

Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., Teller, A.H., Teller, E., 1953. Equation of state calculations by fast computing machines. The journal of chemical physics 21, 1087-1092.

Mina, M., Bugmann, H., Klopcic, M., Cailleret, M., submitted. The devil lies in the management when assessing the impacts of climate change on mountain forest dynamics. Submitted in Regional Environmental Changes.

Minunno, F., van Oijen, M., Cameron, D.R., Cerasoli, S., Pereira, J.S., Tome, M., 2013. Using a Bayesian framework and global sensitivity analysis to identify strengths and weaknesses of two process-based models differing in representation of autotrophic respiration. Environ. Model. Software 42, 99-115.

Monserud, R.A., 1976. Simulation of forest tree mortality. For. Sci. 22, 438-444.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109-123.

Moorcroft, P.R., 2006. How close are we to a predictive science of the biosphere? Trends Ecol. Evol. 21, 400-407.

Moore, A.D., 1989. On the maximum growth equation used in forest gap simulation-models. Ecol. Model. 45, 63-67.

O'Hara, R.B., Arjas, E., Toivonen, H., Hanski, I., 2002. Bayesian analysis of metapopulation data. Ecology 83, 2408-2415.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. Ecol. Monogr. 66, 1-43.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for Global Biodiversity in the 21st Century. Science 330, 1496-1501.

Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S., Hickler, T., Lucht, W., Sitch, S., Smith, B., Sykes, M., 2007. Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell, J., Pataki, D., Pitelka, L. (Eds.), Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, pp. 175-192.

Ramin, M., Arhonditsis, G.B., 2013. Bayesian calibration of mathematical models: Optimization of model structure and examination of the role of process error covariance. Ecol. Inform. 18, 107-116.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2011. Getting a virtual forester fit for the challenge of climatic change. J. Appl. Ecol. 48, 1174-1186.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2012. Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. Ecol. Model. 232, 133-143.

Refsgaard, J.C., van der Sluijs, J.P., Brown, J., van der Keur, P., 2006. A framework for dealing with uncertainty due to model structure error. Advances in Water Resources 29, 1586-1597.

Reinds, G.J., van Oijen, M., Heuvelink, G.B.M., Kros, H., 2008. Bayesian calibration of the VSD soil acidification model using European forest monitoring data. Geoderma 146, 475-488.

Rosenthal, J.S., 2011. Optimal proposal distributions and adaptive MCMC. In: Brooks, S., Gelman, A., Jones, G., Meng, X.L. (Eds.), Handbook of Markov Chain Monte Carlo. CRC press, pp. 93-112.

Rowland, L., Harper, A., Christoffersen, B.O., Galbraith, D.R., Imbuzeiro, H.M.A., Powell, T.L., Doughty, C., Levine, N.M., Malhi, Y., Saleska, S.R., Moorcroft, P.R., Meir, P., Williams, M., Rowland, L., Harper, A., Christoffersen, B.O., Galbraith, D.R., Imbuzeiro, H.M.A., Powell, T.L., Doughty, C., Levine, N.M., Malhi, Y., Saleska, S.R., Moorcroft, P.R., Meir, P., Williams, M., 2014. Modelling climate change responses in tropical forests: similar productivity estimates across five models, but different mechanisms and responses. Geoscientific Model Development Discussions 7, 7823-7859.

Rüger, N., Huth, A., Hubbell, S.P., Condit, R., 2009. Response of recruitment to light availability across a tropical lowland rain forest community. J. Ecol. 97, 1360-1368.

Shao, G.F., Bugmann, H., Yan, X.D., 2001. A comparative analysis of the structure and behavior of three gap models at sites in northeastern China. Clim. Change 51, 389-413.

Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biol. 14, 2015-2039.

Temesgen, H., Mitchell, S.J., 2005. An Individual-Tree Mortality Model for Complex Stands of Southeastern British Columbia. Western Journal of Applied Forestry 20, 101-109.

Valladares, F., Niinemets, U., 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annual Review of Ecology Evolution and Systematics 39, 237-257.

van Oijen, M., Cameron, D.R., Butterbach-Bahl, K., Farahbakhshazad, N., Jansson, P.E., Kiese, R., Rahn, K.H., Werner, C., Yeluripati, J.B., 2011. A Bayesian framework for model calibration, comparison and analysis: Application to four models for the biogeochemistry of a Norway spruce forest. Agric. For. Meteorol. 151, 1609-1621.

van Oijen, M., Reyer, C., Bohn, F.J., Cameron, D.R., Deckmyn, G., Flechsig, M., Härkönen, S., Hartig, F., Huth, A., Kiviste, A., Lasch, P., Mäkelä, A., Mette, T., Minunno, F., Rammer, W., 2013. Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe. For. Ecol. Manage. 289, 255-268.

van Oijen, M., Rougier, J., Smith, R., 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiology 25, 915-927.

Vrugt, J.A., Sadegh, M., 2013. Toward diagnostic model calibration and evaluation: Approximate Bayesian computation. Water Resour. Res. 49, 4335-4345.

Wang, Y.P., Trudinger, C.M., Enting, I.G., 2009. A review of applications of model-data fusion to studies of terrestrial carbon fluxes at different scales. Agric. For. Meteorol. 149, 1829-1842.

Wehrli, A., Zingg, A., Bugmann, H., Huth, A., 2005. Using a forest patch model to predict the dynamics of stand structure in Swiss mountain forests. For. Ecol. Manage. 205, 149-167.

Wunder, J., Brzeziecki, B., Zybura, H., Reineking, B., Bigler, C., Bugmann, H., 2008. Growth-mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. Oikos 117, 815-828.

Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. J. Ecol. 90, 604-615.

Supplemental Material

Appendix A: Model performance for calibration and validation sites

Table A1: Overview of individual likelihood components (stem numbers and basal area increment) and their sum (total likelihood) for calibration and validation sites. Likelihood values were calculated for three ForClim model versions – the current ForClim version 3.3, the model version hosting the empirical mortality function with the original parameter values (ForClim_IR) and the calibrated model versions that yielded the maximum likelihood (BC-MAP). Highest likelihoods per site and component are highlighted in grey.

	Stem numbers			Basal area increment			**Total likelihood**		
	ForClim v3.3	ForClim_IR	BC-MAP	ForClim v3.3	ForClim_IR	BC-MAP	ForClim v3.3	ForClim_IR	BC-MAP
Calibration sites									
Adenberg_03	-23.0	-22.7	-22.9	-7.3	-13.2	-7.3	-30.2	-35.9	-30.2
Bois de Chênes_02	-16.9	-16.3	-15.8	-1.9	-0.6	-1.5	-18.8	-16.8	-17.3
Fuerstenhalde_01	-13.8	-14.8	-14.8	-3.4	-32.6	-5.6	-17.2	-47.4	-20.4
Girstel_04	-30.2	-27.9	-27.4	-17.4	-14.8	-17.3	-47.6	-42.6	-44.7
Leihubelwald_02	-17.0	-14.4	-14.2	-21.6	-4.3	-10.8	-38.6	-18.7	-25.1
Nationalpark_07	-10.5	-8.9	-8.9	-2.3	-6.4	-5.7	-12.8	-15.2	-14.6
St. Jean_01	-23.2	-20.0	-19.2	-25.0	-4.0	-3.5	-48.1	-23.9	-22.7
Tariche Haute Côte_04	-30.5	-23.9	-25.2	-14.7	-17.5	-9.8	-45.1	-41.3	-35.0
Vorm Stein_02	-21.6	-17.6	-17.7	-29.9	-11.7	-10.2	-51.5	-29.3	-27.9
AVERAGE	**-20.7**	**-18.5**	**-18.5**	**-13.7**	**-11.7**	**-8.0**	**-34.4**	**-30.1**	**-26.4**
Validation sites									
Adenberg_01	-21.0	-22.9	-23.4	-9.7	-10.8	-9.4	-30.6	-33.7	-32.7
Adenberg_02	-23.2	-21.2	-22.3	-7.1	-9.0	-5.3	-30.2	-30.2	-27.6
Adenberg_04	-21.0	-22.3	-22.9	-4.0	-10.0	-5.5	-24.9	-32.4	-28.4
Bois de Chênes_01	-20.3	-18.1	-19.9	-32.2	-8.9	-27.1	-52.5	-27.0	-47.0
Bonfol_03	-24.8	-21.0	-21.7	-28.6	-14.6	-23.8	-53.4	-35.5	-45.5
Fuerstenhalde_02	-13.4	-15.0	-13.7	-27.7	-93.7	-42.8	-41.1	-108.7	-56.6
Girstel_11	-11.2	-11.5	-12.7	-8.6	-16.7	-11.1	-19.9	-28.2	-23.9

Leihubelwald_03	-43.3	-16.5	-16.6	-21.9	-45.8	-28.8	-65.2	-62.4	-45.4
Leihubelwald_04	-18.8	-12.0	-12.4	-14.6	-14.7	-17.4	-33.4	-26.7	-29.8
Nationalpark_05	-15.5	-7.8	-8.7	-13.8	-4.1	-3.7	-29.3	-11.9	-12.5
Pfynwald_01	-110.1	-38.0	-29.1	-16.4	-7.1	-7.1	-126.5	-45.1	-36.2
Scatlè_01	-138.4	-98.8	-86.9	-77.9	-91.9	-94.9	-216.3	-190.7	-181.7
St. Jean_02	-29.3	-20.4	-17.7	-3.1	-5.0	-7.2	-32.4	-25.4	-24.9
Tariche Haute Côte_03	-34.4	-17.4	-16.7	-1.4	-31.5	-6.1	-35.8	-48.9	-22.8
Tariche Haute Côte _06	-29.0	-11.9	-11.9	-14.6	-107.3	-34.0	-43.7	-119.2	-46.0
Tutschgenhalden_13	-11.9	-11.7	-12.4	-33.4	-30.0	-26.7	-45.3	-41.6	-39.1
Tutschgenhalden_14	-28.3	-24.9	-28.5	-43.5	-40.8	-41.8	-71.8	-65.7	-70.3
Vorm Stein_01	-15.1	-15.5	-16.2	-18.1	-2.9	-5.0	-33.3	-18.5	-21.2
Weidwald_02	-54.2	-23.8	-24.5	-17.0	-81.4	-24.3	-71.3	-105.2	-48.8
Weidwald_03	-12.9	-12.1	-11.9	-65.8	-181.9	-95.7	-78.7	-193.9	-107.6
Weidwald_04	-30.5	-20.3	-20.5	-24.9	-71.6	-35.9	-55.4	-91.8	-56.3
AVERAGE	**-33.7**	**-22.1**	**-21.5**	**-23.1**	**-41.9**	**-26.4**	**-56.7**	**-63.9**	**-47.8**

Appendix B: Uncertainty in dbh distributions for all validation sites

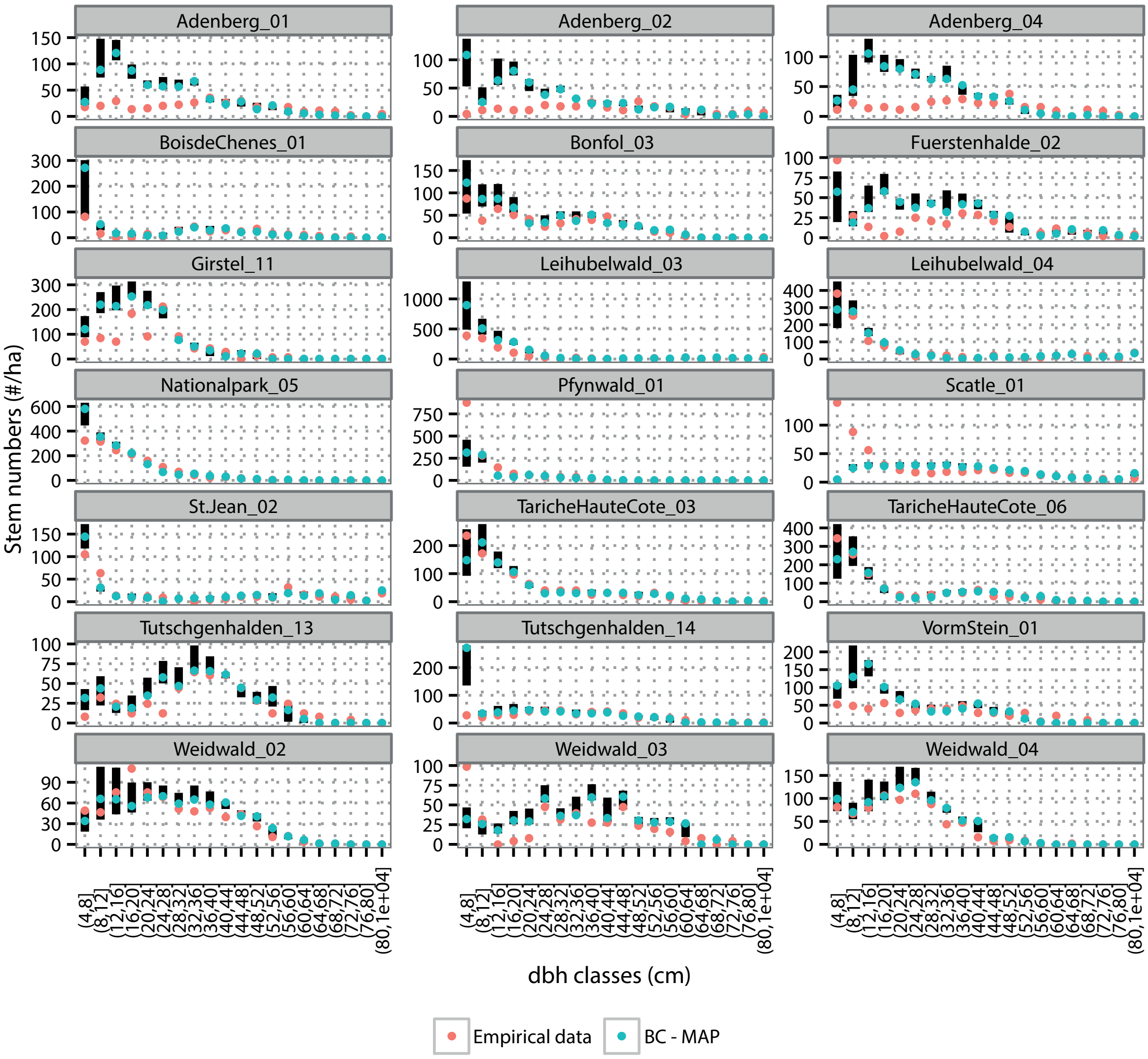


Figure B1: DBH distributions of all validation sites for last year of simulation. Black bars indicate 95% credibility interval from total stem numbers outputs of 1000 ForClim simulations per validation site with different mortality parameter combinations drawn from the posterior distribution. Empirical observations (red points) and simulation results with BC-MAP (blue points) are shown as well.

Appendix C: Posterior uncertainty for individual dbh classes

Table C1: Relative differences between simulated and observed stem numbers in percent (%). Mean, median and the 2.5% respectively 97.5%-quantile are given for each dbh class (cm) based on 1000 simulations per validation site (n=21'000).

dbh class	mean	median	2.5%-quantile	97.5%-quantile
(4,8]	156.5	38.9	-96.5	1867.3
(8,12]	79.0	35.5	-66.8	434.7
(12,16]	317.4	54.7	-68.2	2275.0
(16,20]	352.6	63.1	-44.6	3392.7
(20,24]	128.3	37.7	-52.1	676.3
(24,28]	76.7	35.7	-82.1	423.2
(28,32]	115.4	22.5	-34.2	1612.5
(32,36]	79.6	32.3	-86.1	968.8
(36,40]	23.0	22.5	-79.5	156.7
(40,44]	59.4	26.6	-40.8	500.0
(44,48]	164.5	18.8	-28.8	2968.9
(48,52]	19.9	23.9	-60.3	107.9
(52,56]	14.4	-2.8	-100.0	385.3
(56,60]	26.4	-6.8	-100.0	437.5
(60,64]	20.4	0.0	-100.0	331.8
(64,68]	10.6	0.0	-100.0	306.3
(68,72]	28.4	0.0	-100.0	587.5
(72,76]	-1.6	0.0	-100.0	295.0
(76,80]	43.8	0.0	-100.0	625.0
(80,1e+04]	-20.6	0.0	-100.0	65.2

Appendix D: Relative posterior uncertainty for total basal area and stem numbers

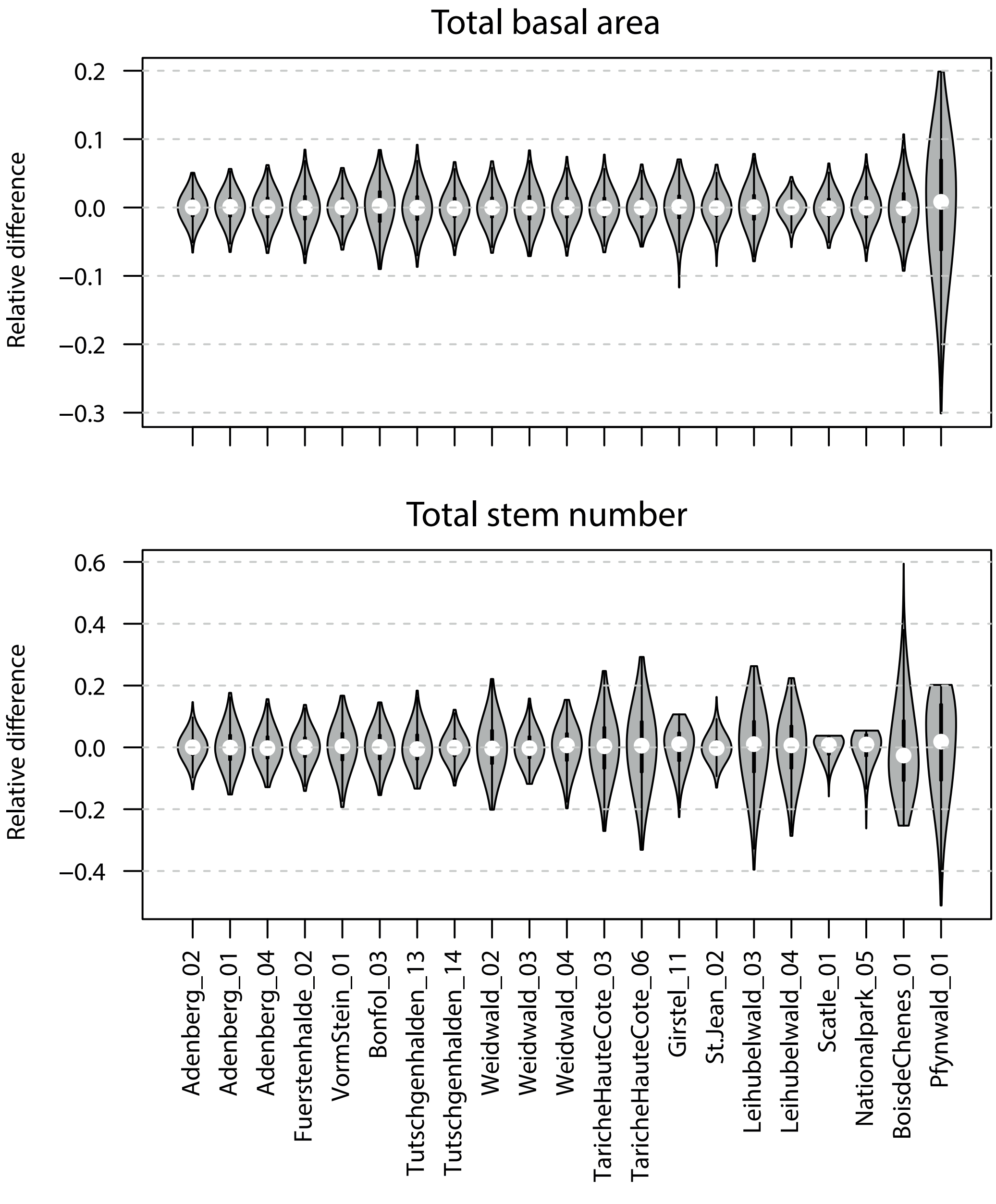


Figure D1: Relative posterior uncertainty for total basal area and stem numbers. Relative uncertainty is expressed by the relative difference between simulations (n=1000) and their mean.

Appendix E: Comparison relbai values and stem numbers for different data sources

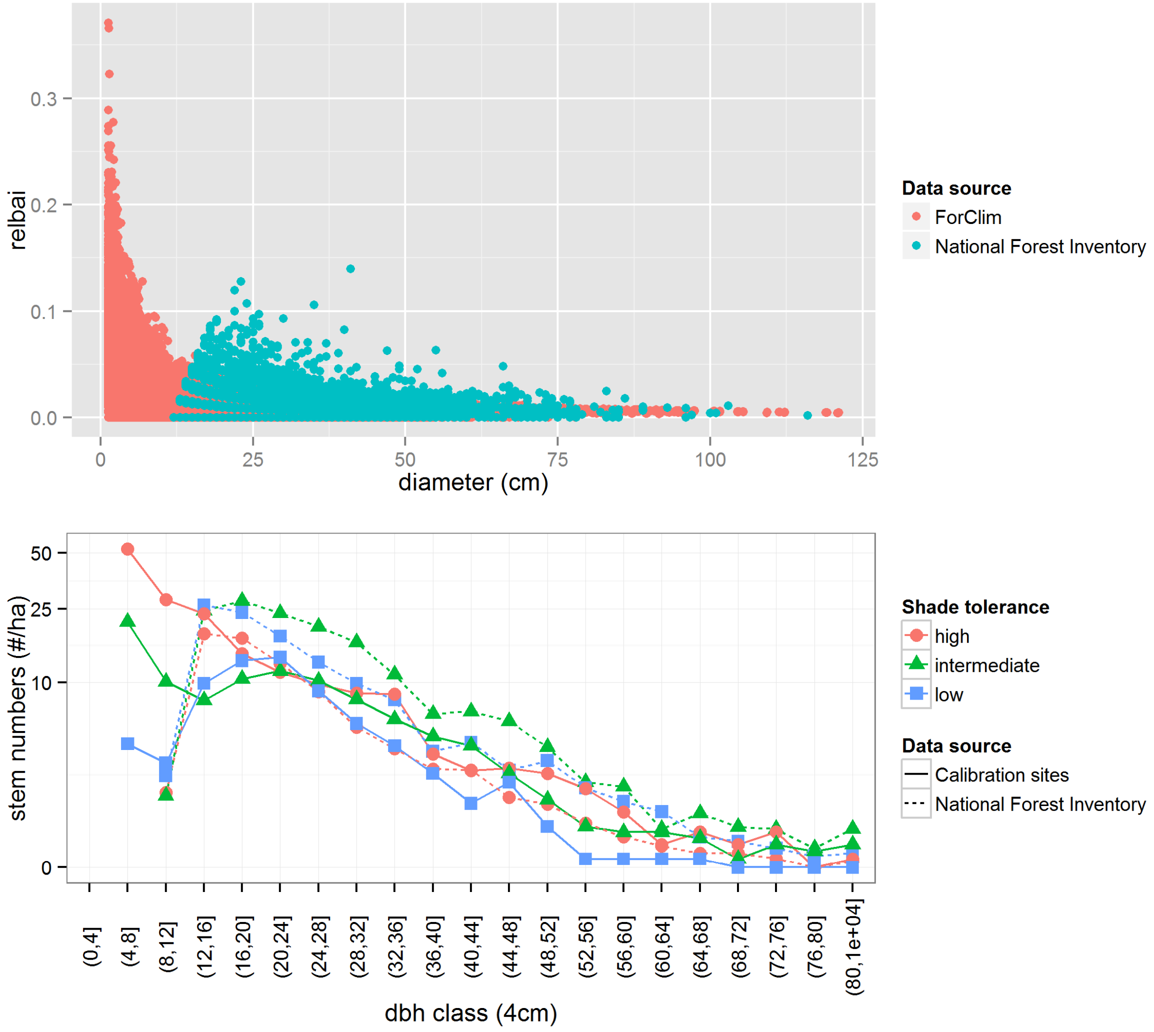


Figure E1: The upper panel shows empirical and simulated values for relative basal area increment (*relbai*) depending on tree diameter. Empirical relbai values were calculated from data of those plots of the Swiss National Forest Inventory that were used to derive the empirical mortality function. Simulated relbai values were derived based on BC-MAP simulations for each validation site. On the lower panel, dbh distributions per dbh class and shade tolerance class are shown for the inventory data used for the derivation of the empirical morality function and for the first inventory of the forest sites used for Bayesian calibration.

Appendix F: Absolut differences in stem numbers across all validation sites

Table F1: Means of absolute differences between observed and simulated stem numbers for different model versions (ForClim v3.3, ForClim_IR, and BC-MAP): Means across all validation sites were calculated for each dbh class and for the three shade tolerance classes (high, intermediate and low).

Shade tolerance	high			intermediate			low		
Dbh class	**FC v3.0**	**BC-MAP**	**FC_IR**	**FC v3.0**	**BC-MAP**	**FC_IR**	**FC v3.0**	**BC-MAP**	**FC_IR**
(4,8]	91.15	57.77	49.36	56.72	44.53	36.38	43.33	36.98	33.13
(8,12]	32.66	21.36	29.33	10.14	11.83	10.88	16.76	13.61	10.95
(12,16]	21.98	28.49	31.59	8.07	8.07	5.97	8.23	10.89	7.17
(16,20]	33.04	27.55	28.69	3.77	6.93	3.48	6.69	8.02	5.74
(20,24]	22.60	18.87	22.50	6.98	8.49	5.81	7.30	7.21	6.43
(24,28]	12.97	9.99	12.85	5.02	5.55	4.98	4.65	8.10	6.04
(28,32]	8.79	7.72	8.06	3.43	4.66	3.59	6.75	8.23	6.80
(32,36]	8.34	7.63	6.52	2.75	3.78	3.32	4.19	6.00	3.76
(36,40]	5.31	6.06	8.20	3.69	3.55	3.54	4.14	3.96	3.39
(40,44]	7.64	7.74	8.46	1.87	2.96	2.56	2.73	3.42	2.96
(44,48]	6.05	5.89	7.96	1.82	1.87	1.90	1.46	1.63	1.71
(48,52]	6.40	6.78	8.82	1.96	1.80	1.93	2.55	3.19	2.75
(52,56]	4.89	3.92	6.92	1.42	1.39	1.30	1.59	1.16	1.27
(56,60]	3.78	4.43	5.21	2.47	2.08	2.53	0.72	1.21	0.70
(60,64]	4.67	4.94	5.40	1.32	1.06	1.16	0.98	0.65	0.90
(64,68]	2.23	2.14	2.58	0.62	1.07	0.81	0.49	0.31	0.49
(68,72]	2.01	2.57	2.29	0.77	1.30	0.76	0.51	0.41	0.49
(72,76]	1.73	2.14	1.79	0.54	0.82	0.51	0.00	0.00	0.00
(76,80]	1.26	1.24	1.40	1.15	0.73	1.21	0.00	0.00	0.00
(80,1e+04]	2.10	1.99	1.88	0.62	0.91	0.81	0.00	0.00	0.00

3

Stratification of the Swiss forest area into typical forest stands

Bircher, N. & Bugmann, H.

Technical Report; not intended for publication

Introduction

Due to the high site diversity of Swiss forests (OcCC, 2007), at least a part of the current forest stands are expected to be substantially influenced by climate change over the coming decades. In this project, the sensitivity of typical Swiss forest stand structures to climate change is assessed using the forest gap model ForClim (Bugmann, 1996). Based on real stand data, we examine whether and to what extent – in terms of biomass, tree species composition, stem numbers and diameter at breast height (DBH) distribution – Swiss forest stands will change in the next 50 to 60 years. There is a special focus on forest stands that – due to their distribution, structure and tree species composition – are typical for the Swiss forest area. Thus, the Swiss forest area needs to be stratified according to quantitative criteria. The challenge of this stratification lies in the appropriate balance between accuracy and feasibility. On the one hand, the essential structural characteristics of forest stands should be considered to allow for a clear distinction. On the other hand, limits to accuracy are set due to data availability as well as to the level of how accurately ForClim is able to portray forest dynamics.

Objective of the stratification

The objective was to derive a set of distinct strata of forest types that, in terms of their stand structure, are typical of current Swiss forests. The stratification must be based on a quantitative and – as far as possible – objective approach. While on the one hand the identified strata need to form distinguishable units, they on the other hand are not required to reach the resolution of classical forest societies (Waldgesellschaften à la NaiS). Stratification criteria should include stand features that are commonly used and accepted among forestry practitioners and forest ecologists.

Material and Methods

The third National Forest Inventory (NFI3; WSL, 2011) served as the data basis for the stratification. It contains a raster of plots systematically distributed over the entire area of Switzerland. For each plot of the NFI3 that was classified as “normal forest”, a wide spectrum of forest stand attributes was collected. Importantly, plot data were completed by a single tree survey, conducted around the center of the plot (Keller, 2005).

The pivotal concept of our stratification was to identify a set of suitable classification criteria, to use them for grouping the NFI plots and, finally, to select those groups of NFI plots with the highest proportion (representativeness).

In a first step, the map of the eco-regions (Standortsregionen) was digitized from the “Guide for sustainability in protection forests” (NaiS; Frehner *et al.*, 2005) in ArcGIS (Figure 1). These eco-regions are well accepted among practitioners and have a better ecological basis than the “production regions” of the NFI.

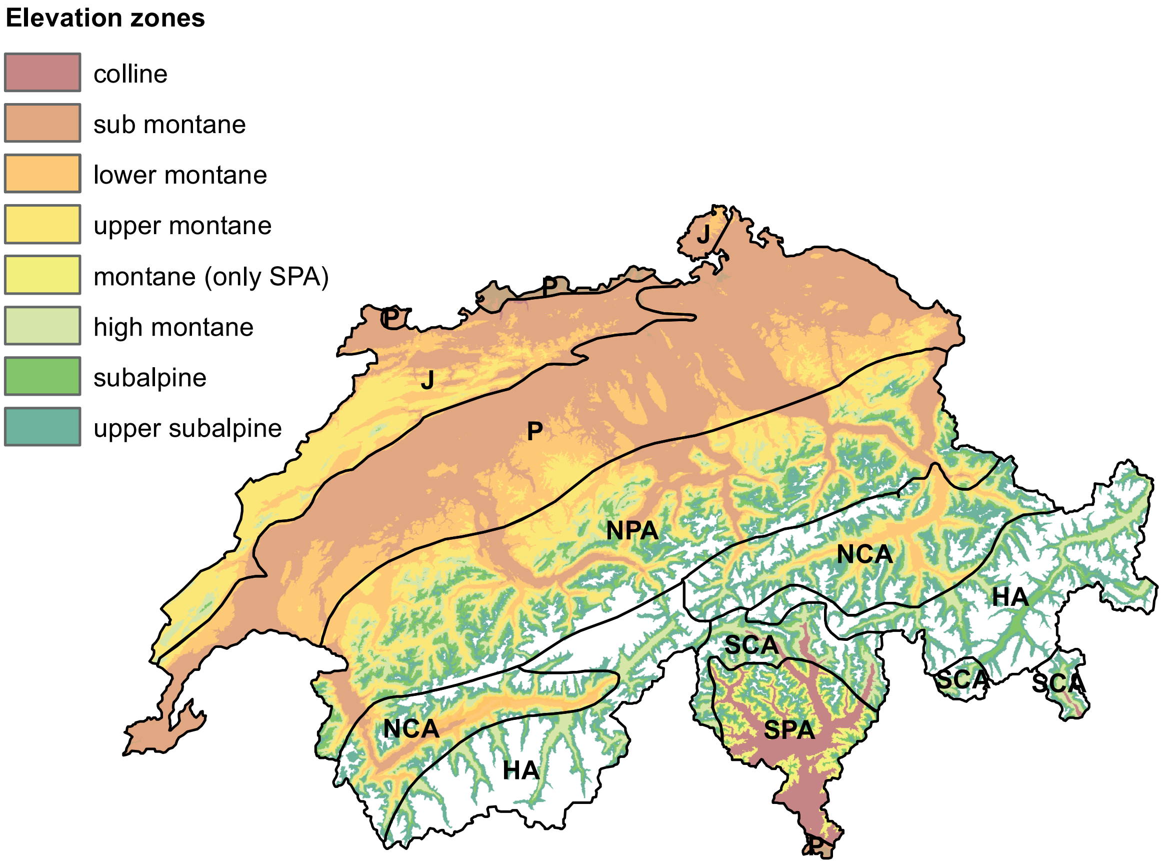


Figure 1: Forest eco-regions (J = Jura, P = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps) and elevation zones of Switzerland modified from Frehner *et al.* (2005). Boundaries for elevation zones represent average estimates (see also Appendix A), white patches represent areas beyond the upper tree line.

For the second step, we decided to stratify the eco-region by elevation, again due to the ecological but also management importance of altitudinal forest zones. Conveniently, the altitudinal vegetation zones of NaiS are defined specifically for each eco-region (Figure 1). Therefore, they were used as the second criterion for the stratification after conferring with Monika Frehner, a sylvicultural expert for Swiss mountain forests and main author of NaiS, based on the classification in NaiS. The boundaries of the elevation zones should be understood as broad-scale averages. In reality, the altitude of a vegetation zone can be fairly variable, depending on local site conditions and topography. However, for an analysis in ArcGIS, the use of fixed thresholds was inevitable. Appendix A shows the classification of the elevation zones and their boundaries.

At this point, the NFI plots were integrated into the stratification. Only plots classified as "normal forest" were considered. The number of NFI plots per elevation zone and eco-region was used to determine the proportion of forest area in each region and altitude. A first threshold was set: **Each elevation zone had to contain at least 10% of the NFI plots in the corresponding eco-region, for it to be retained in the stratification.** Two strata that would thus have been dropped (upper montane Swiss Plateau and the subalpine northern Pre-Alps) lay minimally below the threshold and were retained in the analysis. Appendix B shows the proportion of forest area per eco-region and elevation zone.

Azonal communities (Sonderwaldstandorte) were not considered here because their stand structure does not reflect the prevalent climate und nutrient availability, but rather the disturbance regime, which is not considered in ForClim. Azonal communities among the NFI plots were identified as follows. Based on the vegetation model of Meinrad Küchler (WSL), a unit of the Potential Natural Vegetation was assigned to each NFI plot. If this vegetation unit only contained Sonderwaldstandorte, the corresponding plot was considered to be unsuitable and excluded from the data pool.

In the third step, we considered two forest stand features as being particularly suitable for the further stratification:

Stand structure designates the vertical composition of the reference stand ("massgebender Bestand") (Keller, 2005). Four classes are distinguished: 1= single-layered, 2= multi-layered, 3= stratified, 4= clustered.

The **developmental stage** of the reference stand is determined based on the average DBH of the 100 largest trees per hectare (Keller, 2005), with the following five classes: 1= young growth/thicket (DBH ≤12 cm), 2= pole wood (12-30 cm DBH), 3= small timber (31-40 cm DBH), 4= medium timber (41-50 cm DBH), 5=old timber (≥50 cm DBH).

To identify the combinations of these two features that are quantitatively typical for a particular eco-region and elevation zone, a cross table showing the proportion of all occurring combinations was created for all plots of each particular elevation zone in every eco-region.

Based on a suggestion by Monika Frehner, NFI plots whose **developmental stage** was young growth/thicket were excluded from this step. "Young growth" stands mostly show a considerably lower top height (Oberhöhe) than more mature forest stands. Nevertheless, top height is still used to define their **stand structure**. In this context, the application of this concept for young growth forest stands would be misleading.

Typical forest stands (without young growth)

For each elevation zone of each eco-region, a list with the quantitatively most important combinations of the properties described above was created. To do so, the following rules were established:

- The most common combination was selected first.
- Each selected combination had to have a proportion of at least 10% of the NFI pixels of the respective stratum defined by eco-region and altitudinal belt.
- Altogether, the selected combinations had to reach a proportion of 40% of all occurring combinations in any given elevation zone.

Thus, a **forest stand (=stratum)** at this point was characterized by the following four attributes: a **specific eco-region, elevation zone, specific developmental stage,** and **stand structure**. Note that up to this point, the stratification procedure was based on a purely objective approach.

Finally, the tree species composition of each and every one of these strata was examined. Based on the single-tree data of each NFI plot, stem numbers and basal area per hectare were calculated. These data were then used jointly with expert knowledge (our own and Monika Frehner's) to separate distinct units within each of these strata, if a further splitting was deemed to be required. To this end, rules and thresholds were defined to increase the uniformity of each stratum. The rules mainly referred to the relative basal area of the tree species. Accordingly, plots were regrouped, excluded or transferred based on their species composition (by basal area and tree numbers). Consequently, a fair number of the strata that had been defined so far were split into two or even more strata, containing a lower number of plots with a specific tree species composition. We defined **ten NFI plots to be the minimal number that a stratum was required to contain**, due to initialization constraints of the ForClim model.

Overall, a "typical" forest stand (stratum) in our project is thus characterized by its **eco-region, elevation zone, developmental stage** and **stand structure,** and its **tree species composition**.

Results

Overview

In total, 71 typical forest stands were identified. By that, one fourth (1766 NFI plots) of the total number of available NFI plots classified as “normal forest” (6838) is represented in our final set of typical Swiss forest stands. Table 1 provides an overview of the distribution of these forest stands across the different eco-regions and elevation zones. Typical “young growth” stands will be shown separately.

Table 1: Overview of the number of forest stands per eco-region J = Jura, P = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps) and elevation zone.

	J	P	NPA	NCA*	HA	SCA	SPA	**Total**
colline	–	–	–	–	–	–	6	**6**
sub montane	4	4	–	–	–	–	–	**8**
lower montane	5	4	3	–	–	–	–	**12**
upper montane	6	4	6	–	–	–	–	**16**
high montane	–	–	5	4	2	3	–	**14**
montane**	–	–	–	–	–	–	4	**4**
subalpine	–	–	2	2	3	1	–	**8**
upper subalpine	–	–	–	–	3	–	–	**3**
Total	**15**	**12**	**16**	**6**	**8**	**4**	**10**	**71**

*The Northern Central Alps only includes eco-region b (without beech).

**In the Southern Pre-Alps, the lower, upper and high montane belts are summarized as one single “montane” elevation zone.

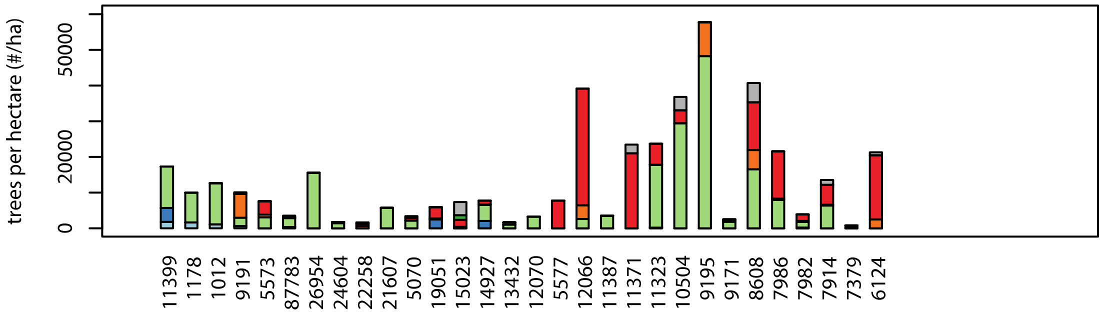
Typical forest stands (without “young growth”)

The structure of each of the 71 forest strata is shown in detail in Appendix C. Each stratum has a label (e.g. J_SM_1a), always consisting of three components: The first letter component refers to the eco-region to which the stratum belongs, going from north to south (J = Jura, P = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps); the second refers to the elevation zone (CO = colline, SM = sub montane, LM = lower montane, UM = upper montane, HM = high montane, SA = subalpine, US = upper subalpine). The digit distinguishes between strata of the same ecoregion and elevation zone, the optional lowercase letter indicates that a stratum was originally part of a larger stratum, which was split due to the tree species composition of the underlying NFI plots. The description includes the number of NFI plots representing the stratum, the volume in cubic meters respectively the basal area in square meters per hectare extrapolated from the single tree survey on each plot,. Bar plots are used to show the DBH distribution of the stratum. For each stratum, tree numbers were calculated for a plot size of 500 m^2. The values of the x-axis represent dbh classes of 4cm.

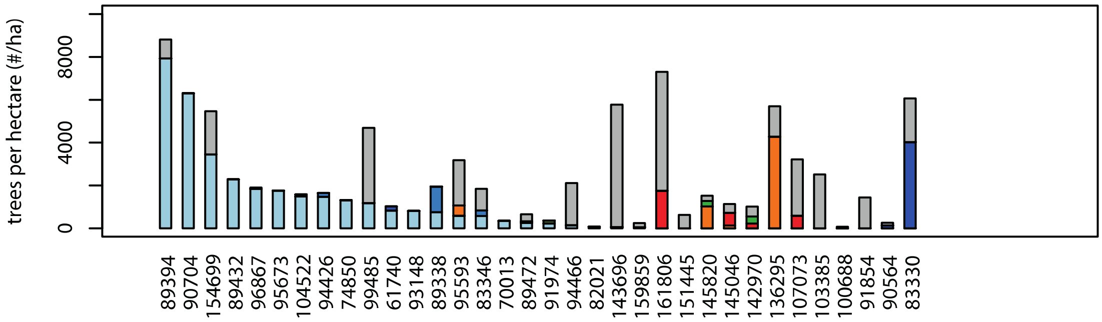
“Young growth” stands

There were six altitudinal vegetation zone with a sufficient proportion (at least 10%) of NFI plots in this developmental stage. However, only three of them consisted of enough plots (at least 10) to form a stratum. Figure 2 shows these three strata with their NFI plots.

a) Jura - sub montane



b) Northern Central Alps - high montane



c) Northern Central Alps - subalpine

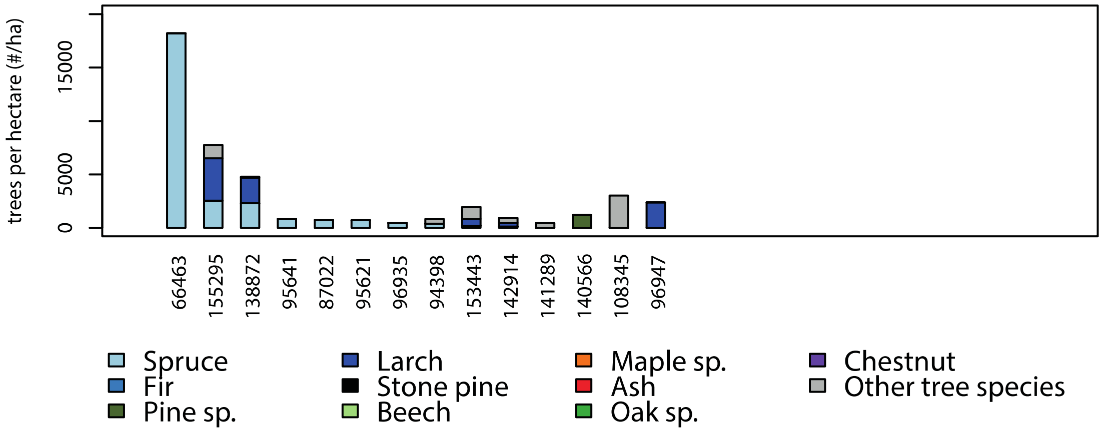


Figure 2: Stem numbers per main tree species and hectare for the three “young growth” strata a) Jura - sub montane, b) Northern Central Alps_b – high montane, and c) Northern Central Alps_b – subalpine.

Discussion

Typical forest stands

We identified 71 strata that are typical in terms of stand structure and tree species composition for the particular eco-region and elevation zone. While the number of strata is rather high, the fraction of the total NFI plots still included is relatively low. However, our aim was to identify *typical* stands, not a *representative* number of LFI plots in the stratification. One has to be aware that an increase of representativeness (by area) would have led to an either very high number of strata, or a far smaller set of criteria for the stratification, thus often leading to artificial stands that one cannot assume to occur in nature. We emphasized the inclusion of all eco-regions and all altitudes, at least as far as possible, and within this set we identified the most common strata. After all, ca. 25% of all NFI plots are represented by the 71 strata, which we view as a reasonable proportion. Our stratified data set demonstrates and reflects the heterogeneity of Swiss forests. The approach we chose allows for a fair distinction of the individual forest stands (strata) by criteria that are known, understood and applied by both practitioners and scientists. With respect to the ensuing problem of generating stand data for the initialization of the ForClim model, our approach is very efficient since the NFI plot data can be used directly and, at least as matters stand right now, a further search for stand data per stratum is not necessary, which is a tremendous advantage for the next steps in the project.

During the stratification, we came across a range of challenges and problems of which we would like to point out the most important ones below.

Single-layered forest stands

According to their stand structure, 29 of the strata are single-layered (stand structure =1), i.e. the top height of the majority of the trees on a plot belongs to the same layer (Keller, 2005). However, if strata are synthesized from different NFI plots, the single-layered character may not be guaranteed as these NFI plots, although each of them is classified as single-layered, may have different top heights. Thus, by consolidating these plots into one stratum, a multi-layered structure may result instead of the intended single-layer structure. Even though it may be assumed that trees with the same DBH should also be similar in their top height, and thus the developmental stage as another criterion of the stratification should mitigate the risk of creating multi-layered forest stands out of single-layered forest plots, nine of the single-layered strata showed a DBH distribution that suggested a multi-layered structure. Although there was the expected peak according to the developmental stage, smaller trees (e.g. the pole wood stage) were also abundant, thus resulting in a second peak. Unfortunately (for our purposes), top height of the individual trees is not recorded in the NFI. Nevertheless, we screened the individual plots of the strata with a conspicuous DBH distribution, and excluded those plots that showed a very high proportion of small trees. This step led to an “improved” DBH distribution for five strata (J_LM_2a, J_LM_2b, NR_UM_2b, NCA_HM_2, and HA_SA_3). Four other strata (NPA_LM_2a, NPA_UM_2a, NPA_HM_1b, and HA_HM_2) were kept without such a manual correction.

The eco-region Northern Central Alps

At the beginning of the stratification we planned to use the seven main eco-regions (Jura, Swiss Plateau, Northern Pre-Alps, Northern Central Alps, High Alps, Southern Central Alps and Southern Pre-Alps) according to NaiS. We did not favor the more detailed classification into subregions (e.g. Northern Central Alps a/b or Southern Pre-Alps a/b) that is used in NaiS because these would have caused too many strata with possibly too few NFI plots. However, when we analyzed the tree species composition of forest stands in the Northern Central Alps, it became obvious that in this case, a separation into the sub regions “a” and “b” (according to NaiS) was necessary. First, the classification of elevation zones for the two subregions is different. Second, tree species like beech, which are only expected to occur in subregion “a”, were mixed with plots located in subregion “b”, making an unequivocal identification of strata nearly impossible. Therefore, the NFI plots of the eco-region Northern Central Alps were allocated to the corresponding subregion. Unfortunately, no altitudinal vegetation belt in subregion “a” had at least ten NFI plots to form an unequivocal stratum. Therefore, in the final set of strata, only the Northern Central Alps “b” region is represented.

“Young growth” strata

As mentioned above, trees with a DBH <12 cm were recorded on one or two separate subplots in the NFI. The three “young growth” strata that we identified (Figure 2) show an extreme heterogeneity in terms of tree numbers. While some subplots contain several ten thousands of young trees (per hectare), others do not have more than a few hundred. The exact location of the subplots and their size (which is variable depending on the site, see Keller (2005)) obviously is decisive for the number of young trees that are recorded. This raises the question whether these data are reliable and do really represent the actual abundance of “young growth” on the individual NFI plots (note that the sampling design has not been intended to provide representative data at the plot level!). Since there were only three “young growth” strata and the available data are questionable, we intend to abandon these for the further work in the project.

Conclusion

We conclude that the stratification of the Swiss Forest area into “typical” stand types has successfully been accomplished, and we will use these data in the next step of the project to initialize ForClim and do test simulations with the model into the future.

Acknowledgments

We are grateful to Monika Frehner for providing expert input for the stratification process. Support by the NFI team at WSL Birmensdorf, particularly by Markus Huber, was indispensable for our work. We greatly appreciate the timely delivery of NFI data for this project.

References

Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055-2074.

Frehner, M., Wasser, B., Schwitter, R., 2005. Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion, Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Keller, M. (Ed.), 2005. Schweizerisches Landesforstinventar. Anleitung für die Feldaufnahmen der Erhebung 2004 - 2007. Eidg. Forschungsanstalt WSL, Birmensdorf.

OcCC, 2007. Klimaänderung und die Schweiz 2050. Erwartete Auswirkungen auf die Umwelt, Gesellschaft und Wirtschaft. OcCC and ProClim, Bern.

WSL, 2011. Schweizerisches Landesforstinventar LFI. Datenbankauszug vom 22. Dezember 2011. Markus Huber. Eidg. Forschungsanstalt WSL, Birmensdorf.

Supplemental Material

Appendix A: Classification and boundaries of the altitudinal vegetation zones

Table A1: Forest eco-regions of Switzerland and their elevation zones modified from NaiS (Frehner *et al.*, 2005). Boundaries of elevation zones are given in meters above sea level (m a.s.l.)

	Jura	**Swiss Plateau**	**Northern Pre-Alps**	**Northern Central Alps**		**High Alps**	**Southern Central Alps**	**Southern Pre-Alps**
				a	**b**			
colline	< 300	< 350	-	-	Zone of downy oak forests (NaiS)*	-	300-1000	300-1000
sub montane	300-650	350-650	350-650	< 500		-	-	-
lower montane	650-900	650-900	650-900	500-1000		-	-	-
upper montane	900-1350	900-1350	900-1350	1000-1350		-	-	-
high montane	1350-1550	>1350	1350-1600	1350-1650	<1650	600-1650	1000-1650	1000-1600 (“montane”)
subalpine	>1550	-	1600-1900	1650-1850	1650-1850	1650-1900	1650-1900	1600-1900
upper subalpine	-	-	-	> 1850	>1850	> 1900	> 1900	> 1900

*Lowest elevation zone is defined by occurrence of downy oak (Q. pubescens) forests.

Appendix B: Proportion of forest area per ecoregion and elevation zone

Table B1: Proportion of forest area per ecoregion and elevation zone. Colors indicate the decision whether a stratum was maintained (see code at the end of the table).

Jura	**number of plots**	**proportion of area (%)**
total	**1048**	
colline	1	0.1
sub montane	300	28.6
lower montane	279	26.6
upper montane	417	39.8
high montane	51	4.9

Northern Central Alps b	**number of plots**	**proportion of area (%)**
total	678	
colline	38	5.6
high montane	444	65.5
subalpine	123	18.1
upper subalpine	73	10.8

Swiss Plateau	**number of plots**	**proportion of area (%)**
total	**1609**	
colline	18	1.1
sub montane	950	59.04
lower montane	489	30.4
upper montane	152	9.4

High Alps	**number of plots**	**proportion of area (%)**
total	**561**	
high montane	178	31.7
subalpine	207	36.9
upper subalpine	176	31.4

Northern Pre-Alps	**number of plots**	**proportion of area (%)**
total	**1739**	
sub montane	109	6.3
lower montane	240	13.8
upper montane	840	48.3
high montane	384	22.1
subalpine	162	9.3
upper subalpine	4	0.2

Southern Central Alps	**number of plots**	**proportion of area (%)**
total	**302**	
colline	24	7.9
high montane	167	55.3
subalpine	73	24.2
upper subalpine	38	12.6

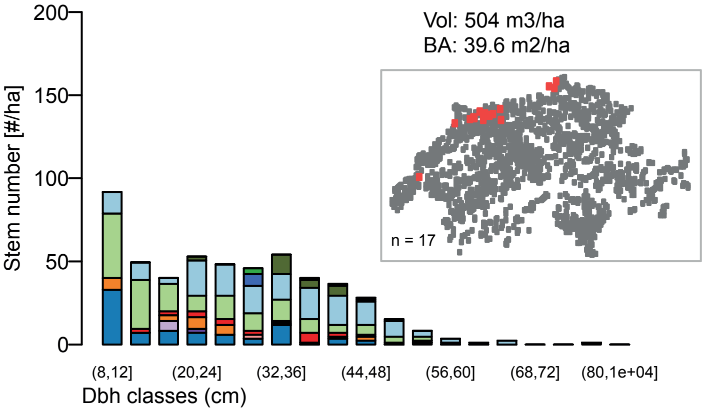
Northern Central Alps a	number of plots	proportion of area (%)
total	**243**	
sub montane	3	1.2
lower montane	77	31.7
upper montane	72	29.6
high montane	53	21.8
subalpine	31	12.7
upper subalpine	7	2.9

Southern Pre-Alps	number of plots	proportion of area (%)
total	**640**	
colline	293	45.8
montane	267	41.7
subalpine	64	10.00
upper subalpine	16	2.5

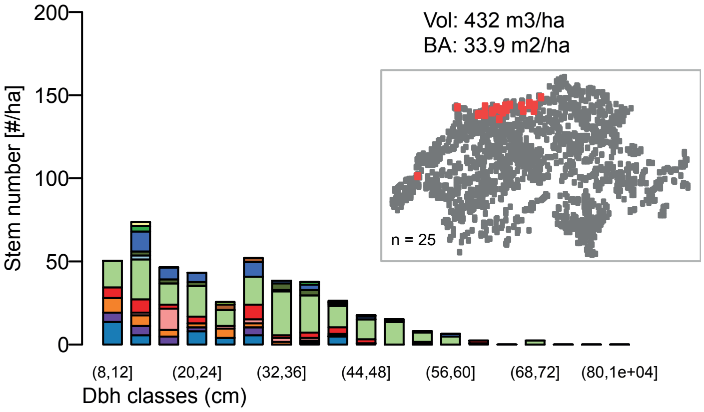
Color codes:	Decision:
well below 10%	Omitted
slightly below 10%	Retained
above 10%	Retained

Appendix C: Overview on typical Swiss forest stands (strata)

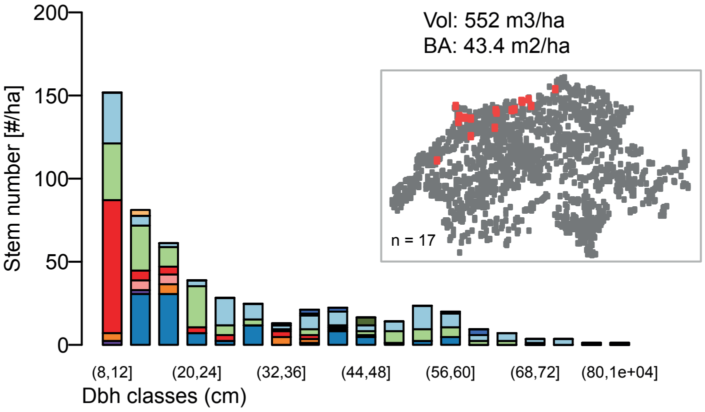
Stratum J_SM_1a



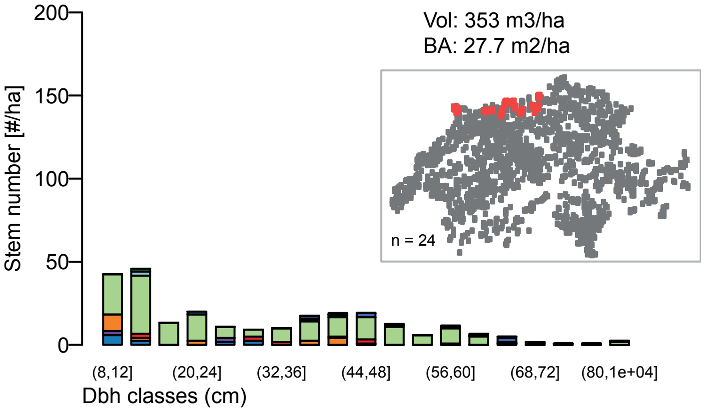
Stratum J_SM_1b



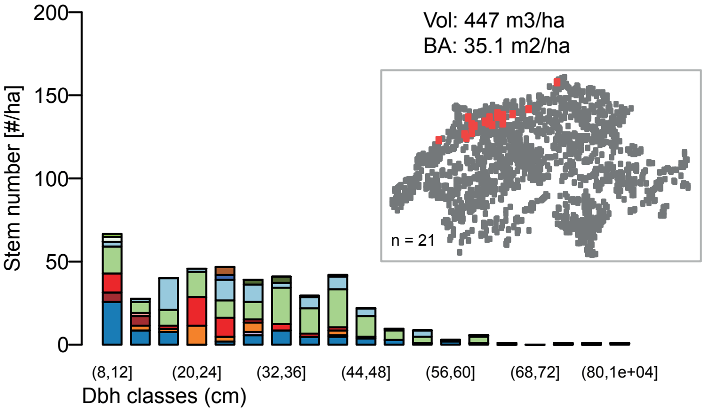
Stratum J_SM_2a



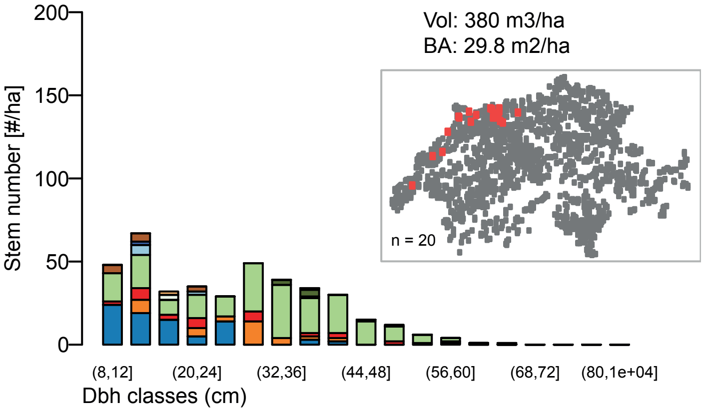
Stratum J_SM_2b



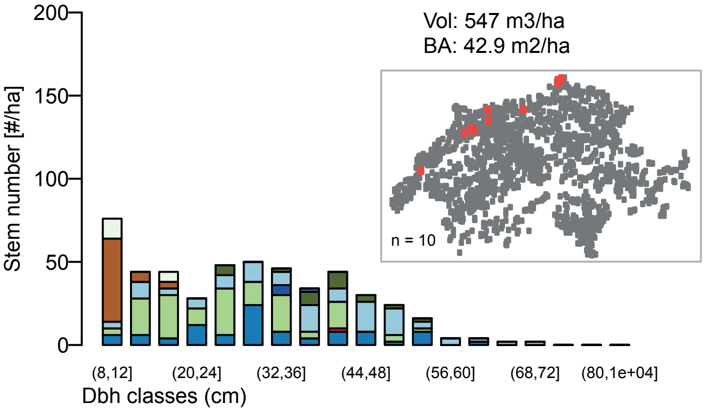
Stratum J_LM_1a



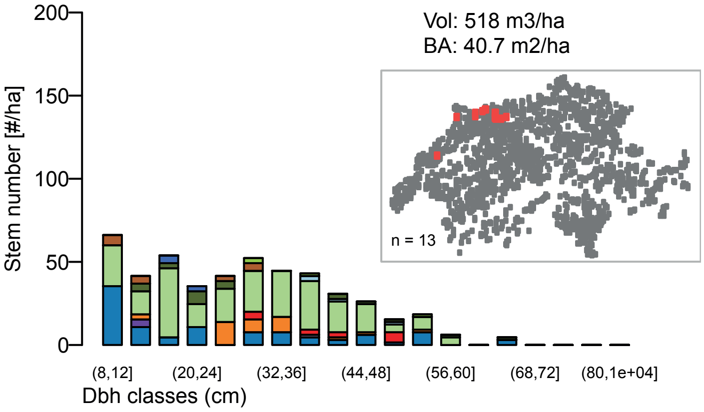
Stratum J_LM_1b

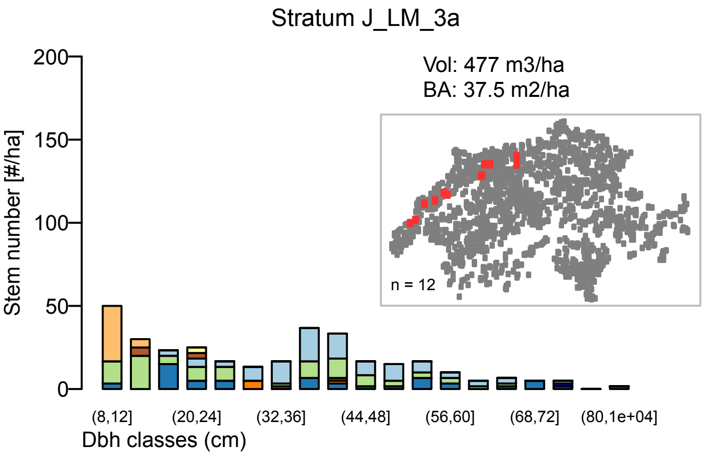


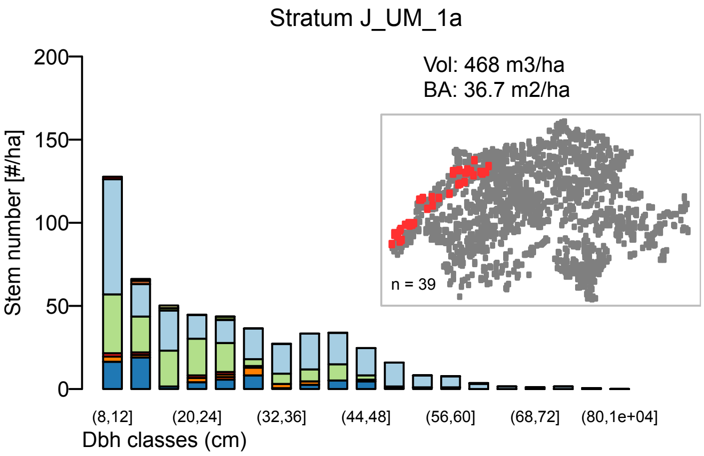
Stratum J_LM_2a

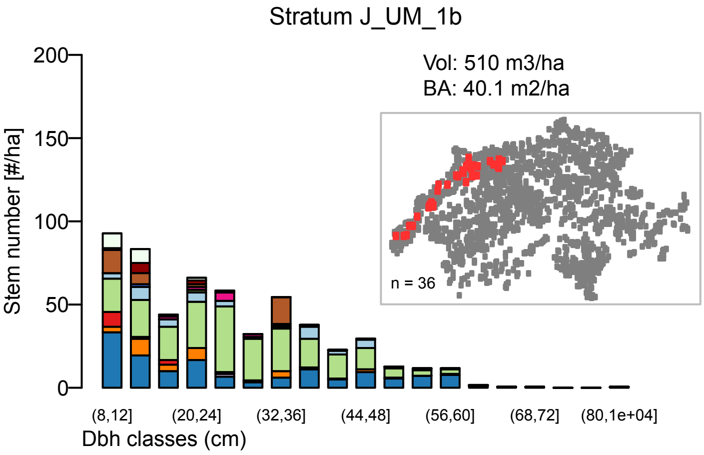


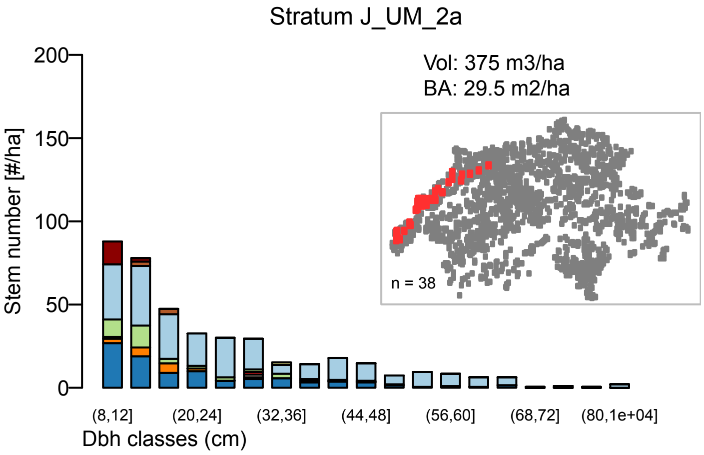
Stratum J_LM_2b

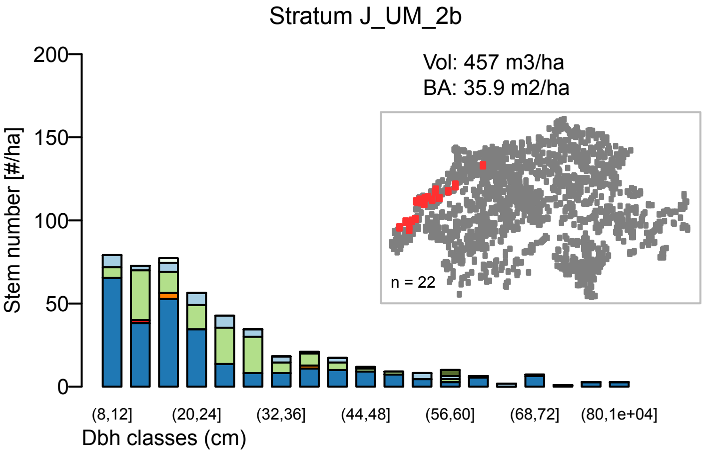


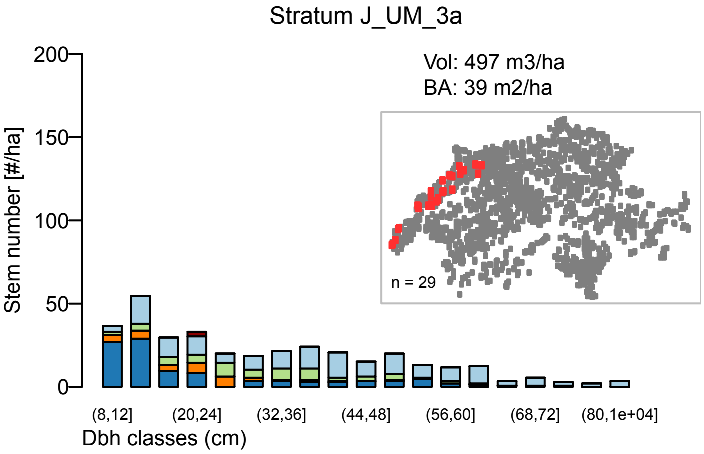

Stratum J_LM_3a
Vol: 477 m3/ha
BA: 37.5 m2/ha
n = 12
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

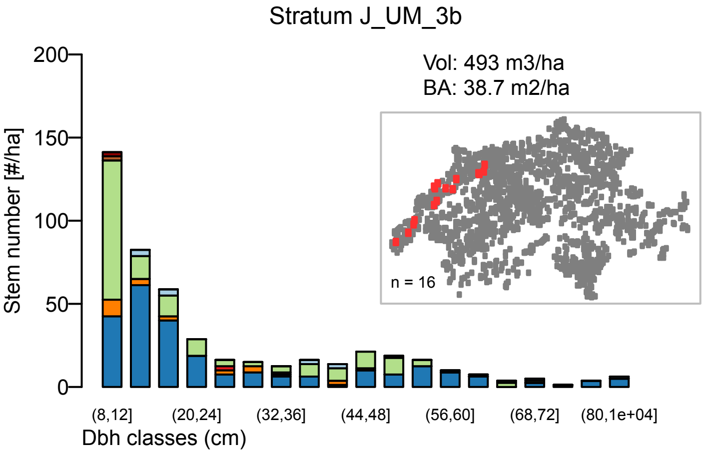

Stratum J_UM_1a
Vol: 468 m3/ha
BA: 36.7 m2/ha
n = 39
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

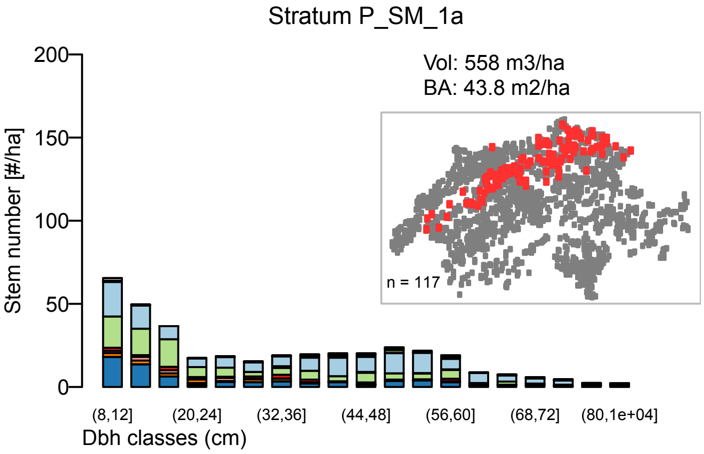

Stratum J_UM_1b
Vol: 510 m3/ha
BA: 40.1 m2/ha
n = 36
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum J_UM_2a
Vol: 375 m3/ha
BA: 29.5 m2/ha
n = 38
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

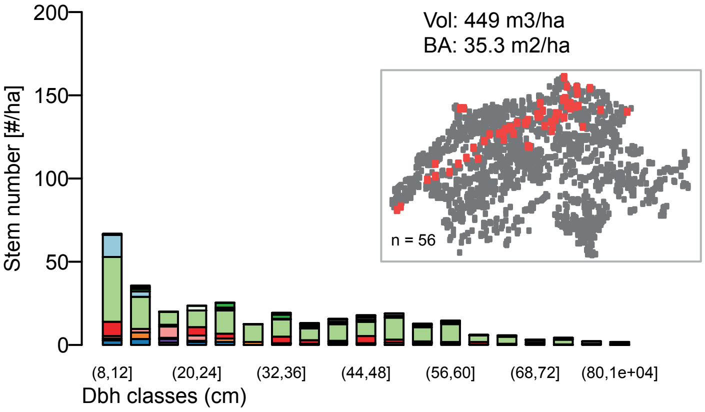

Stratum J_UM_2b
Vol: 457 m3/ha
BA: 35.9 m2/ha
n = 22
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum J_UM_3a
Vol: 497 m3/ha
BA: 39 m2/ha
n = 29
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

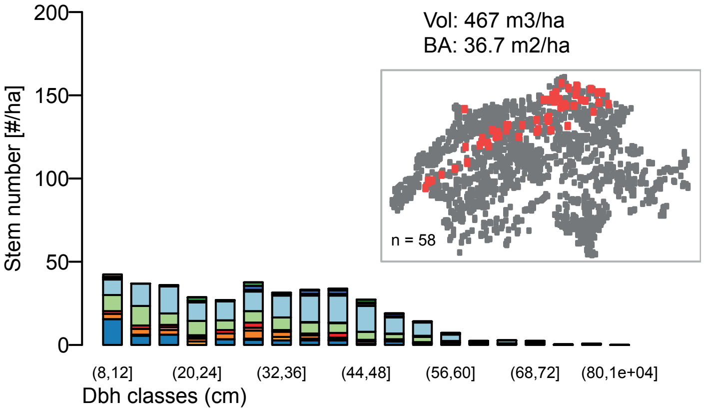

Stratum J_UM_3b
Vol: 493 m3/ha
BA: 38.7 m2/ha
n = 16
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum P_SM_1a
Vol: 558 m3/ha
BA: 43.8 m2/ha
n = 117
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

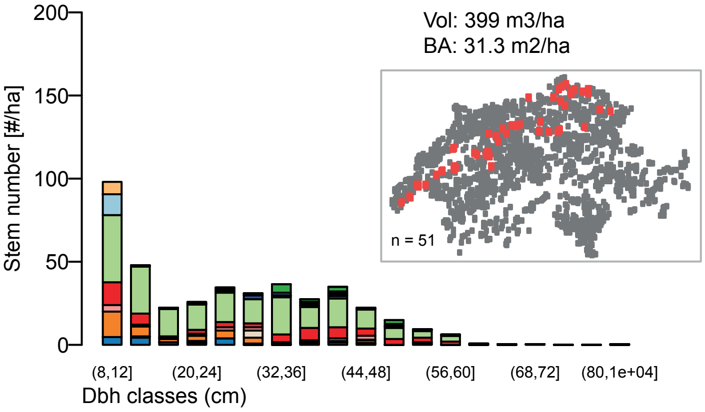
Stratum P_SM_1b



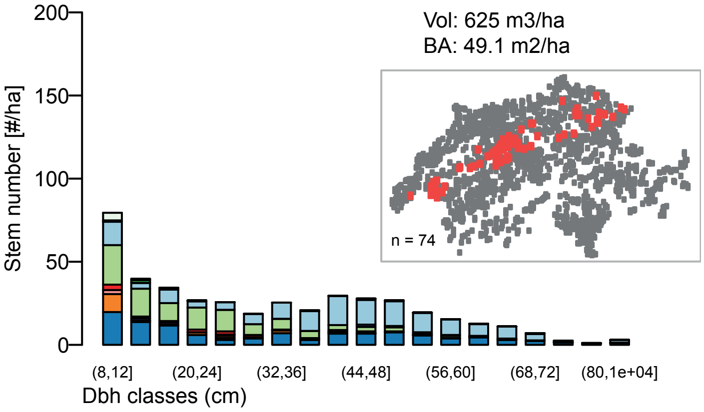
Stratum P_SM_2a



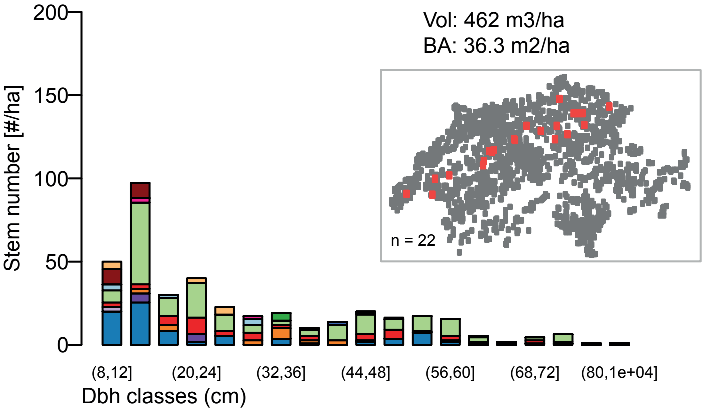
Stratum P_SM_2b



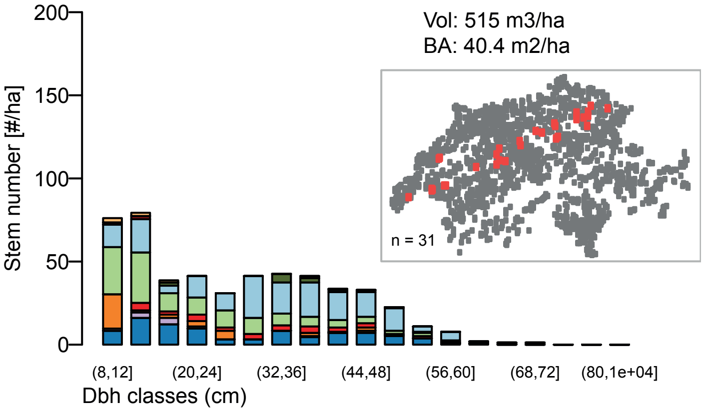
Stratum P_LM_1a



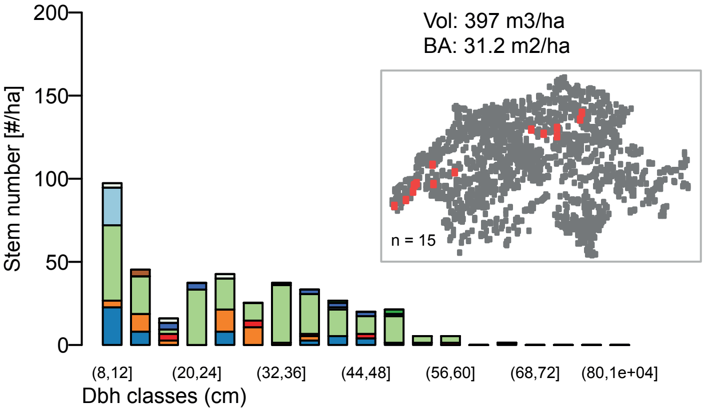
Stratum P_LM_1b



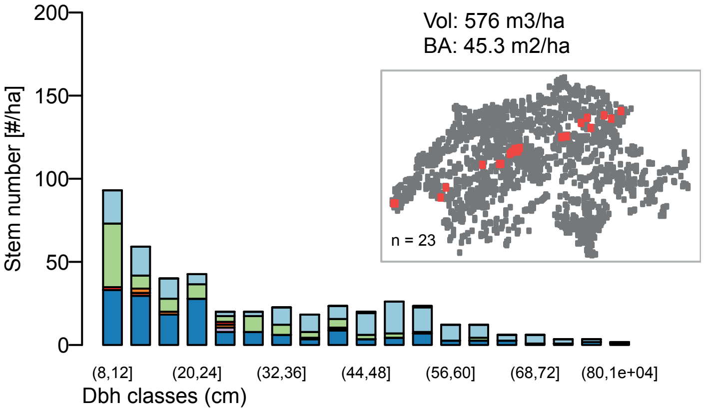
Stratum P_LM_2a

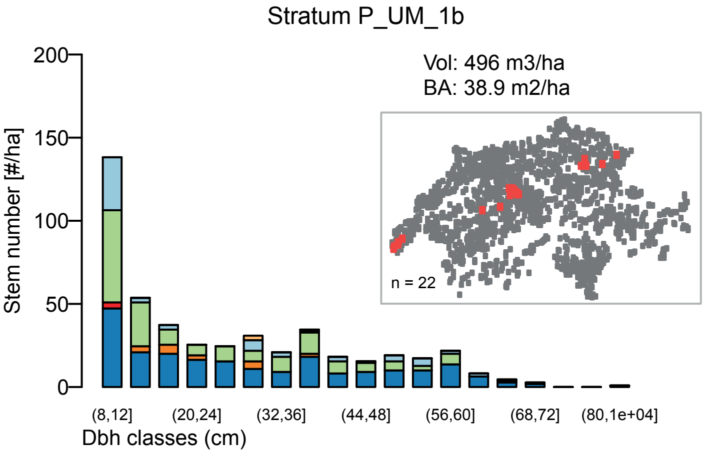


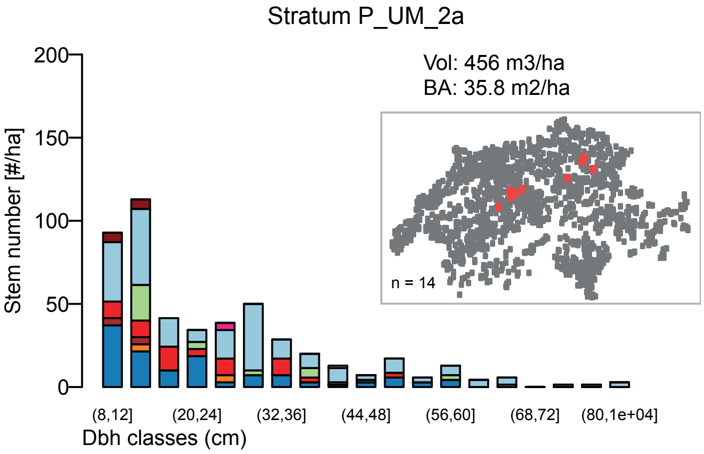
Stratum P_LM_2b

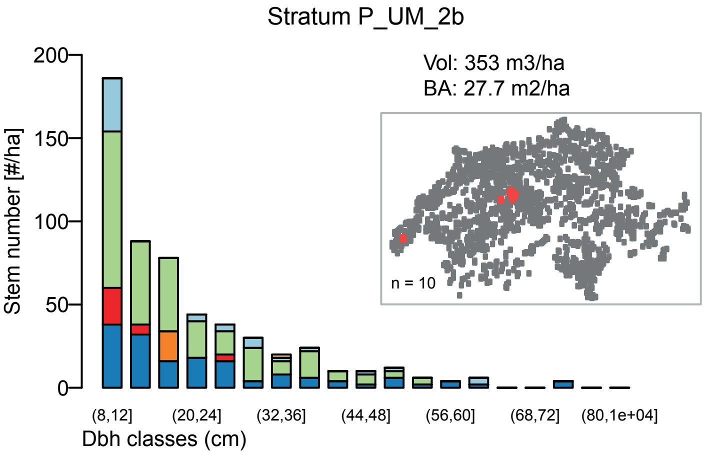


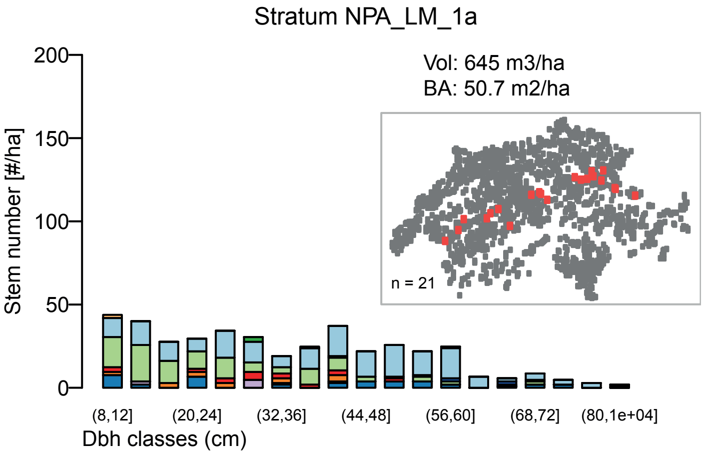
Stratum P_UM_1a

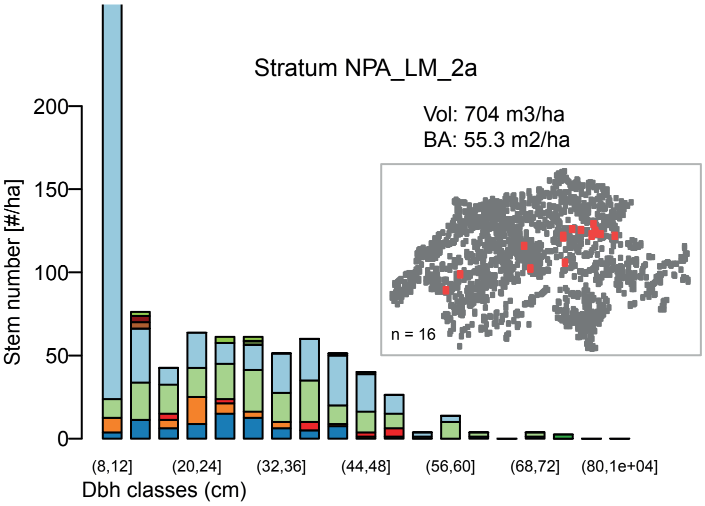


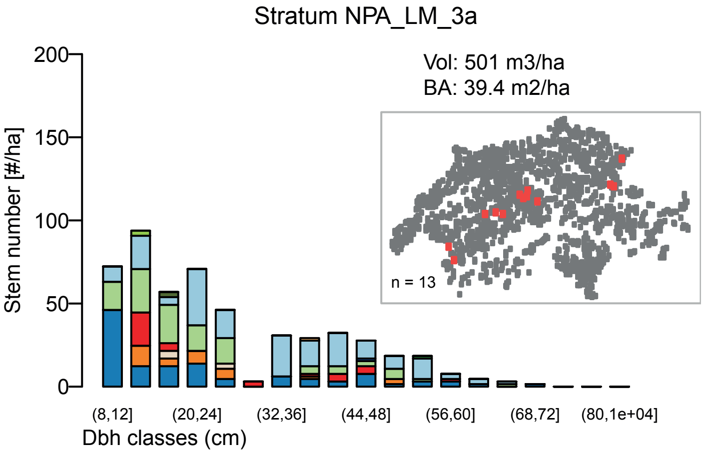

Stratum P_UM_1b
Vol: 496 m3/ha
BA: 38.9 m2/ha
n = 22
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

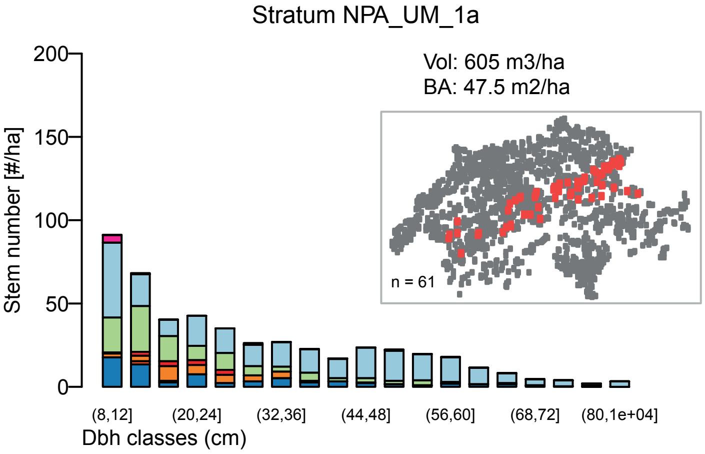

Stratum P_UM_2a
Vol: 456 m3/ha
BA: 35.8 m2/ha
n = 14
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

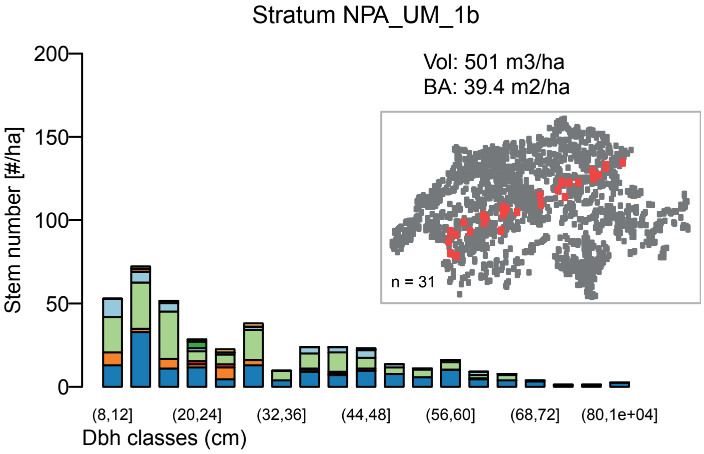

Stratum P_UM_2b
Vol: 353 m3/ha
BA: 27.7 m2/ha
n = 10
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

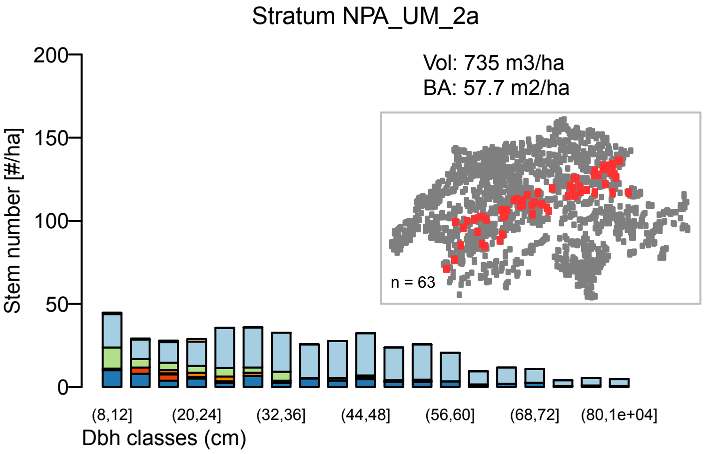

Stratum NPA_LM_1a
Vol: 645 m3/ha
BA: 50.7 m2/ha
n = 21
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

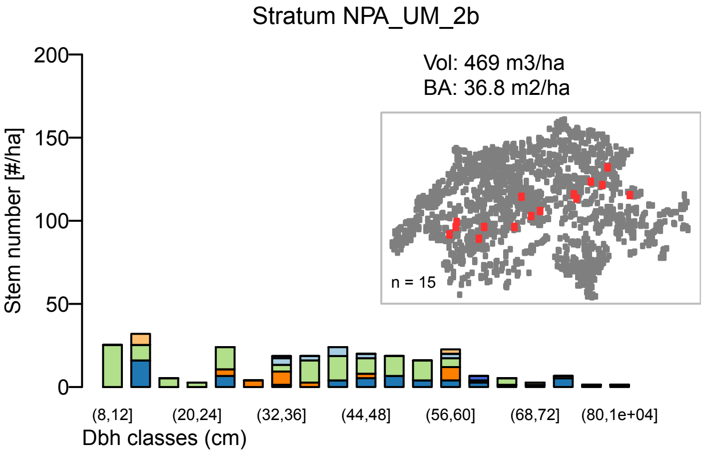

Stratum NPA_LM_2a
Vol: 704 m3/ha
BA: 55.3 m2/ha
n = 16
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

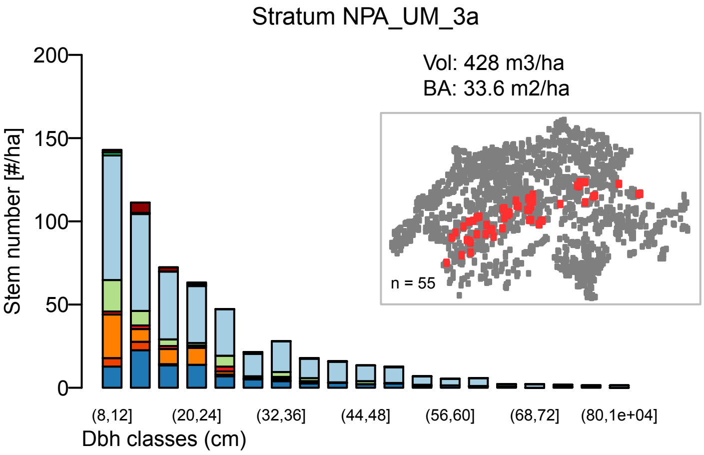

Stratum NPA_LM_3a
Vol: 501 m3/ha
BA: 39.4 m2/ha
n = 13
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

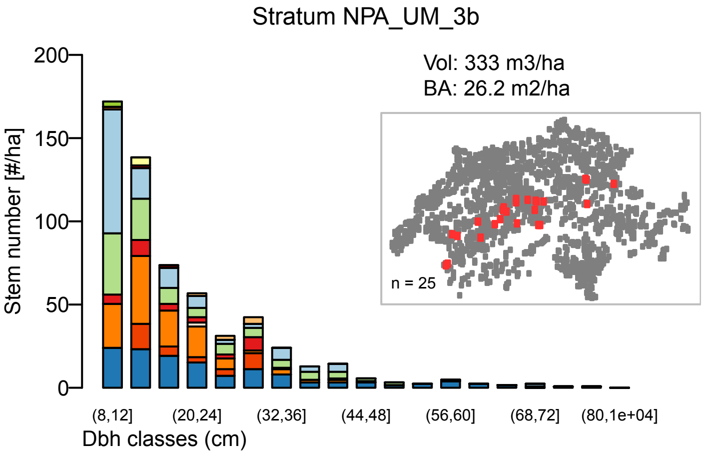

Stratum NPA_UM_1a
Vol: 605 m3/ha
BA: 47.5 m2/ha
n = 61
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

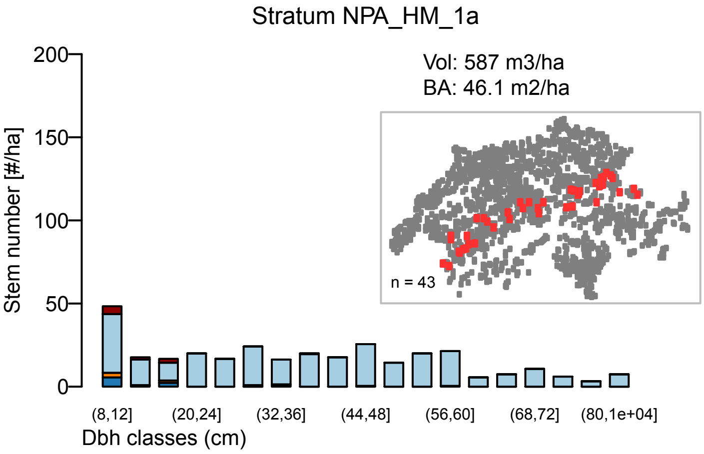

Stratum NPA_UM_1b
Vol: 501 m3/ha
BA: 39.4 m2/ha
n = 31
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

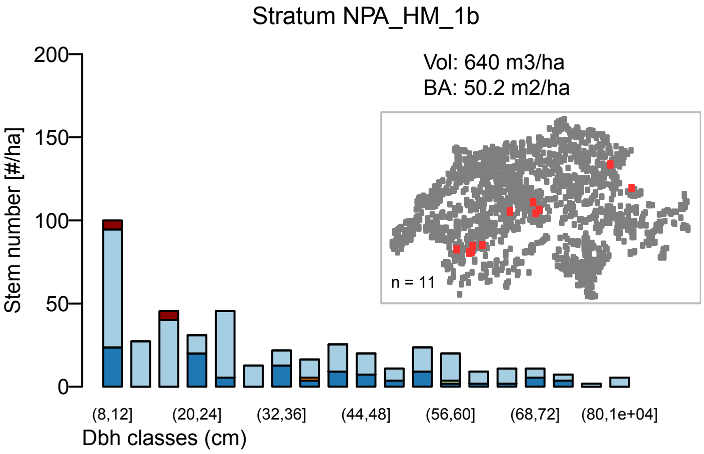

Stratum NPA_UM_2a
Vol: 735 m3/ha
BA: 57.7 m2/ha
n = 63
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

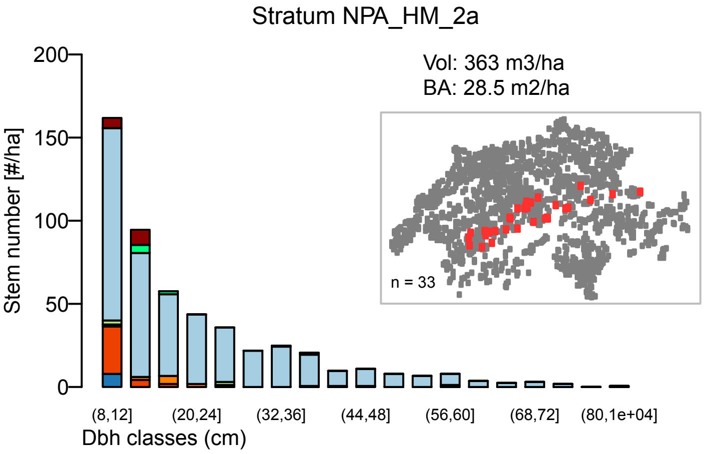

Stratum NPA_UM_2b
Vol: 469 m3/ha
BA: 36.8 m2/ha
n = 15
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

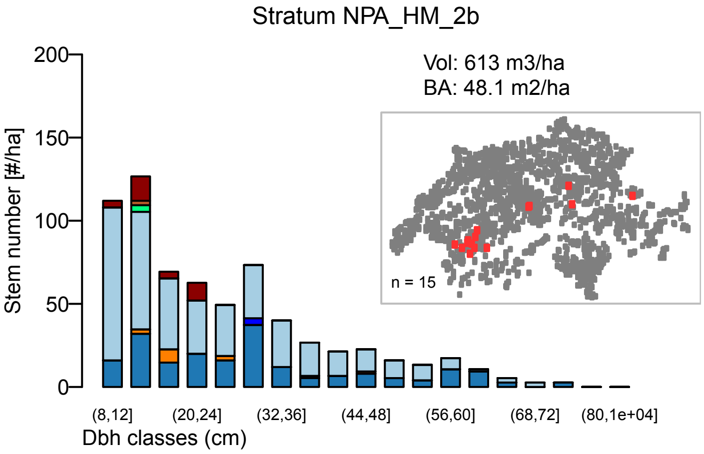

Stratum NPA_UM_3a
Vol: 428 m3/ha
BA: 33.6 m2/ha
n = 55
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum NPA_UM_3b
Vol: 333 m3/ha
BA: 26.2 m2/ha
n = 25
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

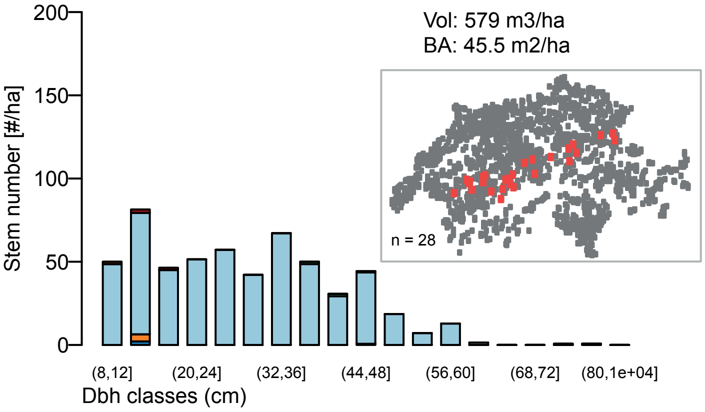

Stratum NPA_HM_1a
Vol: 587 m3/ha
BA: 46.1 m2/ha
n = 43
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum NPA_HM_1b
Vol: 640 m3/ha
BA: 50.2 m2/ha
n = 11
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

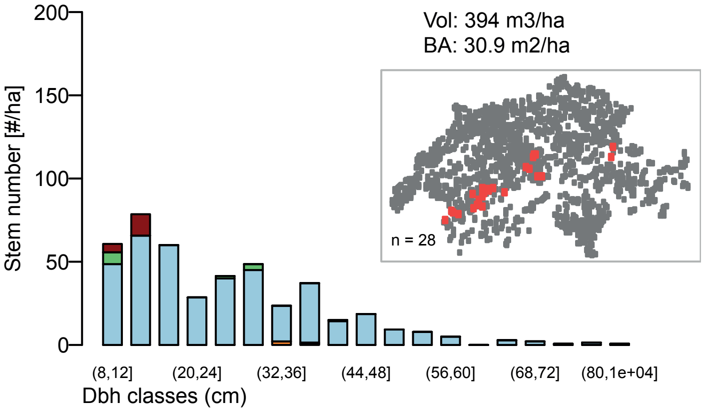

Stratum NPA_HM_2a
Vol: 363 m3/ha
BA: 28.5 m2/ha
n = 33
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum NPA_HM_2b
Vol: 613 m3/ha
BA: 48.1 m2/ha
n = 15
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

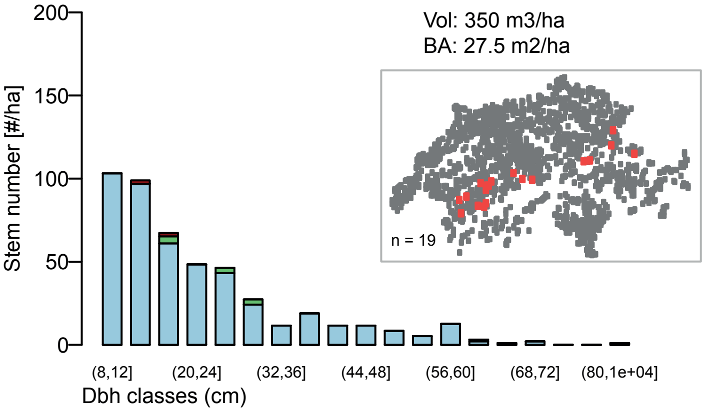
Stratum NPA_HM_3a



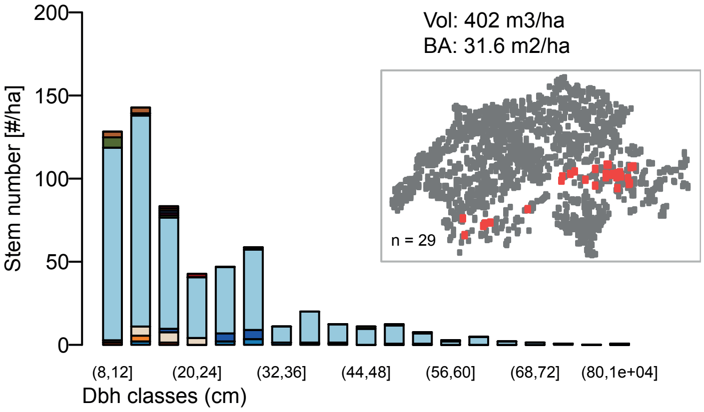
Stratum NPA_SA_1



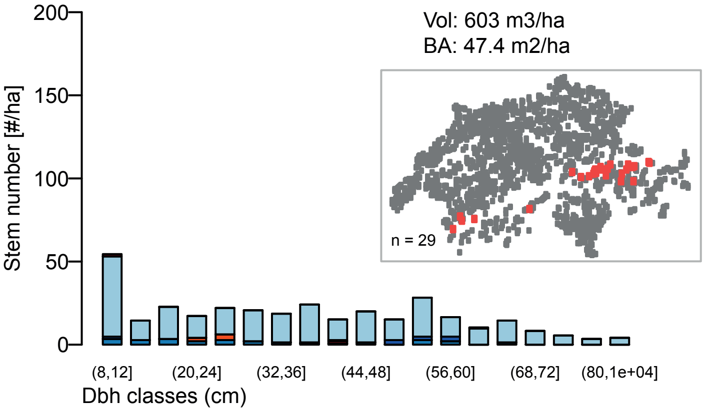
Stratum NPA_SA_2



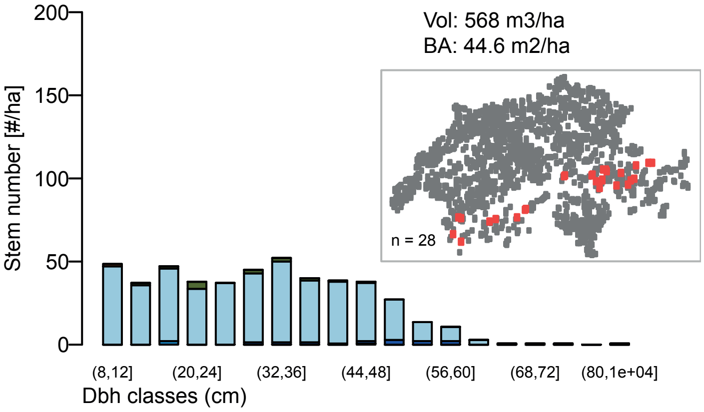
Stratum NCA_HM_1



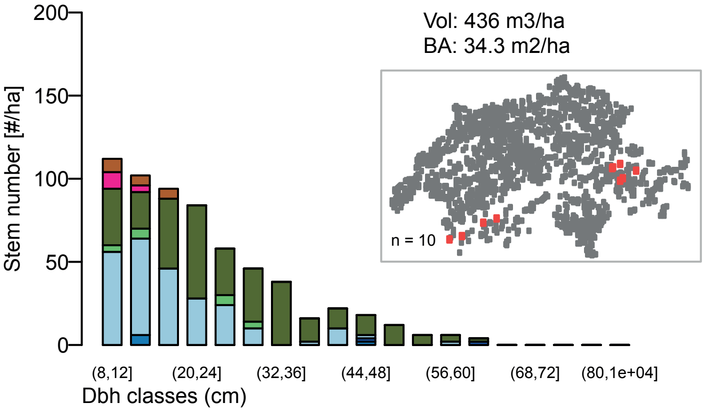
Stratum NCA_HM_2



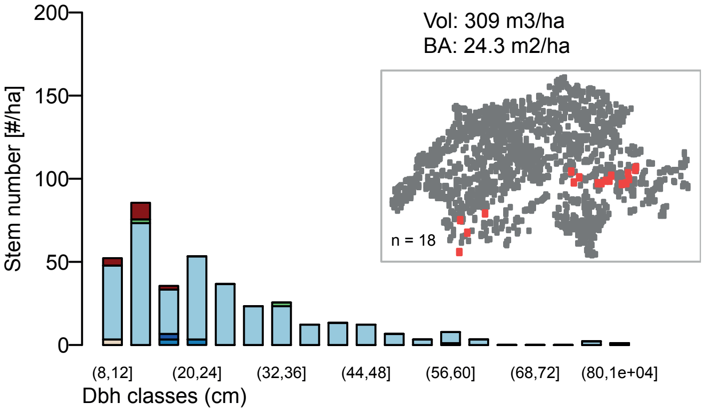
Stratum NCA_HM_3

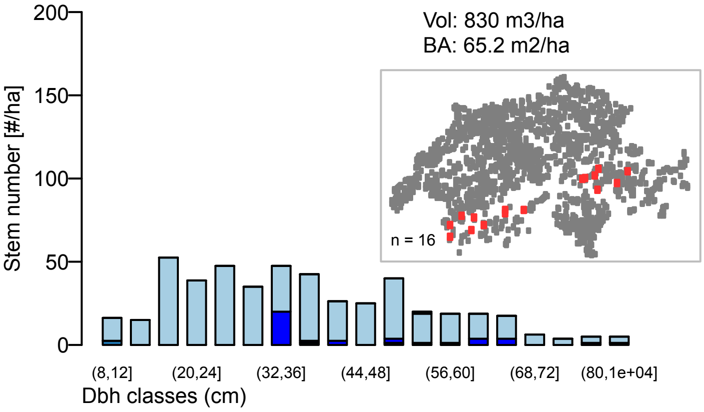


Stratum NCA_SA_3

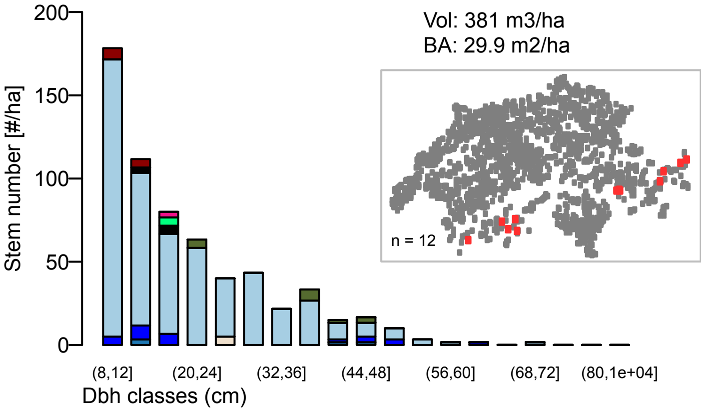


Stratum NCA_SA_1

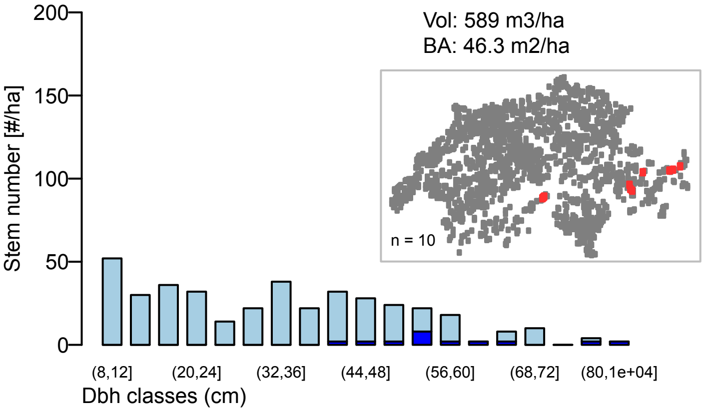




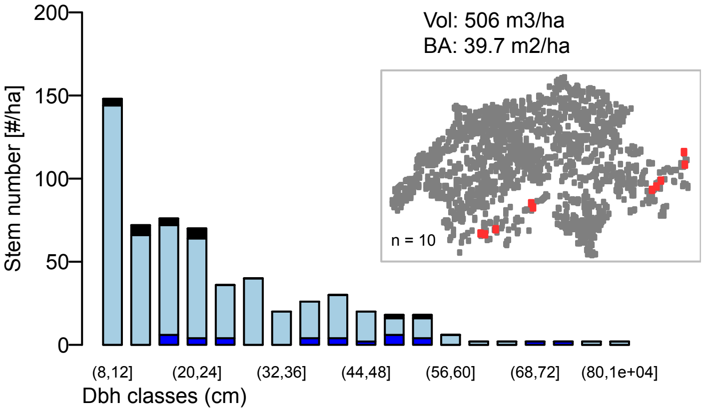
Stratum NCA_SA_2



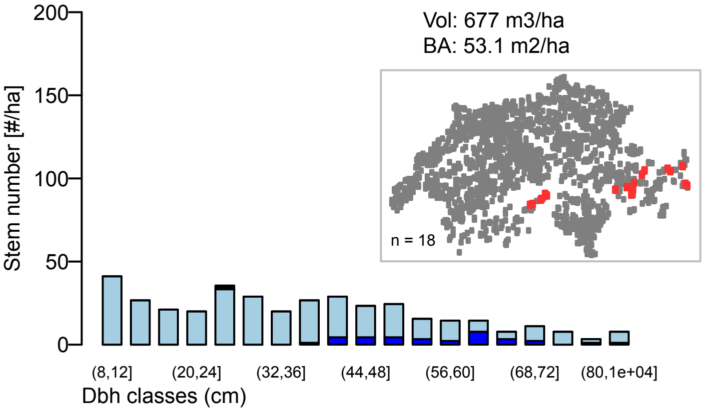
Stratum HA_HM_1



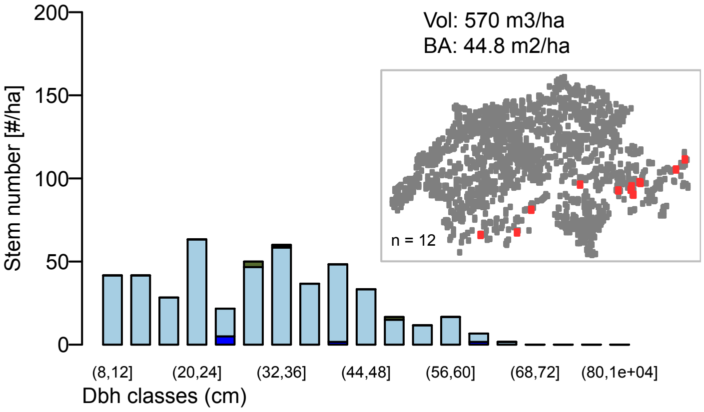
Stratum HA_HM_2



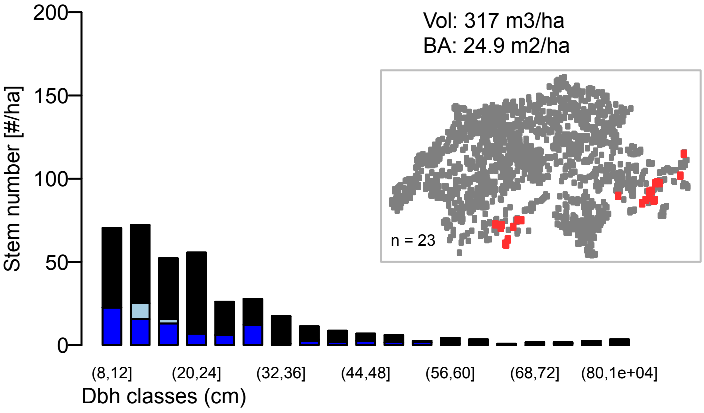
Stratum HA_SA_1



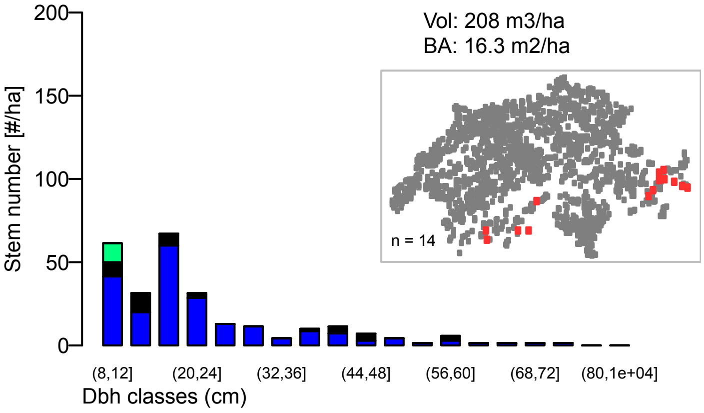
Stratum HA_SA_2



Stratum HA_SA_3

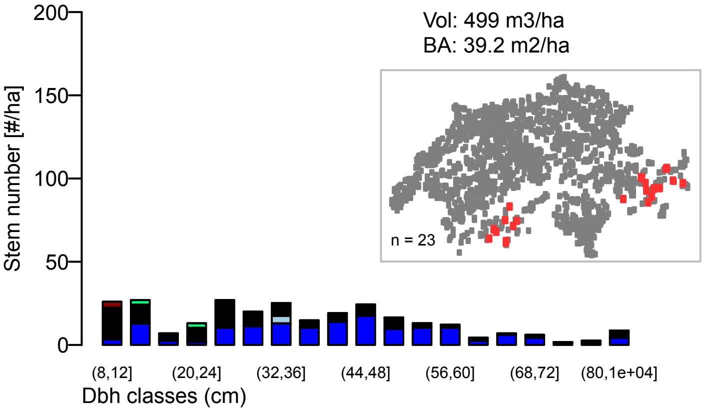


Stratum HA_US_1a

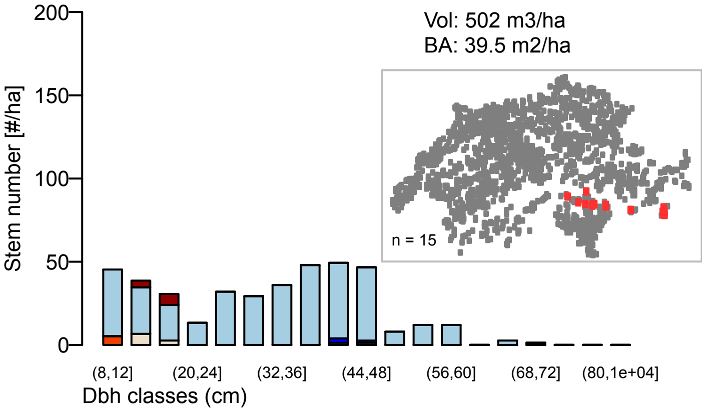


Stratum HA_US_1b

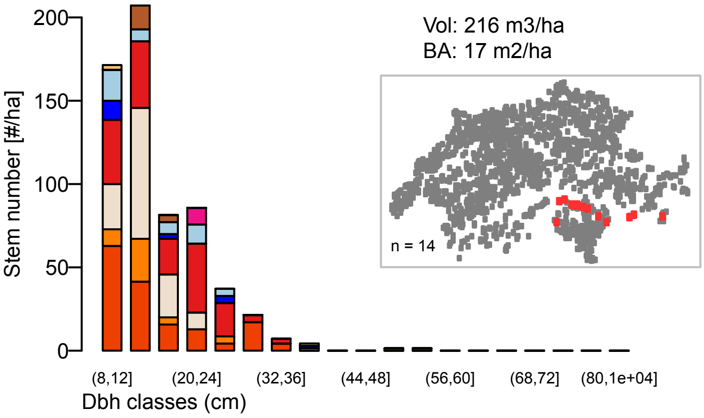
Stratum HA_US_2



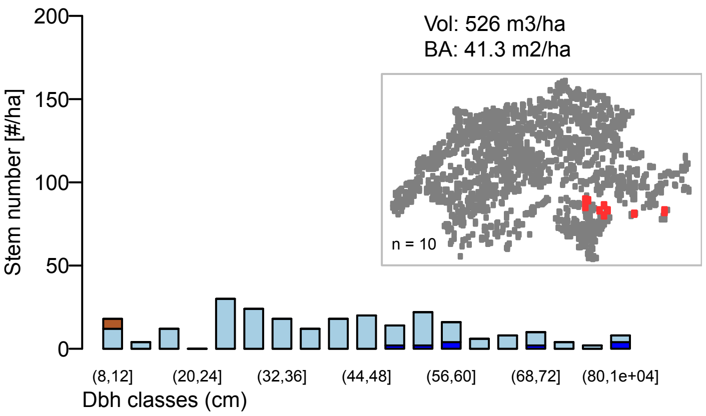
Stratum SCA_HM_1



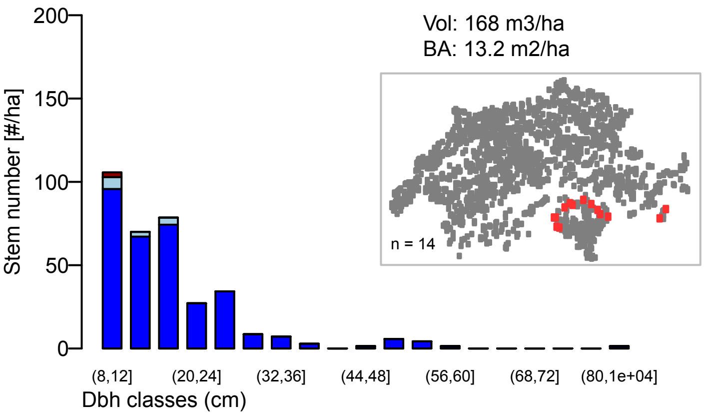
Stratum SCA_HM_2



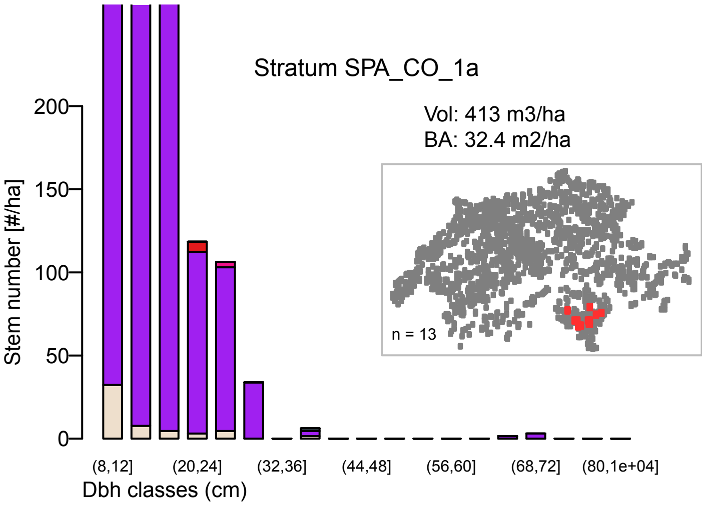
Stratum SCA_HM_3



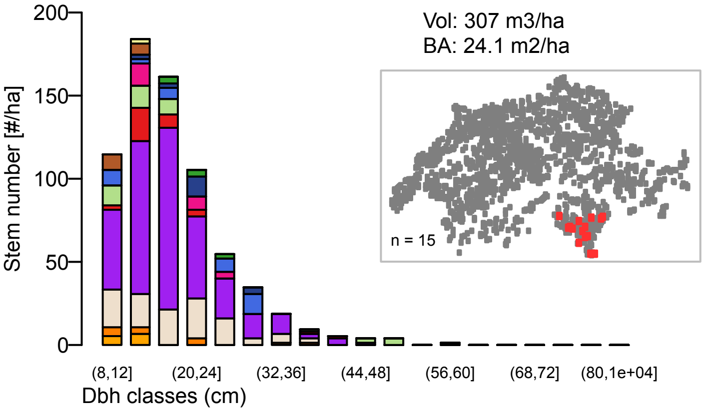
Stratum SCA_SA_1



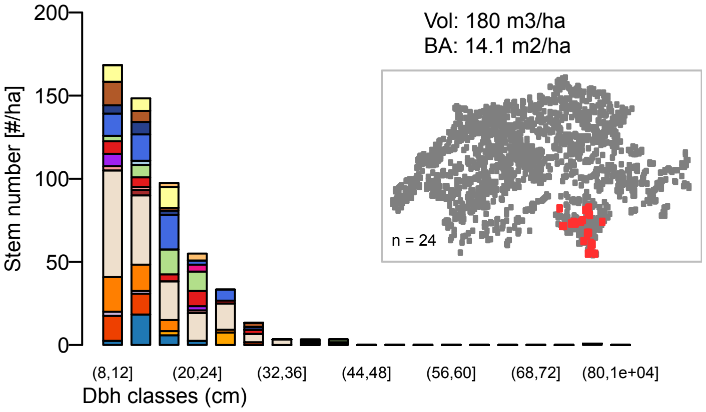
Stratum SPA_CO_1a

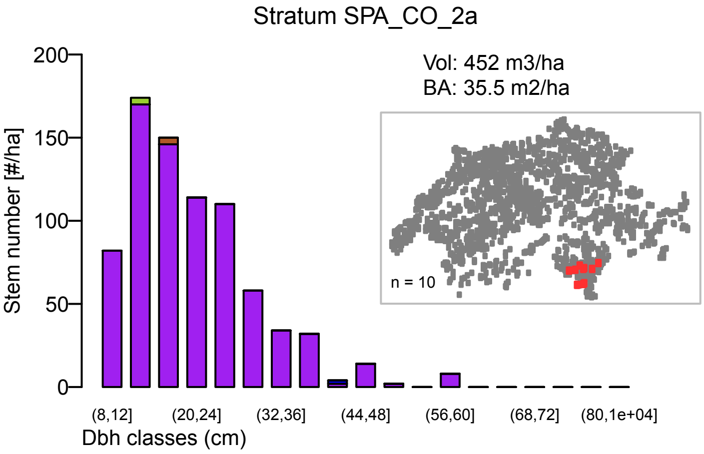


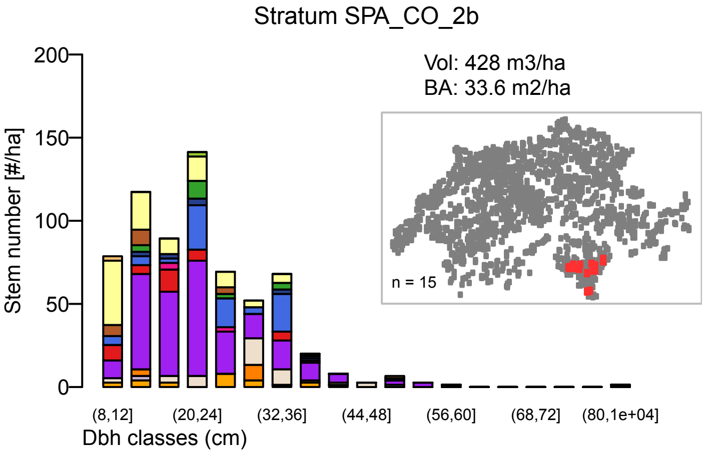
Stratum SPA_CO_1b

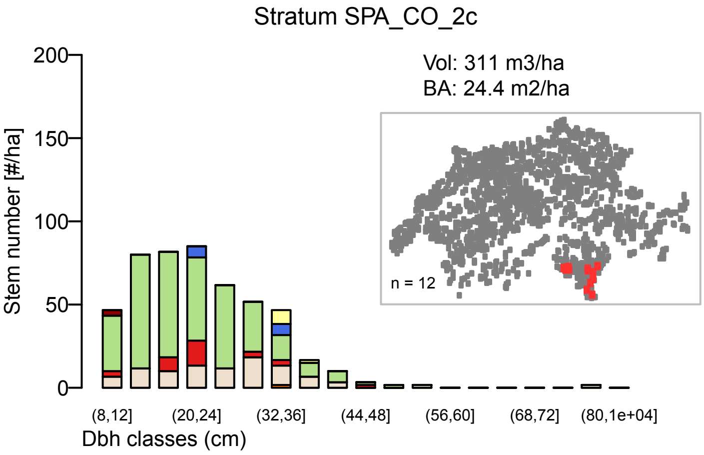


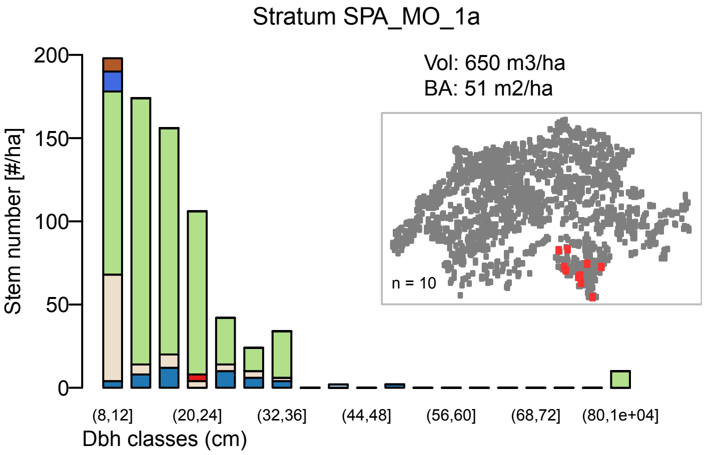
Stratum SPA_CO_1c

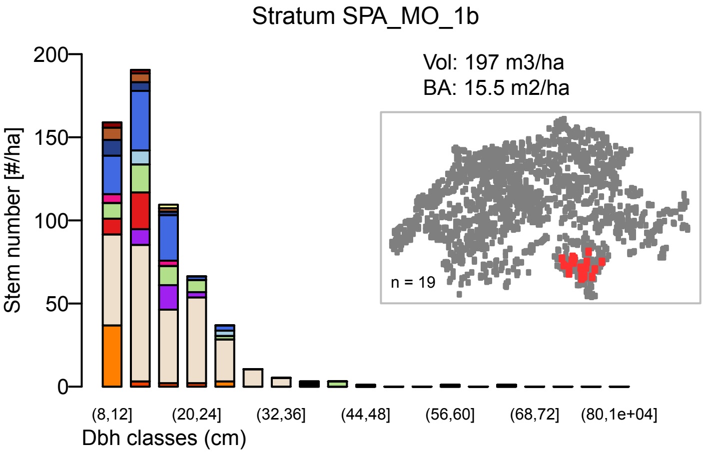


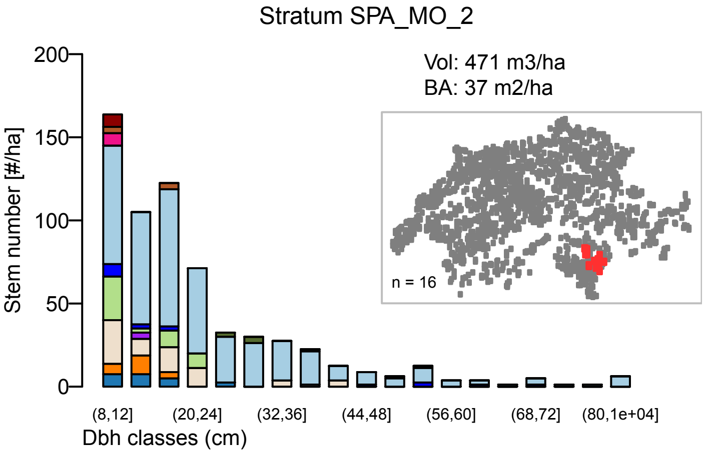

Stratum SPA_CO_2a
Vol: 452 m3/ha
BA: 35.5 m2/ha
n = 10
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

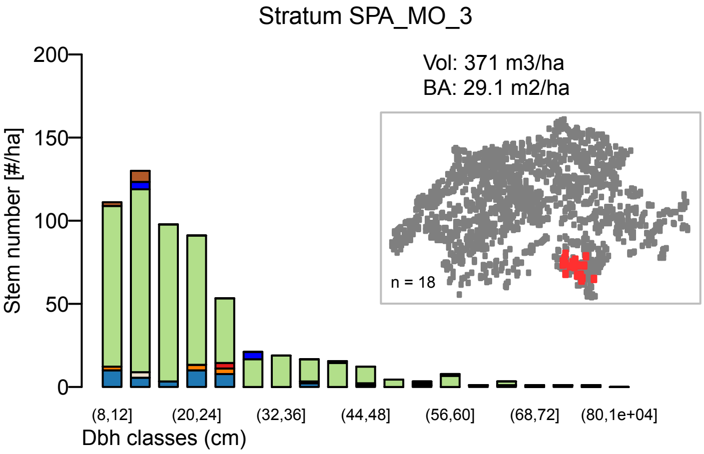

Stratum SPA_CO_2b
Vol: 428 m3/ha
BA: 33.6 m2/ha
n = 15
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)

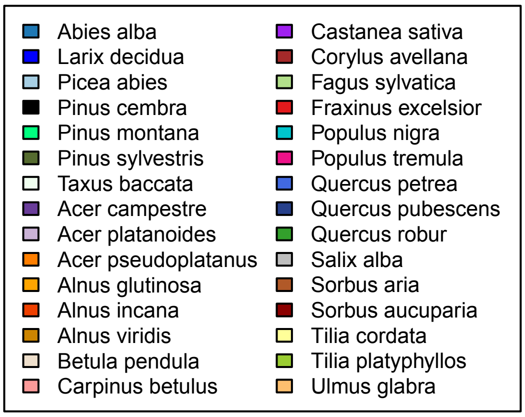

Stratum SPA_CO_2c
Vol: 311 m3/ha
BA: 24.4 m2/ha
n = 12
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum SPA_MO_1a
Vol: 650 m3/ha
BA: 51 m2/ha
n = 10
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum SPA_MO_1b
Vol: 197 m3/ha
BA: 15.5 m2/ha
n = 19
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum SPA_MO_2
Vol: 471 m3/ha
BA: 37 m2/ha
n = 16
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Stratum SPA_MO_3
Vol: 371 m3/ha
BA: 29.1 m2/ha
n = 18
Stem number [#/ha]
0
50
100
150
200
(8,12]
(20,24]
(32,36]
(44,48]
(56,60]
(68,72]
(80,1e+04]
Dbh classes (cm)


Abies alba
Larix decidua
Picea abies
Pinus cembra
Pinus montana
Pinus sylvestris
Taxus baccata
Acer campestre
Acer platanoides
Acer pseudoplatanus
Alnus glutinosa
Alnus incana
Alnus viridis
Betula pendula
Carpinus betulus
Castanea sativa
Corylus avellana
Fagus sylvatica
Fraxinus excelsior
Populus nigra
Populus tremula
Quercus petrea
Quercus pubescens
Quercus robur
Salix alba
Sorbus aria
Sorbus aucuparia
Tilia cordata
Tilia platyphyllos
Ulmus glabra

4

Assessing forest sensitivity to climate change: Accurate reflection of local stand and site characteristics is key

Bircher, N., Cailleret, M., Huber, M., Bugmann, H.

Manuscript; in preparation for Global Change Biology

Abstract

Climate-induced demographic shifts in forests and the sustainable provision of forest ecosystem services have been the target of many modeling projects. However, large uncertainty about local impacts over larger areas remains as most studies adopt a large-scale (i.e. national to continental level) approach and lack sufficient fine-grained resolution, or evaluated a few sites only. Thus, decision makers still lack essential knowledge to plan and develop adaptive management strategies. We provide a comprehensive, high-resolution assessment on forest sensitivity to climate change so as to detail variation in forest stand response due to local conditions, and to evaluate the potential of current management practices. Switzerland was chosen as a case study because it features a complex topography with a wide variety of forest types typical for Central Europe. A stratification of National Forest Inventory (NFI) plots identified 71 strata that reflect typical forest stand structures in different regions and elevation zones. The development of these strata was simulated until 2100 with two versions of the forest succession model ForClim for different conditions, including current "best practice" management and a number of downscaled climate scenarios based on an A2 emission scenario. Legacies of past management and land-use were considered by initializing the model with tree data of NFI plots. Simulation results revealed a mainly negative response of forest strata to climate change, but the high variability in its magnitude demonstrates the importance of drivers of small-scale (i.e., local and stand-specific) forest dynamics such as regional climate, local elevation gradients and current stand composition. Current management regimes showed potential to mitigate adverse impacts of climate change but their effect varied among strata and with forest ecosystem services. We conclude that 1) the development of new adaptive management measures needs to be site- and objective-specific, 2) quantitative, model-based assessments can provide a reliable basis for such efforts only if they accommodate small-scale forest stand characteristics.

Forest gap model

Mortality; Tree ring; Inventory data; Climate change; Forest succession; Modeling

Introduction

Physiological and demographic impacts of anthropogenic climate change (CC) on forest ecosystems are already detectable (e.g., Kullman, 2002; Esper and Schweingruber, 2004; Allen *et al.*, 2010; Rigling *et al.*, 2013). They are likely to substantially influence future forest dynamics (e.g., Jolly *et al.*, 2005) and ecosystem services (ES) (MEA, 2005). Obviously, the sensitivity of forests to CC is highly heterogeneous and depends on several abiotic and biotic factors (cf. Lindner *et al.*, 2010). Regional climate and CC projections often differ remarkably (e.g., CH2011, 2011). In mountain regions, topography plays a key role as it strongly influences local climate (e.g., Engler *et al.*, 2011; Elkin *et al.*, 2013b), soil water regime and light availability (e.g., Austin and Van Niel, 2011), which drive forest dynamics at the stand level (e.g., Zierl and Bugmann, 2007; Hlasny *et al.*, 2011; Seidl *et al.*, 2011a). Edaphic properties such as nitrogen availability (Coudun *et al.*, 2006; Bontemps *et al.*, 2011) or soil pH (Bertrand *et al.*, 2012) contribute to differences in local and stand-specific tree species performance. Biotic interactions such as light competition (e.g., Meier *et al.*, 2010) are further important variables to explain forest structure at the stand scale. In addition, past forest management and land-use have markedly shaped many forests (Bürgi *et al.*, 2013) and often resulted in highly artificial states, e.g. by the promotion or suppression of tree species and stages of forest development (Bürgi, 1998; Motta and Edouard, 2005). Such legacies can strongly impact the future development of forests at the local scale (Kulakowski *et al.*, 2011; Temperli *et al.*, 2012) and require careful consideration when their sensitivity to CC is assessed (cf. Motta and Edouard, 2005; Weber *et al.*, 2008).

Nevertheless, studies that project future forest development often operate with rather coarse model resolution of tens to hundreds of kilometers (e.g., Aber *et al.*, 2001; Peng *et al.*, 2009; Naudts *et al.*, 2014), aggregate results across sub continental regions (e.g., Wamelink *et al.*, 2009; Reyer *et al.*, 2014) or combine these two approaches (e.g., Morales *et al.*, 2007; Galbraith *et al.*, 2010; Hanewinkel *et al.*, 2013). Alternatively, many studies have considered a few sites only (e.g., Elkin *et al.*, 2013b; Rasche *et al.*, 2013; Hlasny *et al.*, 2014). These approaches hinder an adequate assessment of future forest dynamics and ES at the regional scale. On the one hand, the quantification of many ES (e.g. timber production, rockfall or avalanche protection; Elkin *et al.*, 2013b) requires detailed information on forest structure at the stand scale (e.g., Bebi *et al.*, 2001), which cannot be considered in most landscape or global vegetation models (e.g., Hansen *et al.*, 2001). On the other hand, the sensitivity of ecosystems estimated at the continental scale (i.e., hundreds to thousands of kilometers) based on aggregated data may differ considerably from conclusions made at the local level (i.e., <10 km; O'Brien *et al.*, 2004; Elkin *et al.*, 2013a). This is especially problematic for the development of management strategies adapted to future climate, which are usually planned from the local to regional level (Füssel and Klein, 2006).

To date, the challenge to provide a high-resolution, comprehensive assessment of forest dynamics under future climate remains (Lindner *et al.*, 2010). We aim to fill this gap by examining the sensitivity of forest stands to CC that are typical for Switzerland. This country is an ideal case study, as it features a complex topography with highly different bioclimates (OcCC, 2007; Bugmann *et al.*, 2014) where a high diversity of forest ecosystems has evolved, ranging from Mediterranean Scots pine-oak forests to temperate spruce-fir-beech forests and subalpine larch-Stone pine forests (Frehner *et al.*, 2005), which are representative for a wide range of forest types in Central Europe. Forest management is using a broad set of strategies and techniques (cf. Rasche *et al.*, 2011; see also Leibundgut, 1949) serving a wide range of purposes, from even-aged productive fir-beech and spruce stands to protection forests with larch, spruce and Stone pine (Frehner *et al.*, 2005; Brändli, 2010).

We provide a detailed assessment on the sensitivity of typical Swiss forests to CC across a variety of eco-regions (i.e., predefined set of Swiss forest regions with differing topographical and climatic characteristics; Frehner *et al.*, 2005) and elevation zones. Seventy-one typical forest stands were identified using a quantitative stratification based on Swiss National Forest Inventory (NFI) data. Their development until 2100 was simulated with the forest succession model ForClim (Bugmann, 1996; Rasche *et al.*, 2011) under four different situations: (1) current “best practice” management regimes; (2) no management; combined with (3) current climatic conditions (“baseline”) and (4) considering CC. An A2 greenhouse gas emission scenario was chosen for considering cases of strong climate change whereas the variability in CC projections was taken into account by using 11 climate scenarios. The uncertainty of model projections was addressed by discussing the results of two different model versions.

Specifically, we aim to (1) determine how the impact of CC on future forest dynamics would vary according to eco-region, elevation zone, and the initial stand structure and composition; (2) quantify the respective role of each of these variables; (3) identify which tree species would benefit or suffer from CC; and (4) analyze if current management practices would be more appropriate than a situation without management to maintain the provision of forest ES under new climatic conditions.

Materials and methods

Forest stratification

A quantitative stratification of the Swiss forest area (~12’000 sq km, Brändli, 2010) was conducted to identify forest stands that are typical of current forests in terms of stand structure and composition. Data for the stratification were obtained by the National Forest Inventory (NFI; WSL, 2011). The third NFI (NFI3) was based on a regular quadratic grid over the whole of Switzerland with a side length of $\sqrt{2}$ km. On each grid point within the forest, stand structure was described by:

1) A predefined set of forest stand attributes on a 50 m x 50 m plot area, among others canopy cover, vertical stand structure, stand development stage, stand age, degree of mixture, and crown closure (Keller, 2011).

2) Single-tree data sampled using a 200 m^2 circular area around the plot center for trees with 12 cm $\leq$ dbh (1.3 m; diameter at breast height) < 36 cm, and a 500 m^2 circular area for trees with dbh $\geq$ 36 cm.

Keller (2011) provides a detailed account of NFI3 methods and attributes. We used a selection of the forest stand attributes for the stratification. Single-tree data were used to assess tree species composition and for model initialization. We grouped the 6838 forested NFI plots into eco-regions and elevation zones (see Figure 1) according to the “Guide for sustainability in protection forests” that is widely used in Switzerland and other Alpine countries (Frehner *et al.*, 2005). Within each eco-region, we disregarded those elevation zones that contained fewer than 10% of the NFI plots. NFI plots were then segregated into groups according to (1) their vertical stand structure (4 levels), which indicates the number of height layers of the stand, and (2) their developmental stage (6 levels), which is expressed by the average dbh of the 100 largest trees per hectare on the plot (d_{dom}; see Table S1.2). For each eco-region and elevation zone, the groups that included the largest number of NFI plots were selected until 40% of all NFI plots of the zone were considered. In a final step, if recommended by sylvicultural experts, we further divided some groups into deciduous and coniferous-dominated strata, based on tree species composition of their NFI plots. This led to the identification of 71 ‘typical’ forest strata distributed across seven eco-regions and eight elevation zones that cover around 25% of all NFI plots. For each forest stratum, the single-tree data of all associated NFI plots were aggregated to form an artificial but representative forest stand.

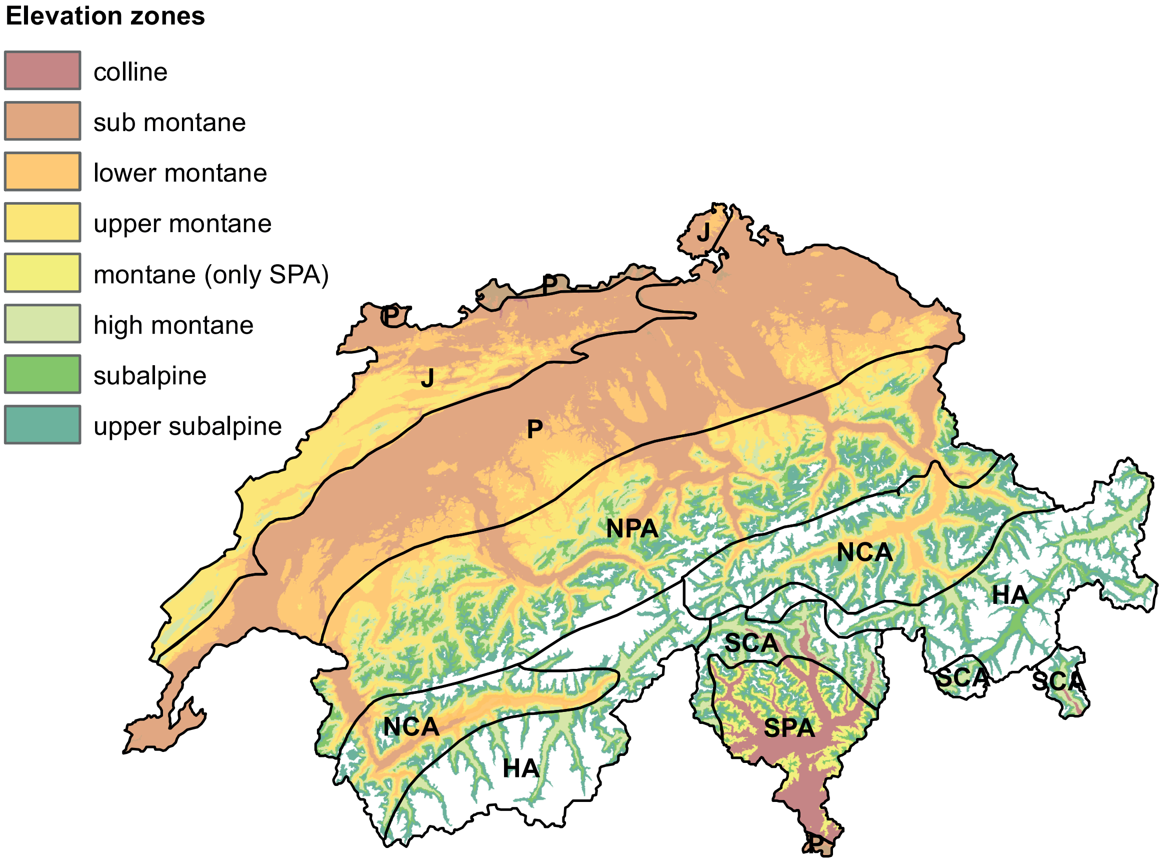


Figure 1: Forest eco-regions (J = Jura, P = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps) and elevation zones of Switzerland, modified from Frehner *et al.* (2005). Boundaries for elevation zones represent average estimates (see Appendix S1), white patches represent areas beyond the upper tree line.

The ForClim model

ForClim (Bugmann, 1996) is a cohort-based forest gap model simulating forest dynamics on a large number (usually, $n = 200$) of small, independent patches (usually, 500 m^2). This patch size allows a few large canopy trees to dominate an entire patch (i.e., complete shading) whose death creates a “gap” in which growth and regeneration rates are enhanced. Forest characteristics at the stand scale are assessed following the mosaic theory of Watt (1947) by averaging them across all simulated patches. Long-term monthly temperature means and precipitation sums, soil water-holding capacity, stand latitude, and topography (slope and aspect) are used to calculate bioclimatic inputs using a modified version of the soil water balance model by Thornthwaite and Mather (1957; Bugmann and Cramer, 1998). These inputs and light availability (calculated using the Beer-Lambert law based on foliage area; Bugmann, 1996) are then used to simulate the establishment of new cohorts (trees of same species and age), their growth, and individual tree mortality. Establishment of saplings with a predefined dbh of 1.27 cm occurs only if a set of biotic and abiotic factors matches species-specific requirements. Annual radial tree growth is determined using a modified version of the carbon budget approach by Moore (1989) where a set of environmental factors including degree-day sum, drought (soil moisture), nutrient availability, light availability and crown length constrain species-specific optimal growth.

In the present study, we implemented the latest developments of *ForClim v3.3* (Mina et al., submitted) and used two model versions with a different mortality function. In *ForClim v3.3*, mortality probability is determined by a constant species-specific mortality rate related to the putative maximum age of each species ("background mortality"), and a stress-induced mortality component that occurs if annual diameter increment falls below 10% of the optimal growth rate or below 3 $mm \cdot yr^{-1}$ for more than two consecutive years (Bircher *et al.*, 2015). This direct link between tree growth and mortality leads to an expectedly high sensitivity of the model under altered climatic conditions. We also used a second ForClim version (*ForClim BC-MAP*) in which tree mortality was simulated using a forest inventory-based function that was re-calibrated with Bayesian statistics to fit the historical development of stand basal area and stem numbers in nine Swiss forest reserves, followed by validation for another 21 reserves (Bircher *et al.*, submitted). As predictor variables, this mortality function uses dbh, relative basal area increment, shade tolerance of the species, and the site-specific degree-day sum. It is less dependent on tree growth and thus is expected to generate lower mortality probabilities. Both model versions have been successfully tested to accurately simulate short-term forest dynamics (i.e., 40-50 yrs) for various forest site conditions (Bircher *et al.*, submitted). We perceive the integration of two model versions to be highly beneficial for this study, as their comparison allows for a more reliable assessment of the signal and magnitude of forest stand sensitivity to CC.

Forest management

Based on the recommendations by sylvicultural experts, we derived one predominant management practice for each elevation zone with a distinction between even-aged and uneven-aged forest stands, which reflects the most common current management practices (Appendix S2).

From the high montane to the upper subalpine elevation zone, a "group plentering" regime (i.e., harvesting a certain percentage of trees by removing entire cohorts) was applied for both uneven- and even-aged stands. Intervals between interventions were increased in length and intervention intensity decreased towards higher altitude to take into account the lower growth potential. A relatively high volume in current even-aged stands was the reason to schedule the first intervention earlier (year 2010) than in uneven-aged forests (2020). From the colline to the upper montane elevation zones, uneven-aged forest stands were managed following a single-tree plentering regime (i.e., basal area is held on a constant residual basal area by removing single trees; Rasche *et al.*, 2011). For even-aged forest stands in these zones, forests with an average $d_{dom} \geq 60$ cm were classified as mature and were completely cut in two interventions that took place within the first 10 years of the simulation (2011 and 2016, respectively), followed by "thinning from above" in constant intervals. This regime was also applied from the beginning of the simulation for stands with $d_{dom} < 60$ cm. Management practices were not adjusted during simulations and all tree species were potentially allowed for regeneration, so as not to hinder the systematic interpretation of CC effects.

Current climate and site parameters

Monthly mean temperature and precipitations sum for the reference period (1980-2009) were obtained from the climatology engineering office METEOTEST (Remund *et al.*, 2014). These data were derived by a spatial interpolation to a 100 m grid of weather data from the MeteoSwiss network using Shepard's Gravity Interpolation method (Zelenka *et al.*, 1992) for all NFI plots. For each forest stratum, we averaged the interpolated weather data of all associated NFI plots, and calculated monthly long-term averages and standard deviations for temperature and precipitation as well as their cross-correlations.

Maximum soil water holding capacity (cm) was aggregated for each stratum based on METEOTEST data from all associated NFI plots (Figure S6.1). Slope and aspect values provided in the NFI data for each plot were converted to one Slope-aspect input parameter [-2...2] as used in ForClim, where the value indicates the slope class (0 = (0-10°], 1 = (10-30°], 2= (30+°]) and the sign denotes North- (-) and South-facing aspect (+), respectively. The slope-aspect parameter was considered for each NFI plot (= ForClim patch) individually in the simulations. Due to the lack of field information on nitrogen availability, all forest stands were given the same averaged value of 80 $kg \cdot ha^{-1} \cdot yr^{-1}$. No other parameters were adjusted locally.

Climate change scenarios

We focused on the extreme greenhouse gas (GHG) emission scenario A2 (Nakicenovic and Swart, 2000). We used the lower, medium and upper estimates of the seasonal absolute changes of temperature (°C) and precipitation (%) (hereafter called 'delta values', albeit they are a factor for precipitation) that were downscaled for five regions of Switzerland (North-eastern Switzerland, Western Switzerland, Western Alps, Eastern Alps, and Southern Switzerland) based on projections from a wide range of Global and Regional Climate Model chains (Fischer *et al.*, 2015). The uncertainty in CC projections was considered by selecting 11 climate scenarios where significant dependencies between climate variables and between seasonal climate delta estimates were taken into account (see Appendix S3).

Simulation setup

For each forest stratum, the model was initialized with the single-tree data of all associated NFI plots; each NFI plot corresponded to one forest patch in the model. Simulations were run from the year 2006 (last year of NFI3) to 2100. For running simulations with CC, we applied the delta change method on the current climate using linear interpolation for the delta values between the central years of the three scenario time slices (2035, 2060, and 2085). All forest stands were run with both model versions, 12 climate scenarios ("current/reference climate" + 11 CC scenarios), and with and without management (i.e., 3408 simulation runs in total).

Statistical analysis: factors affecting forest dynamics under climate change

Due to the wealth of simulation results obtained, statistical methods had to be used to detect response patterns across the strata. We applied general linear mixed effects models (GLME) to investigate the respective role of potential explanatory variables for the mean relative change in stand basal area (BA) caused by CC (change in BA under CC compared to BA under current climate in the year 2100; n = 71). Models were fitted with the R language and environment (R Core Team, 2014) using the package *lme4* (Bates *et al.*, 2014). The explanatory variables included as fixed effects in the global model were the elevation of the forest stratum, initial species richness (iniSpecRich; initial number of species that contributes to a least 1% of stand basal area), soil water capacity (SWC), initial d_{dom} and Shannon's index of diversity in tree height (VSSDI). We further considered the initial proportion of silver fir *Abies alba*, Norway spruce *Picea abies*, and European beech *Fagus sylvatica* (initProp.Abies, initProp.Picea, and initProp.Fagus, respectively), as they currently are the most abundant tree species in Switzerland (Brändli, 2010). In order to analyze how the relative change in BA and how the effect of elevation varies among the eco-regions, random effects were estimated for the intercept, with eco-region as grouping variable.

To make the interpretation of parameter estimates easier, all fixed effects were standardized using the *arm* package (Gelman and Su, 2014). The corrected Akaike Information Criterion (AIC_c) was used to select the best model in which the random effects were analyzed. To analyze the respective effects of each explanatory variable, we also used a model averaging approach Grueber *et al.* (2011) by considering all the models whose ΔAIC_c (AICc of the best model – AICc of the current model) was below 4, using the R package *MuMIn* (Barton, 2014).

Indicators of forest ecosystem services

In Switzerland, the most important forest ES are timber production, protection against natural hazards, biodiversity, and recreation (Brändli, 2010).

Timber production was calculated by averaging the annual harvested basal area ($m^2 \cdot ha \cdot yr^{-1}$) for two time periods (2006-2060 and 2061-2100, respectively).

The capacity of a forest stand to protect against gravitational hazards is critically influenced by its species mixture, structural profile, rooting stability and regeneration potential (Frehner *et al.*, 2005). We incorporated these characteristics in a gravitational protection forest index (GPFI) that takes tree density ($\theta_{density}$), structural diversity of large trees (θ_{LC}), structural diversity of small trees (θ_{SC}) and species diversity (θ_{SD}) into account (details in Appendix S4):

$$\mathrm{GPFI} = 50 * \theta_{density} + 25 * \theta_{LC} + 10 * \ \theta_{SC} + 15 * \ \theta_{SD} \tag{1}$$

For biodiversity and recreation, we applied Shannon's stand structural index (SSI), which represents the average of Shannon's diversity index on tree species, tree height and tree dbh (cf. Staudhammer and LeMay, 2001; Elkin *et al.*, 2013b). The use of this index is based on the assumption that high structural diversity is beneficial not only for biodiversity but also for recreational purposes due to higher aesthetical value (cf. Rasche *et al.*, 2013).

Timber production was assessed for all forest strata. The other indices, however, were assessed only in those elevation zones where they are particularly relevant for human society, i.e. the colline to upper montane zone for SSI and the high montane to upper subalpine zone for GPFI, respectively.

Results

Future climate

Under an A2 emission scenario, relative to the 1980-2009 period mean temperatures would rise in Switzerland by 4.1 °C until the end of the century (SD: 1.1 °C; ensemble of the 11 CC scenarios), with a peak in the summer season (4.9 ±1.1 °C). Projected changes in precipitation are unevenly distributed across seasons and regions (Figure S3.1). Precipitation is expected to decrease in summer (-23 ±11%) and increase in winter (+12 ±16%). There is rather large uncertainty regarding future precipitation changes in spring (-1.3 ±15%) and fall (-2 ±14%).

Overall change in basal area

In 2060, ForClim v3.3 projected a slight overall change in stand BA due to CC considering all simulated forest strata (Figure 2; left panels) with slightly larger changes in higher elevations (upper montane to upper subalpine) if management was applied. A negative effect was found only for forest stands in the lowest elevation zones of the Jura (sub montane and lower montane) and the Swiss Plateau (sub montane) with median changes of basal area ranging between -8% and -1%. Simulated BA increased at higher elevations, particularly in the highest zones of the Southern Central Alps (median change: +12%) and the High Alps (median change: +12%).

In 2100, there was a clearly stronger impact of CC on stand BA, but this response varied across the CC scenarios (see standard deviations in Figure 2; Figure S3.2). On average, there was a decline of BA (compared to BA under current climate) in the Jura (-2.4%), the Swiss Plateau (-0.7%) and the Southern Pre-Alps (-1.2%). In the other regions, an increase of BA could be observed, which differed in magnitude (e.g. Northern Pre-Alps: +4.1% vs. Northern Central Alps: +0.5%). From the colline to the lower montane elevation zone, CC caused a decline of BA in most regions. In the sub montane strata of the Jura (mean absolute BA 55 $m^2 \cdot ha^{-1}$ under current climate), average decline was highest (-14.9%). Compared to the Jura, losses of BA in strata of the Swiss Plateau were lower at same elevations. In higher elevations, BA under CC was increasing. In particular, an increase could be observed for the subalpine (+5.4%) and the upper subalpine elevation zone (+23.5%). Again, the average response for the same elevation zone varied among regions (e.g. high montane of Northern Pre-Alps: +2.9% vs. high montane of Northern Central Alps: -3.0%).

Using the *ForClim BC-MAP* model version, simulations run without management showed similar results as *ForClim v3.3* regarding forest dynamics under CC (Fig. S5.1), albeit with lower magnitude, i.e. this version projected a lower decrease in BA for those forest stands that were negatively affected by CC.

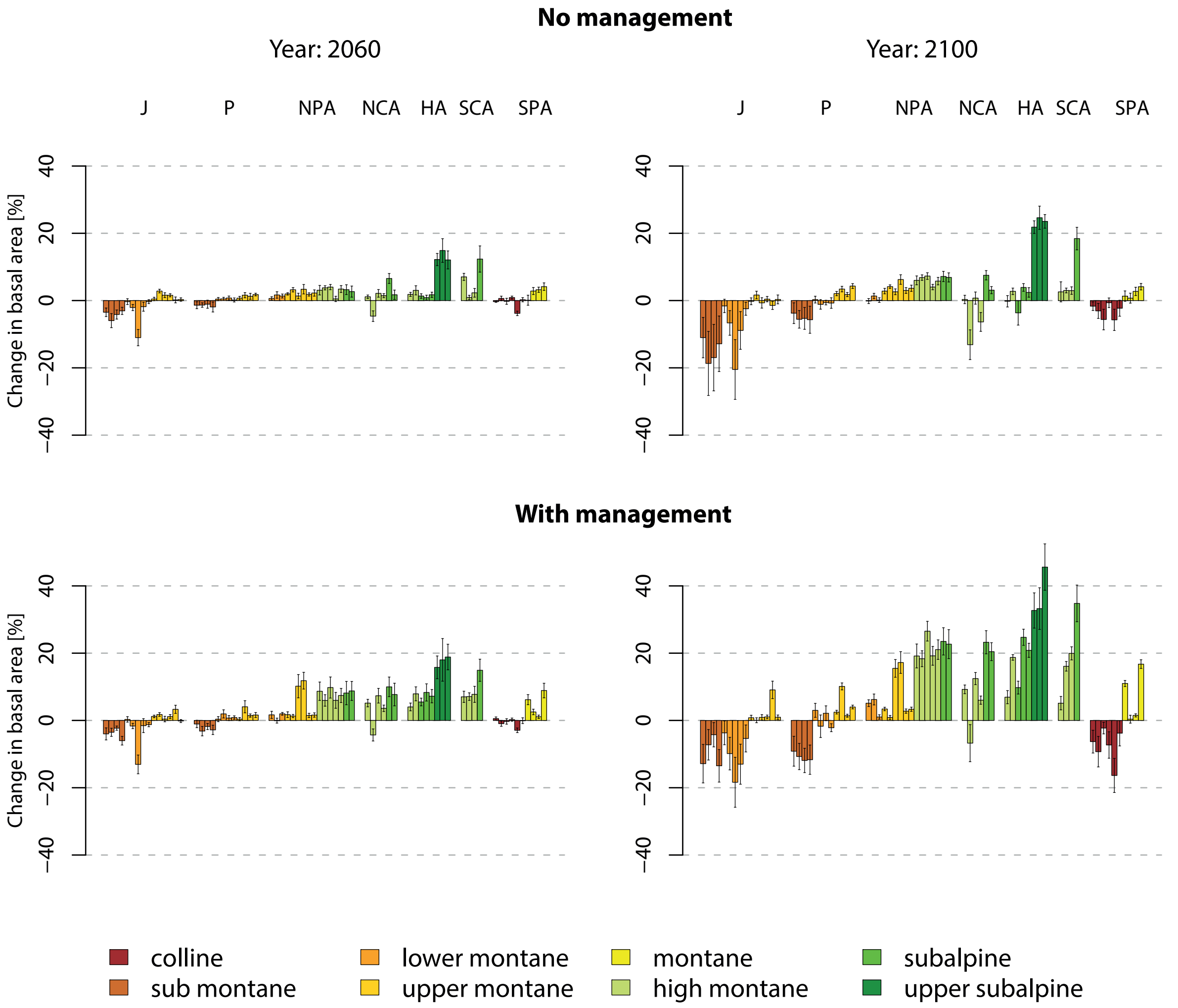


Figure 2: Relative difference of basal area (%) for simulations under CC and under current climatic conditions with ForClim v3.3 for the year 2060 (left panels) and 2100 (right panels) without (upper panels) and with management (lower panels). Each bar represents one forest stratum, ordered by eco-region (J = Jura, M = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps) and elevation zones (lowest elevations on the left). The vertical bars are one standard deviation, resulting from the variability of changes in basal area under the 11 CC scenarios.

Effect of forest management

On average, forest management positively impacted stand BA for the year 2100 when using *ForClim v3.3* (lower panels in Figure 2; Figure 3, left). This is especially true for high elevation stands (from the montane to the upper subalpine zone), indicating that the decrease in BA was lower or its increase was stronger compared to simulations without management (mean difference: +13.0 ±4.2%). For example, BA in strata of the upper subalpine zone of the High Alps increased by 33% when management was applied (cf. +23.5% without management). In contrast, there was no significant positive effect of management on stand BA at low elevations (colline to upper montane elevation zones; mean difference: -0.1 ±3.7%). The same trend was found for *ForClim BC-MAP* simulations (Figure 3, right). The effect of management on stand BA was also positive at high elevations (mean difference: +12.0 ±4.6%), but no clear effect was visible at low elevations (mean difference: -0.25 ±2.2%).

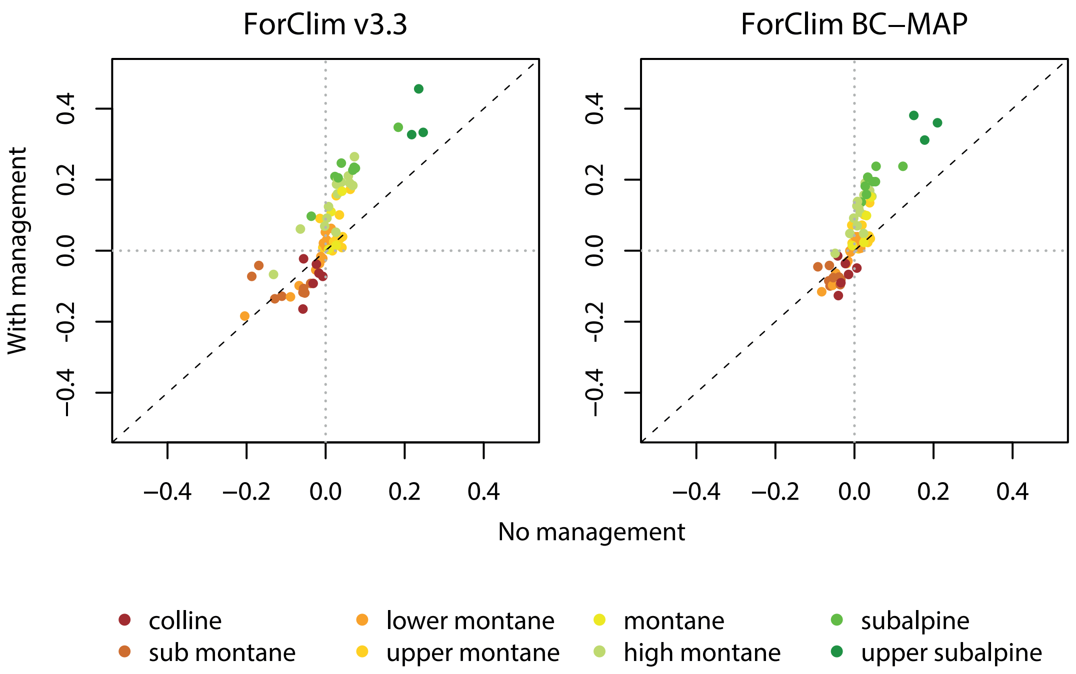


Figure 3: Mean relative difference in BA between CC and current climate in simulations with and without forest management (y- and x-axis, respectively) for the year 2100. Simulated relative differences are shown for the model versions ForClim v3.3 (left) and ForClim BC-MAP (right).

Factors modifying the effect of climate change on stand basal area

The estimates of the GLME model highlighted that elevation was the main factor that determines the effect of CC on stand BA, with a positive relationship between both variables for all model versions ($P<0.001$; Table 1). Water holding capacity had a positive effect as well, which was significant ($P<0.05$) except in the average models for simulations without management. The BA of strata with a high initial proportion of Norway spruce was affected more strongly by CC than strata dominated by beech or silver fir. The initial abundance of Norway spruce was negatively correlated with the magnitude of BA changes throughout all model versions and, with one exception, at a significant level. The initial species richness showed a negative correlation as well, but just partly at a significant level. The initial proportion of European beech was relevant in simulations without management but not as strong as Norway spruce. The initial proportion of silver fir was neither a relevant nor a significant factor. Regarding forest stand structure, the vertical diversity index (VSSDI) was negatively and significantly correlated with change of BA under CC but only in simulations without management. In contrast, the initial d_{dom} was positively correlated at a significant level but only in simulations with management.

Table 1: Estimates of the linear mixed-effects models fitted on the relative change in basal area (year 2100; n = 71). Fixed effects of the best model and of that obtained using a model averaging approach are shown for both the ForClim 3.3 and BC-MAP version, and for simulations with and without management. Grey background colors indicate significant effects ($p<0.05$ for the lighter and $p<0.01$ respectively $p<0.001$ for the darker colors). The set of explanatory variables included the initial number of species that contributes to a least 1% of stand BA (initSpecRich), median soil water capacity (SWC_median), initial d_{dom}, initial proportion (initProp) of silver fir, Norway spruce and European beech, and Shannon's index of diversity in tree height (VSSDI).

	ForClim v3.3				ForClim BC-MAP			
	No management		With management		No management		With management	
Model name	Average model	Best model	Average model	Best model	Average model	Best model	Average model	Best model
Fixed effects								
(Intercept)	0.11	0.02	5.81	5.81	0.73	0.67	5.47	5.48
Elevation	15.03	14.77	25.18	26.00	9.60	9.57	21.97	21.97
initSpecRich	-2.19	-2.87	-1.19	–	-2.23	-2.34	-0.23	–
initProp.Abies	0.27	–	-0.11	–	0.35	–	0.00	–
initProp.Picea	-5.97	-6.36	-3.80	-3.96	-4.62	-4.81	-3.30	-3.51
initProp.Fagus	-1.99	-2.56	0.08	–	-1.43	-1.66	0.09	–
SWC_median	2.45	3.15	4.06	4.19	2.04	2.01	2.70	2.79
ddom	0.19	–	4.74	5.15	0.08	–	2.80	3.11
VSSDI	-3.13	-3.33	0.00	–	-2.11	-2.14	-0.37	–

Considering the eco-regions as random effects in the GLME models resulted in a better performance of the best models for simulations without management as shown in Table 2. However for simulations with management, model performance was rather equal, indicating a lower importance of eco-regions as drivers of managed forests' sensitivity to CC.

Table 2: Model performance for best models with and without random effects (With / No RE). Random effects were estimated for the intercept, with eco-regions as grouping variable. The explained variance R^2 and the corrected Akaike Information Criterion (AICc) were used to assess model performance (cf. Nakagawa and Schielzeth, 2013). The grey background colour indicates whether the model with or without random effects showed higher performance (i.e., high R^2 and/or low AICc). The best models were compared for both the ForClim 3.3 and BC-MAP version, and for simulations with and without management.

	ForClim v3.3				ForClim BC-MAP			
	No management		With management		No management		With management	
	No RE	With RE	No RE	With RE	No RE	With RE	No RE	With RE
R^2	0.7636	0.8352	0.8584	0.8668	0.8421	0.8758	0.8830	0.8861
AICc	413.26	406.99	448.38	449.66	323.32	322.67	404.29	406.67

Tree species affected by climate change

Both coniferous and deciduous species showed a decline in BA at low elevations (Figure 4). At intermediate and high elevations, deciduous species benefit more from management interventions than conifers.

Within the conifers, BA of silver fir remained more or less constant (range of medians across elevation zones: 0.0 – 0.3 $m^2 \cdot ha^{-1}$). On average, Norway spruce showed a decline of BA under CC in most elevation zones (-0.7 – -0.1 $m^2 \cdot ha^{-1}$) except of the colline and montane zone (median change: 0.0 $m^2 \cdot ha^{-1}$) and the upper subalpine zone (+0.7 $m^2 \cdot ha^{-1}$). Loss of spruce BA was highest in the sub montane (median: -3.1 $m^2 \cdot ha^{-1}$: maximum: -9.2 $m^2 \cdot ha^{-1}$) and lower montane zone (median: -1.3 $m^2 \cdot ha^{-1}$; maximum: -10.3 $m^2 \cdot ha^{-1}$) of the Jura. However, declines were also observed in the high montane elevation zone of the Northern Central Alps (median: -4.1 $m^2 \cdot ha^{-1}$: maximum: -8.9 $m^2 \cdot ha^{-1}$) and the subalpine zone of the High Alps (median: -1.1 $m^2 \cdot ha^{-1}$: maximum: -2.2 $m^2 \cdot ha^{-1}$). Under the current forest management regime, maximum losses of spruce BA was reduced (Figure 4, bottom). The BA of other conifers (e.g., European larch *Larix decidua*, Scots pine *Pinus sylvestris*) remained constant or decreased somewhat across nearly all elevation zones (median range: -0.1 – 0.3 $m^2 \cdot ha^{-1}$). However, an increase could be observed in the upper subalpine zone (+6.5 $m^2 \cdot ha^{-1}$), in particular for European larch and Stone pine *Pinus cembra*. Under current forest management, BA of other conifers decreased slightly from the upper montane to the sub alpine zone (median range: -0.7 – -0.1 $m^2 \cdot ha^{-1}$). The increase of BA in the upper subalpine zone was less pronounced (+2.8 $m^2 \cdot ha^{-1}$).

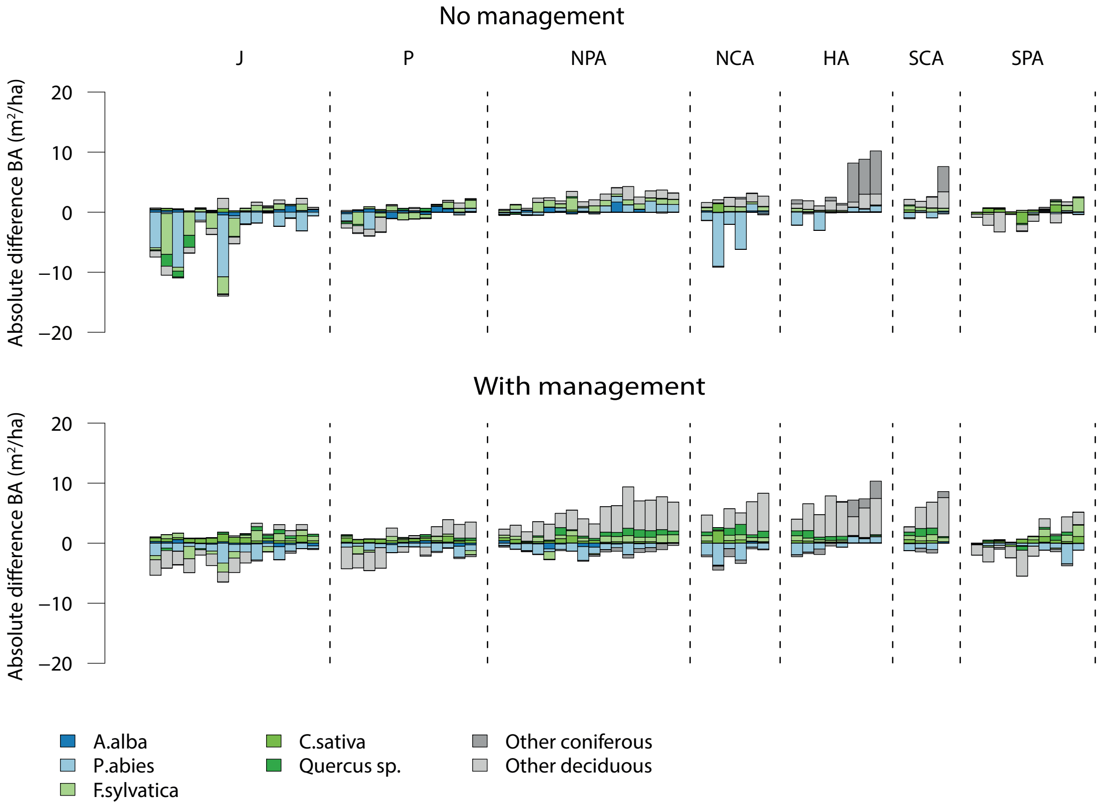


Figure 4: Averages of absolute difference of species-specific basal area for the year 2100 between CC and current climate per forest stand using ForClim v3.3. Forest stands are ordered within eco-regions according to increasing elevation.

For deciduous species, ForClim v3.3 simulated a decline of BA at low elevations. For beech, BA was reduced in the sub montane (median change: -2.4 and -0.4 $m^2 \cdot ha^{-1}$, respectively) and lower montane (-2.6 and -0.8 $m^2 \cdot ha^{-1}$, respectively) of the Jura and the Swiss Plateau. However, there was a slight increase in beech BA from the upper montane to the upper subalpine elevation zone (0.2 – 1.0 $m^2 \cdot ha^{-1}$) in all regions. Similarly to Norway spruce, maximum losses of beech at low elevations were smaller if management was applied. Oak species showed a decline of BA in the sub montane zone of the Jura (-1.5 $m^2 \cdot ha^{-1}$) but remained constant otherwise (-0.1 – +0.1 $m^2 \cdot ha^{-1}$). Under current forest management, BA of Oak species (Pendunculate oak *Quercus robur* and Sessile oak *Q. petraea*) slightly increased from the upper montane to the subalpine elevation zone (range of medians: 0.2 – 1.1 $m^2 \cdot ha^{-1}$). European chestnut *Castanea sativa* hardly showed any changes of BA under CC. A slight increase of chestnut BA was visible from the colline to the subalpine elevation zone under management (0.1 – 0.7 $m^2 \cdot ha^{-1}$). For the other deciduous species such as European ash *Fraxinus excelsior* or Sycamore maple *Acer pseudoplatanus*, BA decreased on average in the colline (-1.0 $m^2 \cdot ha^{-1}$) and sub montane elevation zone (-1.1 $m^2 \cdot ha^{-1}$), while it remained constant at intermediate elevations (lower montane to upper montane zone: 0.1 – 0.5 $m^2 \cdot ha^{-1}$) and slightly increased at higher elevations (high montane to upper subalpine zone: 1.1 – 1.8 $m^2 \cdot ha^{-1}$). With forest management, the decline of other deciduous species at lowest elevations was more pronounced, while its increase from the upper montane to the upper subalpine elevation zone (1.7 – 5.6 $m^2 \cdot ha^{-1}$) was clearly higher.

Similar patterns were obtained from *ForClim BC-MAP* (see Figure S5.2), although the decline of spruce, beech and oak BA at low elevations was less pronounced. Similarly, increase of beech and oak BA at higher elevation did occur to a lesser degree.

Projections of key ecosystem services

According to the model version ForClim 3.3 under current climatic conditions and using “best-practice” management regimes, the ability of forests to provide protection (GPFI) would decrease until the year 2060 in the Northern Pre-Alps, Central Alps, and the High Alps (Table 3), mainly due to reduced density of trees with dbh >24 cm (Figure S4.2). This was not the case for simulations without management, where GPFI increased in all regions (see Table S4.2). Stand structural diversity (SSI) clearly decreased in the Jura, Swiss Plateau and Northern Pre-Alps but remained constant in the Southern Pre-Alps (Table 3) when management was applied. Generally, an increase in species diversity was facing reduced structural diversity regarding tree height and dbh (Figure S4.2). Without management, SSI increased in the latter region but remained constant across the others.

During the second period (2061-2100), the quantity of harvestable timber was slightly higher than during the first period (2006-2060). Independent of management, forest protection slightly decreased in all eco-regions compared to the year 2060 with the exception of the Southern Central Alps, where GPFI decreased if no management was applied (Table S4.2). SSI slightly increased in the Jura and the Swiss Plateau but remained constant in the Northern and Southern Pre-Alps. In simulations without management, SSI further increased in all regions. Projected absolute values of ES were very similar when ForClim BC-MAP was used (Table S4.1).

Under CC, there was hardly any effect on the considered ES (median range of Diff-CC60: -2.1 – 2.2%) compared to current climate for the year 2060. However, the effect of CC was stronger for the year 2100 (Diff-CC100; Table 3): The quantity of harvested timber was negatively affected in the Jura and the Swiss Plateau, though these effects were not significant. A significant increase of harvest was found in alpine region such as the Northern

Pre-Alps, the High Alps, and the Southern Central Alps. The effect of CC on GPFI in managed strata was positive (range of medians: 4.4 – 7.9%) and usually significant. Without management (Table S4.2), however, the median effect of CC was generally weaker and in some cases even negative (-0.1 – 1.2%). Stand structural diversity was projected to decrease in managed strata under CC in three out of four regions (increase of SSI under CC in Northern Pre-Alps). Without management, median effects of CC were very similar. However, large standard deviations for all relative differences (Diff-CC100) indicate a high variability among forest stands within an eco-region, primarily due to strong regional elevation gradients (cf. Figure S4.1).

The response of ES in simulations with *ForClim BC-MAP* to CC was consistent with ForClim v3.3, albeit smaller in magnitude (Table S4.1).

Table 3: Ecosystem service metrics (median and standard deviation) of harvest, protection (GPFI), and biodiversity/recreation (SSI) simulated by ForClim v3.3 for each eco-region with forest management. Mean annual harvested basal area (m^{2}ha^{-1}yr^{-1}) was calculated under current climate for two periods (2006-2060, 2061-2100). The average relative differences (%) under CC compared to simulations under current climatic conditions are listed as well (Diff-CC). For GPFI and SSI, absolute estimates (current climate) are given for the initial state of the forest stand (year 2006) and the years 2060 and 2100. For the latter, the average relative differences under to CC (Diff-CC) are shown as well.

	Harvest				GPFI					SSI				
Region	2006-2060 [m^2/ha.yr]	Diff-CC60 [%]	2061-2100 [m^2/ha.yr]	Diff-CC100 [%]	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]
Jura	0.5 ±0.1	0.9 ±5.1	0.6 ±0.1	-3.1 ±17.6	–	–	–	–	–	2.1 ±0.4	1.3 ±0.4	-2.1 ±5.8	1.5 ±0.4	-7.3 ±6.1
Swiss Plateau	0.6 ±0.1	0.6 ±2.4	0.8 ±0.1	-0.3 ±9.2	–	–	–	–	–	2.1 ±0.5	1.3 ±0.4	-0.3 ±3.3	1.5 ±0.4	-1.4 ±7.2
Northern Pre-Alps	0.4 ±0.2	1.7 ±3.2	0.5 ±0.2	13.4 ±8.2	77.4 ±8.2	68.3 ±3.9	1.6 ±1.0	66.7 ±6.7	7.2 ±5.2	2.1 ±0.3	1.8 ±0.5	2.4 ±3.6	1.7 ±0.4	2.4 ±3.6
Northern Central Alps	0.4 ±0.1	1.1 ±1.5	0.5 ±0.1	8.3 ±13.2	78.4 ±9.9	67.6 ±5.1	0.8 ±1.5	64.4 ±6.7	4.4 ±5.7	–	–	–	–	–
High Alps	0.4 ±0.1	2.2 ±3.3	0.4 ±0.2	17.9 ±10.9	76.7 ±10	64.7 ±4.7	1.1 ±1.2	61.8 ±7.1	7.9 ±5.3	–	–	–	–	–
Southern Central Alps	0.3 ±0.2	1.4 ±5.7	0.4 ±0.1	11.3 ±6.2	62 ±20.3	67.3 ±4.4	0.7 ±0.5	64.3 ±9.7	7.8 ±5.9	–	–	–	–	–
Southern Pre-Alps	0.5 ±0.1	1.4 ±3.4	0.6 ±0.1	0.2 ±10.1	–	–	–	–	–	1.2 ±0.6	1.2 ±0.3	0.0± 5.6	1.3 ±0.3	-3.4 ±8.2

Discussion

Addressing forest dynamics under CC beyond the regional scale used to be the domain of bioclimatic envelope modeling techniques (Thuiller *et al.*, 2005) or dynamic global vegetation models (Prentice *et al.*, 2007). However, such large-scale applications come with considerable limitations including the assumption of species in equilibrium without competition (Pearson and Dawson, 2003; Svenning and Skov, 2004), simulating potential natural vegetation and/or excluding forest management. In contrast, process-based models have not often found consideration in projections of vegetation dynamics at larger scale (Hickler *et al.*, 2012) but are rather used in local assessments for a few sites only (Badeck *et al.*, 2001).

We applied a process-based model at a large number of sites; this represents a new combination as it provides at national perspective while keeping a high spatial resolution at the stand scale. We addressed the sensitivity of common forest types to CC in Switzerland by simulating the dynamics of 71 representative forest strata, based on stand initialization data, current forest management and under 11 climate change scenarios. Thus, we are able to discuss the impacts of climate change on Swiss forests and ES at the national level covering large ecological and bioclimatic gradients. Below, we will first discuss general trends of Swiss forests under climate change. This is followed by a detailed discussion on abiotic and biotic factors including stand elevation, tree species composition, regional climatic conditions, and forest management that explain the high variability in the sensitivity to CC among the different forest strata that we examined.

According to our simulations, under an extreme, although unfortunately not unlikely, high-end emission scenario (IPCC, 2014), the composition and structure of Swiss forests and the ES they provide would change only slightly until the middle of this century. In contrast, clear impacts of CC must be expected towards the end of the century (cf. Zierl and Bugmann, 2007; Seidl *et al.*, 2011a). This temporal scale is also in accordance with other studies that expect Central European forests (Morales *et al.*, 2007) respectively Swiss forests (Schmid *et al.*, 2006) to change from carbon sinks to sources at the end of this century. For Switzerland, a reduced potential of carbon storage must be expected in particular at low elevations from the colline to the lower montane zone where BA was simulated to decrease compared to current climate due to drier conditions (Zingg and Bürgi, 2008). The projected forest dynamics resemble current observations made in Southern European forests with low water availability (cf. Vayreda *et al.*, 2012; Ruiz-Benito *et al.*, 2014). In addition, they are in agreement with negative impacts of CC on forest growth expected at large scale for Central European forests at low altitudes (cf. review of Lindner *et al.*, 2014). At high elevations, Swiss forests are expected to increase in BA under CC compared to current climate, which agrees with the results of other studies regarding alpine elevations (Morales *et al.*, 2007; Reyer *et al.*, 2014).

Analogously to expected changes in BA, the effect of CC on the examined ES would vary considerably among forest stands. At low elevations, simulated decreases of harvestable basal area, tree species diversity, and the lower heterogeneity of size structure would have negative consequences for the forestry sector and the social and recreational value of these stands (cf. Dale *et al.*, 2001; Hanewinkel *et al.*, 2013). However, at high elevations and in cold-wet sites, the rise in temperatures would enhance forest productivity, harvestable timber and the ability of forests to protect against natural hazards (cf. Elkin *et al.*, 2013b).

The main factor that affects forest sensitivity to CC in terms of stand basal area was elevation, which is consistent with other modeling studies in Europe (e.g., Seidl *et al.*, 2011a; Elkin *et al.*, 2013b). The projected strong decrease of tree growth at low elevations was related to the increase of drought intensity and frequency during the vegetation period due to reduced precipitation and higher temperature (e.g., Jump *et al.*, 2006; Macias *et al.*, 2006). In contrast, this may positively impact productivity of high-elevation stands, analogously to Northern regions (Piao *et al.*, 2011; Ruiz-Benito *et al.*, 2014), due to an increase in the rates of growth and regeneration. The same dependency was found for those forest ES that are strongly related to site-specific stand structure (Elkin *et al.*, 2013b). Therefore, the variation in ES sensitivity along elevation was consistent with simulated forest stand dynamics and explains the large variability of ES response to CC within eco-regions. These findings are underlining the need to assess the impact of CC on ES separately across different vegetation zones (cf. Rocca *et al.*, 2014).

For beech, declines of BA have to be expected, partly to a high degree, at lower sites due to increased drought (Zingg and Bürgi, 2008) while also other deciduous trees species were hardly thriving at such places as drought levels exceeded the species' tolerance. This raises concern regarding tree regeneration at forest sites that are supposed to face a more severe climate in the future. However, these results should be viewed with caution, as our modeling approach did not consider any plasticity and adaptability of species' traits, nor migration of more drought-adapted tree species e.g. from the Mediterranean area (e.g., *Quercus ilex*, Henne *et al.*, 2013). In contrast, we found a positive response to CC for beech (cf. Hlasny *et al.*, 2011) and other deciduous tree species at medium and higher elevations in Swiss forests. The projected behavior of beech along a bioclimatic gradient can already be observed today along its southern distribution range where declining growth (Kint *et al.*, 2012) is combined with a shift of the species to higher elevations (Penuelas and Boada, 2003; Jump *et al.*, 2006). Hlasny *et al.* (2011) expect beech to similarly react along an elevational gradient in the Carpathian mountains.

Although these findings underline the strong relationship between elevation and forest growth, our results also highlight other factors that drive forest dynamics under CC: increased temperatures might lead to improved tree regeneration conditions and higher productivity due to an extended growing season at higher elevations (Ruiz-Benito *et al.*, 2014). However, except for the highest elevation zone, the basal area increment of supposedly thriving deciduous species was rather marginal. Assuming that future climatic conditions are actually favorable for such more drought-adapted species, their transition seems to be a more time-consuming process (cf. review of Lindner *et al.*, 2014) whose assessment would require a time horizon beyond the year 2100. In the same line, species distribution models project oak to shift northwards in Europe even under a less extreme A1B scenario (Hanewinkel *et al.*, 2013). We only found such a response along the elevational gradient if management was applied. Mette *et al.* (2013) explain delayed response of oak to CC with subdued regeneration due to dominance of beech. Our findings based on current forest data imply that a response could even remain completely absent unless stand structure is changed by management interventions. This is further supported by our GLME models showing a significant negative relationship between Shannons tree height diversity index (VSSDI) and the relative change of stand basal area in simulations without management. This relationship was, however, not significant anymore if trees with a height <= 130 cm (i.e., regeneration) were neglected (not shown). We take this result as an indication for the long lasting influence of the current stand structure, in this case its current regeneration, on the future forest dynamics. Both current stand data and forest management, however, are hardly considered in species distribution models.

Speaking about the influence of the current stand structure on a forest's sensitivity to CC, this is becoming an even more relevant subject in the context of Norway spruce: As revealed by the GLME models, we notably found a clear negative relationship between current proportion of spruce in the forest stand and the stand's BA under CC compared to current climate. Although the reaction of spruce to CC along elevation zones was similar with beech (cf. Zingg and Bürgi, 2008), its response to CC at higher elevation such as the high montane and subalpine zone was much less uniform. These zones represent core areas of its natural distribution range under current climate (Ellenberg and Leuschner, 2010) and are expected to remain one of the last suitable spruce habitats in Central Europe under CC (cf. Hanewinkel *et al.*, 2013). However according to our simulation results, even here we found distinct loss of spruce BA illustrating that growth dynamics under climate change are not solely depending on the elevational gradient. The decline in Norway spruce BA at higher elevations was mainly observed for the Central Alps and the High Alps but not for the Northern Pre-Alps. High sensitivity of Norway spruce to drought in particular during the summer season (Levesque *et al.*, 2014) can explain the regionally non-uniform response across highly similar elevation zones. Kellomäki *et al.* (2008) detected Norway spruce in Scandinavia to find refuge under CC only at elevated sites with highest moisture. The northern edge of the Alps is characterized by high annual precipitation (Frehner *et al.*, 2005), which can alleviate the impact of future CC. In contrast, forests at lower elevations of the inner-alpine regions have already faced increasing drought conditions (e.g., Rebetez and Dobbertin, 2004; Bigler *et al.*, 2006) that would continue in the future (Rössler *et al.*, 2012; see also Figure S6.2). Thus, our results clearly advocate a detailed consideration of regional, local and topographic heterogeneity when assessing the impact of CC on forest dynamics and tree species behavior.

Impact of current management practices

The adequate management of forest ecosystems represents a major challenge for the forestry sector especially in the context of fast CC (Lindner *et al.*, 2010; Seidl *et al.*, 2011a). Knowledge on the effects of forest management practices under CC is a valuable input to develop adaptive measures (cf. Lasch *et al.*, 2005). Regarding the relative changes in stand BA, our results mainly suggest a positive effect of management on BA change under CC. Removal of large trees increased simulated light availability at the forest floor, which promoted regeneration and hence the transition to more adapted tree species than under unmanaged conditions (cf. Lindner *et al.*, 2000). For example at intermediate and high elevations, beech, oak, and other deciduous species showed higher basal area increment compared to simulations without forest management (cf. Figure 5). For Scandinavian forests, Briceño-Elizondo *et al.* (2006) found a similar positive effect of thinning regimes on tree growth under climate change. Forest management also mitigated the risk of sudden forest die-backs by reducing the stock of tree species like Norway spruce that showed limited potential for regeneration and growth under future CC. In fact, this effect is adopted in conversion strategies to transform mono-specific forests to more drought-adapted mixed-species stands (e.g., Kint *et al.*, 2009; Temperli *et al.*, 2012). At low elevations, simulation results of both model versions suggest currently applied forest management practices being capable of reducing decline maxima of spruce and beech. However, comparison with simulations without management also implies an insufficient natural regeneration under CC at those sites. To guarantee a continuous development of forest in these zones, further evaluation on the species' potential to adapt and regenerate under CC remains an urgent need (e.g., Bolte *et al.*, 2009).

Regarding forest ES, our results imply that current forest management regimes are not sufficient to compensate for negative impacts of CC on forest ES (Lasch *et al.*, 2005). We further found that forest management affects trade-offs not only among forest ES (Fürstenau *et al.*, 2007; Briceño-Elizondo *et al.*, 2008; Temperli *et al.*, 2012) but also regarding the mitigation of negative CC effects. For example, although management counteracted negative CC impacts on forest protection against gravitational hazards, no clear effect was evident for biodiversity or recreation (see SSI in Table 3 and S5.2). These results give weight for the development of nuanced adaptive management strategies that focus on specific sites and ES (cf. Temperli *et al.*, 2013; Rasche, 2014).

Uncertainties in model projections

Simulation results of dynamic vegetation models often diverge, depending on model choice (e.g., Moorcroft, 2006) and applied processes (Rowland *et al.*, 2014). On the one side, physiological effects such as raising CO2 levels or increased nitrogen deposit on forest growth are under debate (Kahle *et al.*, 2008). However, considering those factors in simulation studies on future forest dynamics lead to rather diverging results while uncertainty on accurate implementation remains high (e.g., Wamelink *et al.*, 2009; Reyer *et al.*, 2014). In our study, we did not include the potential effect of changes in CO_2 levels on forest growth. However, such an effect is considered to be rather irrelevant for Swiss forests (cf. Körner, 2003; Dawes *et al.*, 2015). Possible negative effects of nitrogen saturation on tree growth (Braun *et al.*, 2010; Kint *et al.*, 2012) were neglected as well. Nitrogen availability was set to be a non-limiting factor. On the other side, the choice of applied demographic processes such as tree mortality can significantly influence the outcome of a simulation study (e.g., Friend *et al.*, 2014; Bircher *et al.*, 2015). In order to provide more robust projections and a quantitative assessment of their uncertainty, a multi-model or multi-process approach is often advocated (Valle *et al.*, 2009; Hlasny *et al.*, 2014). The two model versions used in this study, albeit differing strongly with respect to the formulation of tree mortality, provided similar qualitative responses of forest properties to CC. Although model projections of forest dynamics under CC cannot be tested for accuracy (cf. Elkin *et al.*, 2013b), ForClim has been successfully tested for long-term projections of potential natural vegetation (Bugmann, 1996), and both model versions applied here have proven to reliably simulate initialized forest stands under current climate (Rasche *et al.*, 2012; Bircher *et al.*, 2015; Bircher *et al.*, submitted). Thus, we are confident that based on the simulation results of two model versions, a reliable assessment of the magnitude of CC impacts on Swiss forests until 2100 is possible, which goes far beyond the accuracy of earlier assessments (Bugmann, 1997; Elkin *et al.*, 2013b; Rasche *et al.*, 2013).

The GLME models imply that the current stand structure (i.e. initial tree species richness, d_{dom}, VSSDI and initial proportion of certain tree species) of the examined forest strata can have a long-lasting effect on forest sensitivity to CC. In addition, stand structure can critically affect forest vulnerability to natural disturbances (cf. Schelhaas *et al.*, 2003), which are expected to further grow in frequency and intensity under CC (Seidl *et al.*, 2011b; Seidl *et al.*, 2014). In turn, they are capable to trigger rapid shifts in forest stand structure and composition (e.g., Frelich and Reich, 2010; Turner, 2010). However, since such disturbances are not explicitly considered in ForClim, our study does not allow a comprehensive assessment of feedbacks between stand structure, natural disturbances and climate change.

Another source of uncertainty arises from the future climate scenarios (Elkin *et al.*, 2013b), as simulated forest responses depend heavily on the climate scenario that is applied (cf. Figure 2 and Figure S3.2). For an examined forest stand, change of BA compared to current climate differed on average by 6.1% depending on the applied CC scenario. However, in particular for lower sites, change of BA could differ by up to 26% among CC scenarios. Thus, even within a single GHG emission scenario, the variability of future climate projections remains substantial among climate models (cf. Fischer *et al.*, 2012). Furthermore, assessments that aggregate results from various climate models are confronted with high uncertainty regarding dependencies between estimates of temperature and precipitation (e.g., correlation between seasonal estimates; CH2014-Impacts, 2014; Fischer *et al.*, 2015). This renders the simple use of average estimates problematic (e.g., Knutti *et al.*, 2010; CH2014-Impacts, 2014) and highlights the relevance of using an ensemble approach, as supported by our results. The A2 greenhouse gas emission scenario, which is among the most extreme estimations of future greenhouse gas concentrations (IPCC, 2007), was deliberately chosen here to discuss the possible degree of CC severity. However, as greenhouse gas emissions continue to increase on unchecked or even increased rates (World Meteorological Organisation, 2014), our projections of future forest dynamics are based on climatic conditions that are absolutely realistic for the end of this century.

Acknowledgments

We are grateful to Ché Elkin for valuable feedbacks on the development of metrics to quantify forest ecosystem services such as the gravitational protection forest index. We appreciate the support of Harald von Waldow (ETH Center for Climate Systems Modeling; C2SM) on the selection and appropriate use of climate change scenarios in the simulations.

References

Aber, J., Neilson, R.P., McNulty, S., Lenihan, J.M., Bachelet, D., Drapek, R.J., 2001. Forest processes and global environmental change: Predicting the effects of individual and multiple stressors. Bioscience 51, 735-751.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. J. Biogeogr. 38, 1-8.

Badeck, F.-W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M., Mouillot, F., Schaber, J., Smith, B., 2001. Tree Species Composition in European Pristine Forests: Comparison of Stand Data to Model Predictions. Clim. Change 51, 307-347.

Barton, K., 2014. MuMIn: Multi-Model Inference. R package, version 1.12.1., http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. Lme4: Linear mixed-effects models using Eigen and S4. R package, version 1.1-7. http://CRAN.R-project.org/package=lme4.

Bebi, P., Kienast, F., Schönenberger, W., 2001. Assessing structures in mountain forests as a basis for investigating the forests' dynamics and protective function. For. Ecol. Manage. 145, 3-14.

Bertrand, R., Perez, V., Gegout, J.C., 2012. Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: the case of Quercus pubescens in France. Global Change Biol. 18, 2648-2660.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330-343.

Bircher, N., Cailleret, M., Bugmann, H., 2015. The agony of choice: different empirical mortality models lead to sharply different future forest dynamics. Ecol. Appl. 25, 1303-1318.

Bircher, N., Hartig, F., Hülsmann, L., Heiri, C., Bugmann, H., Cailleret, M., submitted. Bayesian statistics provide new insights on structural realism of a dynamic vegetation model. Submitted in Ecological Applications.

Bolte, A., Ammer, C., Lof, M., Madsen, P., Nabuurs, G.J., Schall, P., Spathelf, P., Rock, J., 2009. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. Scand. J. For. Res. 24, 473-482.

Bontemps, J.-D., Hervé, J.-C., Leban, J.-M., Dhôte, J.-F., 2011. Nitrogen footprint in a long-term observation of forest growth over the twentieth century. Trees 25, 237-251.

Brändli, U.-B., 2010. Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Bundesamt für Umwelt (BAFU), Birmensdorf, Bern.

Brang, P., Schonenberger, W., Frehner, M., Schwitter, R., Thormann, J.J., Wasser, B., 2006. Management of protection forest in the Eruopean Alps: an overview. Forest Snow Landscape Research. 80, 23-44.

Braun, S., Thomas, V.F.D., Quiring, R., Flückiger, W., 2010. Does nitrogen deposition increase forest production? The role of phosphorus. Environ. Pollut. 158, 2043-2052.

Briceño-Elizondo, E., Garcia-Gonzalo, J., Peltola, H., Matala, J., Kellomäki, S., 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. For. Ecol. Manage. 232, 152-167.

Briceño-Elizondo, E., Jäger, D., Lexer, M.J., Garcia-Gonzalo, J., Peltola, H., Kellomäki, S., 2008. Multi-criteria evaluation of multi-purpose stand treatment programmes for Finnish boreal forests under changing climate. Ecol. Indicators 8, 26-45.

Bugmann, H., 1997. Sensitivity of forests in the European Alps to future climatic change. Clim. Res. 8, 35-44.

Bugmann, H., Brang, P., Elkin, C., Henne, P., Jakoby, O., Lévesque, M., Lischke, H., Psomas, A., Rigling, A., Wermelinger, B., Zimmermann, N.E., 2014. Climate change impacts on tree species, forest properties, and ecosystem services. In: CH2014-Impacts (2014) (Ed.), Toward Quantitative Scenarios of Climate Change Impacts in Switzerland. OCCR, FOEN, MeteoSwiss, C2SM, Agroscope, and ProClim, Bern, Switzerland, pp. 79-89.

Bugmann, H., Cramer, W., 1998. Improving the behaviour of forest gap models along drought gradients. For. Ecol. Manage. 103, 247-263.

Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055-2074.

Bürgi, M., 1998. Habitat alterations caused by long-term changes in forest use in northeastern Switzerland. In: Kirby, K., Watkins, C. (Eds.), The ecological history of European forests: based on presentations given at the International conference on advances in forest and woodland history, held at the University of Nottingham in September 1996. CAB INTERNATIONAL, pp. 203-211.

Bürgi, M., Gimmi, U., Stuber, M., 2013. Assessing traditional knowledge on forest uses to understand forest ecosystem dynamics. For. Ecol. Manage. 289, 115-122.

CH2011, 2011. Swiss climate change scenarios CH2011. C2SM, MeteoSwiss, ETH, NCCR Climate and OcCC, Zurich, Switzerland, p. 88.

CH2014-Impacts, 2014. Toward quantitative scenarios of climate change impacts in Switzerland. OCCR, FOEN, MeteoSwiss, C2SM, Agroscope, and ProClim, Bern, Switzerland.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12, 351-366.

Coudun, C., Gégout, J.-C., Piedallu, C., Rameau, J.-C., 2006. Soil nutritional factors improve models of plant species distribution: an illustration with Acer campestre (L.) in France. J. Biogeogr. 33, 1750-1763.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. Bioscience 51, 723-734.

Dawes, M.A., Philipson, C.D., Fonti, P., Bebi, P., Hattenschwiler, S., Hagedorn, F., Rixen, C., 2015. Soil warming and CO2 enrichment induce biomass shifts in alpine tree line vegetation. Global Change Biol. 21, 2005-2021.

Elkin, C., Cailleret, M., Bugmann, H., 2013a. Climate change impacts on forest ecosystem services at local and landscape scale: the challenge of creating representative regional projections. Impacts World 2013 Conference Proceedings, Potsdam: Potsdam Institute for Climate Impact Research, pp. 637-647.

Elkin, C., Gutiérrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., Bugmann, H., 2013b. A 2 °C warmer world is not safe for ecosystem services in the European Alps. Global Change Biol. 19, 1827-1840.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht. Verlag Eugen Ulmer, Stuttgart.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araujo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J.C., Gomez-Garcia, D., Grytnes, J.A., Heegaard, E., Hoistad, F., Nogues-Bravo, D., Normand, S., Puscas, M., Sebastia, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P., Guisan, A., 2011. 21st century climate change threatens mountain flora unequally across Europe. Global Change Biol. 17, 2330-2341.

Esper, J., Schweingruber, F.H., 2004. Large-scale treeline changes recorded in Siberia. Geophys. Res. Lett. 31, 5.

Fischer, A.M., Liniger, M.A., Appenzeller, C., 2015. Climate scenarios of seasonal means: inter-variable and inter-seasonal correlations of change estimates. CH2011 Extension Series No. 3. MeteoSwiss and Center for Climate Systems Modeling, Zurich, Switzerland.

Fischer, A.M., Weigel, A.P., Buser, C.M., Knutti, R., Künsch, H.R., Liniger, M.A., Schär, C., Appenzeller, C., 2012. Climate change projections for Switzerland based on a Bayesian multi-model approach. Int J Climatol 32, 2348-2371.

Frehner, M., Wasser, B., Schwitter, R., 2005. Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion, Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Frelich, L.E., Reich, P.B., 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? Front. Ecol. Environ. 8, 371-378.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., Woodward, F.I., 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Acad. Sci. U.S.A. 111, 3280-3285.

Fürstenau, C., Badeck, F.W., Lasch, P., Lexer, M.J., Lindner, M., Mohr, P., Suckow, F., 2007. Multiple-use forest management in consideration of climate change and the interests of stakeholder groups. European Journal of Forest Research 126, 225-239.

Füssel, H.M., Klein, R.J.T., 2006. Climate change vulnerability assessments: An evolution of conceptual thinking. Clim. Change 75, 301-329.

Galbraith, D., Levy, P.E., Sitch, S., Huntingford, C., Cox, P., Williams, M., Meir, P., 2010. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. New Phytol. 187, 647-665.

Gelman, A., Su, Y.-S., 2014. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package, version 1.7-07., http://CRAN.R-project.org/package=arm.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699-711.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.J., Nabuurs, G.J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203-207.

Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R., Bartlein, P.J., 2001. Global Change in Forests: Responses of Species, Communities, and Biomes: Interactions between climate change and land use are projected to cause large shifts in biodiversity. Bioscience 51, 765-779.

Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., Tinner, W., 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. Landscape Ecol. 28, 819-833.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kuhn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecol. Biogeogr. 21, 50-63.

Hlasny, T., Barcza, Z., Barka, I., Merganicova, K., Sedmak, R., Kern, A., Pajtik, J., Balazs, B., Fabrika, M., Churkina, G., 2014. Future carbon cycle in mountain spruce forests of Central Europe: Modelling framework and ecological inferences. For. Ecol. Manage. 328, 55-68.

Hlasny, T., Barcza, Z., Fabrika, M., Balazs, B., Churkina, G., Pajtik, J., Sedmak, R., Turcani, M., 2011. Climate change impacts on growth and carbon balance of forests in Central Europe. Clim. Res. 47, 219-236.

IPCC, 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jolly, W.M., Dobbertin, M., Zimmermann, N.E., Reichstein, M., 2005. Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. Geophys. Res. Lett. 32, L18409.

Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Global Change Biol. 12, 2163-2174.

Kahle, H.P., Karjalainen, T., Agren, G.I., Kellomäki, S., van Oijen, M., Prietzel, J., Spiecker, H. (Eds.), 2008. Causes and consequences of forest growth trends in Europe: Results of the RECOGNITION project conclusions. Brill.

Keller, M. (Ed.), 2011. Swiss National Forest Inventory. Manual of the field survey 2004–2007. Swiss Federal Research Institute WSL, Birmensdorf, CH.

Kellomäki, S., Peltola, H., Nuutinen, T., Korhonen, K.T., Strandman, H., 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philosophical Transactions of the Royal Society B-Biological Sciences 363, 2341-2351.

Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A., Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901-2008. Clim. Change 115, 343-363.

Kint, V., Lasch, P., Lindner, M., Muys, B., 2009. Multipurpose conversion management of Scots pine towards mixed oak-birch stands-A long-term simulation approach. For. Ecol. Manage. 257, 199-214.

Knutti, R., Furrer, R., Tebaldi, C., Cermak, J., Meehl, G.A., 2010. Challenges in Combining Projections from Multiple Climate Models. J. Clim. 23, 2739-2758.

Körner, C., 2003. Carbon limitation in trees. J. Ecol. 91, 4-17.

Kulakowski, D., Bebi, P., Rixen, C., 2011. The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120, 216-225.

Kullman, L., 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. J. Ecol. 90, 68-77.

Lasch, P., Badeck, F.W., Suckow, F., Lindner, M., Mohr, P., 2005. Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). For. Ecol. Manage. 207, 59-74.

Leibundgut, H., 1949. Grundzüge der schweizerischen Waldbaulehre. Forstw Cbl 68, 257-291.

Levesque, M., Rigling, A., Bugmann, H., Weber, P., Brang, P., 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric. For. Meteorol. 197, 1-12.

Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Reyer, C., Delzon, S., van der Maaten, E., Schelhaas, M.J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., Hanewinkel, M., 2014. Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? J. Environ. Manage. 146, 69-83.

Lindner, M., Lasch, P., Erhard, M., 2000. Alternative forest management strategies under climatic change - Prospects for gap model applications in risk analyses. Silva Fenn. 34, 101-111.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698-709.

Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutierrez, E., 2006. Increasing aridity is enhancing Silver fir (Abies alba Mill.) water stress in its south-western distribution limit. Clim. Change 79, 289-313.

MEA, 2005. Millennium Ecosystem Assessment, Island Press, Washington, D.C.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.-C., Thuiller, W., Araújo, M.B., Guisan, A., Zimmermann, N.E., 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. Ecography 33, 1038-1048.

Mette, T., Dolos, K., Meinardus, C., Brauning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., Wellstein, C., 2013. Climatic turning point for beech and oak under climate change in Central Europe. Ecosphere 4, 19.

Mina, M., Bugmann, H., Klopcic, M., Cailleret, M., submitted. The devil lies in the management when assessing the impacts of climate change on mountain forest dynamics. Submitted in Regional Environmental Changes.

Moorcroft, P.R., 2006. How close are we to a predictive science of the biosphere? Trends Ecol. Evol. 21, 400-407.

Moore, A.D., 1989. On the maximum growth equation used in forest gap simulation-models. Ecol. Model. 45, 63-67.

Morales, P., Hickler, T., Rowell, D.P., Smith, B., T Sykes, M., 2007. Changes in European ecosystem productivity and carbon balance driven by regional climate model output. Global Change Biol. 13, 108-122.

Motta, R., Edouard, J., 2005. Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley, Piedmont, Italypper Susa Valley, Piedmont, Italy. Can J Forest Res 35, 21-36.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4, 133-142.

Nakicenovic, N., Swart, R., 2000. Special report on emissions scenarios. Special Report on Emissions Scenarios, Edited by and Robert Swart, pp. 612. ISBN 0521804930. Cambridge, UK: Cambridge University Press, July 2000. 1.

Naudts, K., Ryder, J., J. McGrath, M., Otto, J., Chen, Y., Valade, A., Bellasen, V., Berhongaray, G., Bönisch, G., Campioli, M., Ghattas, J., De Groote, T., Haverd, V., Kattge, J., MacBean, N., Maignan, F., Merilä, P., Penuelas, J., Peylin, P., Pinty, B., Pretzsch, H., Schulze, E.D., Solyga, D., Vuichard, N., Yan, Y., Luyssaert, S., 2014. A vertically discretised canopy description for ORCHIDEE (SVN r2290) and the modifications to the energy, water and carbon fluxes. Geosci. Model Dev. Discuss. 7, 8565-8647.

O'Brien, K., Sygna, L., Haugen, J.E., 2004. Vulnerable or resilient? A multi-scale assessment of climate impacts and vulnerability in Norway. Clim. Change 64, 193-225.

OcCC, 2007. Klimaänderung und die Schweiz 2050. Erwartete Auswirkungen auf die Umwelt, Gesellschaft und Wirtschaft. OcCC and ProClim, Bern.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecol. Biogeogr. 12, 361-371.

Peng, C., Zhou, X., Zhao, S., Wang, X., Zhu, B., Piao, S., Fang, J., 2009. Quantifying the response of forest carbon balance to future climate change in Northeastern China: Model validation and prediction. Global Planet. Change 66, 179-194.

Penuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biol. 9, 131-140.

Piao, S.L., Wang, X.H., Ciais, P., Zhu, B., Wang, T., Liu, J., 2011. Changes in satellite-derived vegetation growth trend in temperate and boreal Eurasia from 1982 to 2006. Global Change Biol. 17, 3228-3239.

Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S., Hickler, T., Lucht, W., Sitch, S., Smith, B., Sykes, M., 2007. Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell, J., Pataki, D., Pitelka, L. (Eds.), Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, pp. 175-192.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/.

Rasche, L., 2014. The importance of climate variability changes for future levels of tree-based forest ecosystem services. International Journal of Biodiversity Science Ecosystem Services & Management 10, 187-197.

Rasche, L., Fahse, L., Bugmann, H., 2013. Key factors affecting the future provision of tree-based forest ecosystem goods and services. Clim. Change 118, 579-593.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2011. Getting a virtual forester fit for the challenge of climatic change. J. Appl. Ecol. 48, 1174-1186.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2012. Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. Ecol. Model. 232, 133-143.

Rebetez, M., Dobbertin, M., 2004. Climate change may already threaten *Scots pine* stands in the Swiss Alps. Theor Appl Climatol 79, 1-9.

Remund, J., Rihm, B., Huguenin-Landl, B., 2014. Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert. Meteotest, Bern.

Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., Pilz, T., 2014. Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. Ann. For. Sci. 71, 211-225.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Global Change Biol. 19, 229-240.

Rocca, M.E., Brown, P.M., MacDonald, L.H., Carrico, C.M., 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For. Ecol. Manage. 327, 290-305.

Rössler, O., Diekkruger, B., Loffler, J., 2012. Potential drought stress in a Swiss mountain catchment-Ensemble forecasting of high mountain soil moisture reveals a drastic decrease, despite major uncertainties. Water Resour. Res. 48, 19.

Rowland, L., Harper, A., Christoffersen, B.O., Galbraith, D.R., Imbuzeiro, H.M.A., Powell, T.L., Doughty, C., Levine, N.M., Malhi, Y., Saleska, S.R., Moorcroft, P.R., Meir, P., Williams, M., Rowland, L., Harper, A., Christoffersen, B.O., Galbraith, D.R., Imbuzeiro, H.M.A., Powell, T.L., Doughty, C., Levine, N.M., Malhi, Y., Saleska, S.R., Moorcroft, P.R., Meir, P., Williams, M., 2014. Modelling climate change responses in tropical forests: similar productivity estimates across five models, but different mechanisms and responses. Geoscientific Model Development Discussions 7, 7823-7859.

Ruiz-Benito, P., Madrigal-Gonzalez, J., Ratcliffe, S., Coomes, D.A., Kandler, G., Lehtonen, A., Wirth, C., Zavala, M.A., 2014. Stand structure and recent climate change constrain stand basal area change in European forests: A comparison across boreal, temperate, and mediterranean biomes. Ecosystems 17, 1439-1454.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biol. 9, 1620-1633.

Schmid, S., Thürig, E., Kaufmann, E., Lischke, H., Bugmann, H., 2006. Effect of forest management on future carbon pools and fluxes: A model comparison. For. Ecol. Manage. 237, 65-82.

Seidl, R., Rammer, W., Lexer, M.J., 2011a. Climate change vulnerability of sustainable forest management in the Eastern Alps. Clim. Change 106, 225-254.

Seidl, R., Schelhaas, M.-J., Lexer, M.J., 2011b. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biol. 17, 2842-2852.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nature Clim. Change 4, 806-810.

Staudhammer, C.L., LeMay, V.M., 2001. Introduction and evaluation of possible indices of stand structural diversity. Can. J. For. Res. 31, 1105-1115.

Svenning, J.-C., Skov, F., 2004. Limited filling of the potential range in European tree species. Ecol. Lett. 7, 565-573.

Temperli, C., Bugmann, H., Elkin, C., 2012. Adaptive management for competing forest goods and services under climate change. Ecol. Appl. 22, 2065-2077.

Temperli, C., Zell, J., Bugmann, H., Elkin, C., 2013. Sensitivity of ecosystem goods and services projections of a forest landscape model to initialization data. Landscape Ecol. 28, 1337-1352.

Thornthwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology, Drexel Institute of Technology, Centerton, New Jersey 10, 185-311.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. U.S.A. 102, 8245-8250.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833-2849.

Valle, D., Staudhammer, C.L., Cropper, W.P., Gardingen, P.R., 2009. The importance of multimodel projections to assess uncertainty in projections from simulation models. Ecol. Appl. 19, 1680-1692.

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Retana, J., 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Global Change Biol. 18, 1028-1041.

Wamelink, G.W.W., Wieggers, H.J.J., Reinds, G.J., Kros, J., Mol-Dijkstra, J.P., van Oijen, M., de Vries, W., 2009. Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on carbon sequestration by European forests and forest soils. For. Ecol. Manage. 258, 1794-1805.

Watt, A.S., 1947. Pattern and Process in the Plant Community. J. Ecol. 35, 1-22.

Weber, P., Rigling, A., Bugmann, H., 2008. Sensitivity of stand dynamics to grazing in mixed Pinus sylvestris and Quercus pubescens forests: A modelling study. Ecol. Model. 210, 301-311.

World Meteorological Organisation, 2014. WMO Greenhouse gas bulletin-the state of greenhouse gases in the atmosphere using global observations through 2013. WMO Geneva.

WSL, 2011. Schweizerisches Landesforstinventar LFI. Datenbankauszug vom 22. Dezember 2011. Markus Huber. Eidg. Forschungsanstalt WSL, Birmensdorf.

Zelenka, A., Czeplak, G., D'Agostino, V., Weine, J., Maxwell, E., Perez, R., Noia, M., Ratto, C., Fest, R., 1992. Techniques for supplementing solar radiation network data.

Zierl, B., Bugmann, H., 2007. Sensitivity of carbon cycling in the European Alps to changes of climate and land cover. Clim. Change 85, 195-212.

Zingg, A., Bürgi, A., 2008. Trockenperioden seit 1900 und Waldwachstum: eine Analyse langfristiger Datenreihen. Schweizerische Zeitschrift für Forstwesen 159, 352-361.

Supplemental Material

Appendix S1: Forest stratification

Table S1.1: Forest eco-regions of Switzerland and their elevation zones modified from NaiS (Frehner *et al.*, 2005). Boundaries of elevation zones are given in meters above sea level (m a.s.l.)

	Jura (J)	**Swiss Plateau (M)**	**Northern Pre-Alps (NPA)**	**Northern Central Alps (NCA)***	**High Alps (HA)**	**Southern Central Alps (SCA)**	**Southern Pre-Alps (SPA)**
colline	< 300	< 350	-	Downy oak forests (NaiS)**	-	300-1000	300-1000
sub montane	300-650	350-650	350-650		-	-	-
lower montane	650-900	650-900	650-900		-	-	-
upper montane	900-1350	900-1350	900-1350		-	-	-
montane	-	-	-	-	-	-	1000-1600
high montane	1350-1550	>1350	1350-1600	<1650	600-1650	1000-1650	-
subalpine	>1550	-	1600-1900	1650-1850	1650-1900	1650-1900	1600-1900
upper subalpine	-	-	-	>1850	> 1900	> 1900	> 1900

*Only subregion “b” was considered. ** Lowest elevation zone is defined by occurrence of downy oak (Q. pubescens) forests.

Table S1.2: Overview of the NFI attributes stand structure and stand development that were used for the forest stratification. The description of the levels follows Keller (2011).

Stand structure*		**Stand development**	
Levels	Description	Levels	Description
Single-layered	Crowns of the trees forming the stand extend into the upper layer	*Young growth/thicket*	$d_{dom} < 12$ cm
Multi-layered	Two or more uniform layers	*Pole wood*	$d_{dom} = 12–30$ cm
All-aged/all-sized	Stands with several indistinct layers	*Young timber*	$d_{dom} = 31–40$ cm
Clustered	Crowded groups of trees with different heights.	*Medium timber*	$d_{dom} = 41–50$ cm
		Old timber	$d_{dom} > 50$ cm
		Mixed	Collective of the 100 strongest trees/ha varies over at least 3 diameter classes

*The proportion of different height layers (lower, medium upper) defines the stand structure (Keller, 2011).

Appendix S2: Forest management

Table S2.1: Overview about forest management for different elevation zones and forest types. Information about applied forest management regimes include the management type, year of first management intervention in the simulation (start), interval between interventions, harvest intensity and affected dbh classes. For the plentering management regime, residual basal area (m^2ha^{-1}) and target dbh (cm) are listed.

Elevation zone	Forest type	Management type	Start (Year)	Interval (Years)	Intensity (%)	Managed dbh classes	Residual basal area (for plentering)	Target dbh (for plentering)
upper subalpine	uneven-aged	MF-Ple	2020	35	25	<40cm:20% >40cm:80%	-	-
	even-aged	MF-Ple	2010	35	25	<30cm:20% >30cm:80%	-	-
subalpine	uneven-aged	MF-Ple	2020	30	30	<40cm:20% >40cm:80%	-	-
	even-aged	MF-Ple	2010	30	30	<30cm:20% >30cm:80%	-	-
high montane	uneven-aged	MF-Ple	2020	25	30	<40cm:20% >40cm:80%	-	-
	even-aged	MF-Ple	2010	25	30	<30cm:20% >30cm:80%	-	-
upper montane montane lower montane sub montane colline	uneven-aged	Ple	2020	10	-	-	Initial basal area	dbh>=80cm
	even-aged (rh)	FC / FC /TA…	2010 (FC)	5 FC)/ 12(TA)	33/67/15	All		
	even-aged (n-rh)	TA	2016	12	15	Larger dbh classes*	-	-

Terms/definitions:

MF-Ple = mountain forest plentering
Ple = plentering
TA = thinning from above
FC = final cutting
rh = ready for cutting (only even-aged forest; ddom>=60cm)
n-hf = not ready for cutting (only even-aged forest; ddom <60cm)

Residual basal area =Remaining basal area after harvest intervention
Initial basal area= Stand basal area at beginning of simulation (plentering)
Target dbh = Trees with dbh above this threshold are harvested first to reach residual basal area (plentering)
* For thinning, a Weibull function is applied across dbh distribution. For thinning from above, more trees of the larger dbh classes are harvested.
All tree species present in the forest stand are harvested.

Appendix S3: Climate change scenarios

Seasonal climate delta values assuming an A2 greenhouse gas emission scenario (Nakicenovic and Swart, 2000) were used (absolute °C change in temperature, relative change in precipitation) that were downscaled for five regions of Switzerland (North-eastern Switzerland, Western Switzerland, Western Alps, Eastern Alps, and Southern Switzerland) based on projections from 20 Global and Regional climate model chains (Fischer *et al.*, 2015). For the years 1980-2009 as reference period, projections were made for three different climate periods (2020-2049, 2045-2074, and 2070-2099) including a medium (i.e., “best guess”) estimate of climate deviation and, in addition, lower and upper estimates to define projection uncertainties.

Given no statistically significant dependencies between seasons within and between temperature and precipitation, a rigorous consideration of seasonal estimate uncertainty would basically require running simulation tests with all 6561 possible estimate combinations (CH2014-Impacts, 2014). In collaboration with the ETH Center for Climate Systems Modeling (C2SM), we developed an approach to consider uncertainty in climate projections appropriately while still reducing the full set of possible estimate combinations to a feasible number. Since simulations were supposed to be conducted until 2100, we focused on the last climate period (2070 - 2099) for the selection of estimate combinations. Here, a few significant dependencies for seasonal estimates did exist (Andreas Fischer, personal communication): 1) Positive correlations between seasonal estimates for temperature, 2) a negative correlation between estimates of temperature and precipitation in summer, and 3) a positive correlation between estimates of fall and winter for precipitation. Assuming these dependencies holding equally true for all regions, the initial set of 6561 estimate combination was reduced to 45. Out of this final set, 10 combinations of climate estimates were drawn randomly while the combination holding all medium estimates for temperature and precipitation was chosen deliberately, resulting in a set of 11 climate scenarios for the simulations of future forest dynamics.

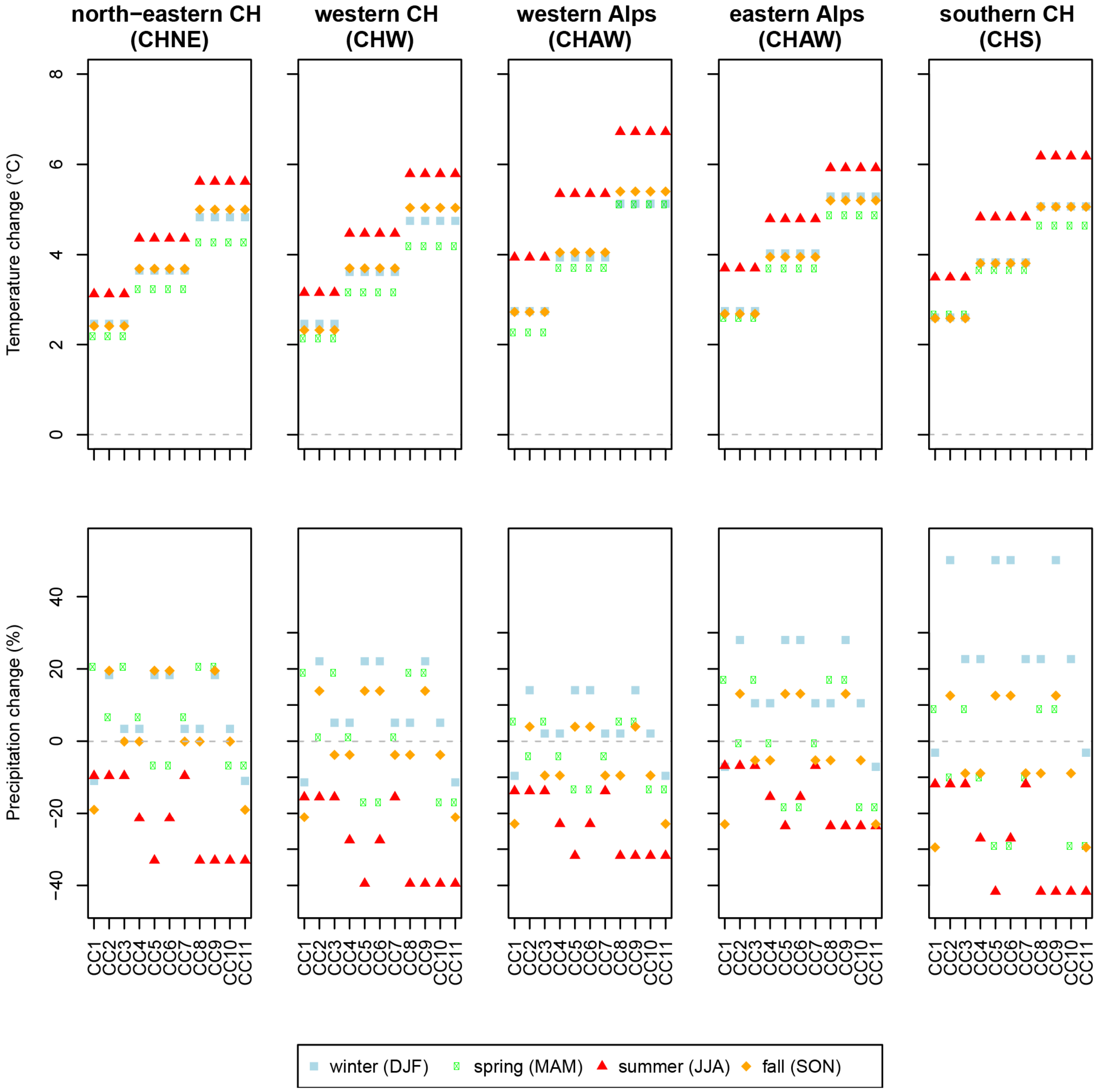


Figure S3.1: Climate change delta values assuming an A2 emission scenario for temperature (absolute °C change: upper panels) and precipitation (percent change: lower panels) for the five regions of Switzerland based on the CH2011 report (2011; 2015). Delta values are given for the 11 climate scenarios and seasons of the year.

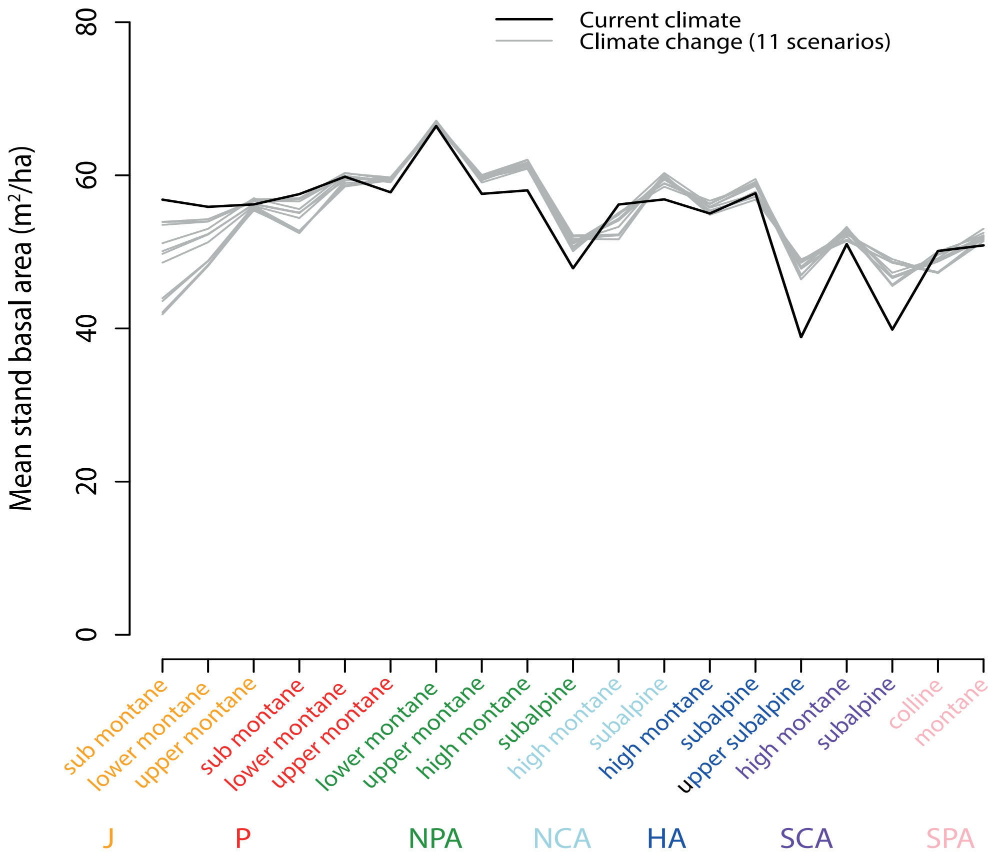


Figure S3.2: Simulated stand basal area (year 2100) under current climate (black line) and under 11 climate change scenarios (grey lines). Mean values across all strata of each elevation zone per eco-region are shown.

Appendix S4: Indices for forest ecosystem services

In mountain regions, forests commonly play an integral role in providing protection from gravitational hazards such as snow avalanches, rockfall, and landslides (Brang *et al.*, 2006; Chave *et al.*, 2009). Frehner *et al.* (2005) developed guidelines for sustainability in protection forests (NaiS) defining requirements for forest stands to provide effective protection against various natural hazards. Using these guidelines we developed a general index that represents the protective capability of forests across a range of gravitational hazard risks.

The general ability of a forest to protect against gravitational hazards depends on the species mixture, vertical structure, rooting stability of live trees and regeneration potential (Frehner *et al.*, 2005). We incorporated these characteristics into a single Gravitational Protection Forest Index (GPFI) that includes measurements of the density of trees $(\theta_{density})$, structural diversity of large trees (θ_{LC}), structural diversity of small trees (θ_{SC}), and species diversity (θ_{SD}):

$$GPFI = 50 * \theta_{density} + 25 * \theta_{LC} + 10 * \ \theta_{SC} + 15 * \ \theta_{SD} \tag{1}$$

The weight that was assigned to each of the characteristics in eq. (1) reflects the view that achieving a forest structure that protects against gravitational hazards is of principle importance, while maintaining a mixed forest and a high level of regeneration potential is of secondary importance.

Minimal requirements for the individual characteristics of this index were derived based on minimal and ideal profiles for protection forests (Frehner *et al.*, 2005). By default, minimal requirements were defined for a forest cell of 25 x 25 m (625m^2). Applications using a different cell size (i.e. patch size = 500m^2) need to consider a correction factor ($corrF = {}^{actual\ cell\ size[m^2]}/_{625}$):

$$\theta_{density} = \min\left[\left(\frac{\#\,trees/ha\ \ with\ DBH > 24}{400}\right), 1\right] \tag{2}$$

$$\theta_{LC} = \min\left[\left(\frac{\#cohorts\ with\ trees > 24\ cm\ DBH}{(4 * corrF)}\right), 1\right] \tag{3}$$

$$\theta_{SC} = \min\left[\left(\frac{\#\ cohorts\ with\ trees < 12\ cm\ DBH}{(2 * corrF)}\right), 1\right] \tag{4}$$

$$\theta_{SD} = \min\left[\left(\frac{\#\ species}{(3 * corrF)}\right), 1\right] \tag{5}$$

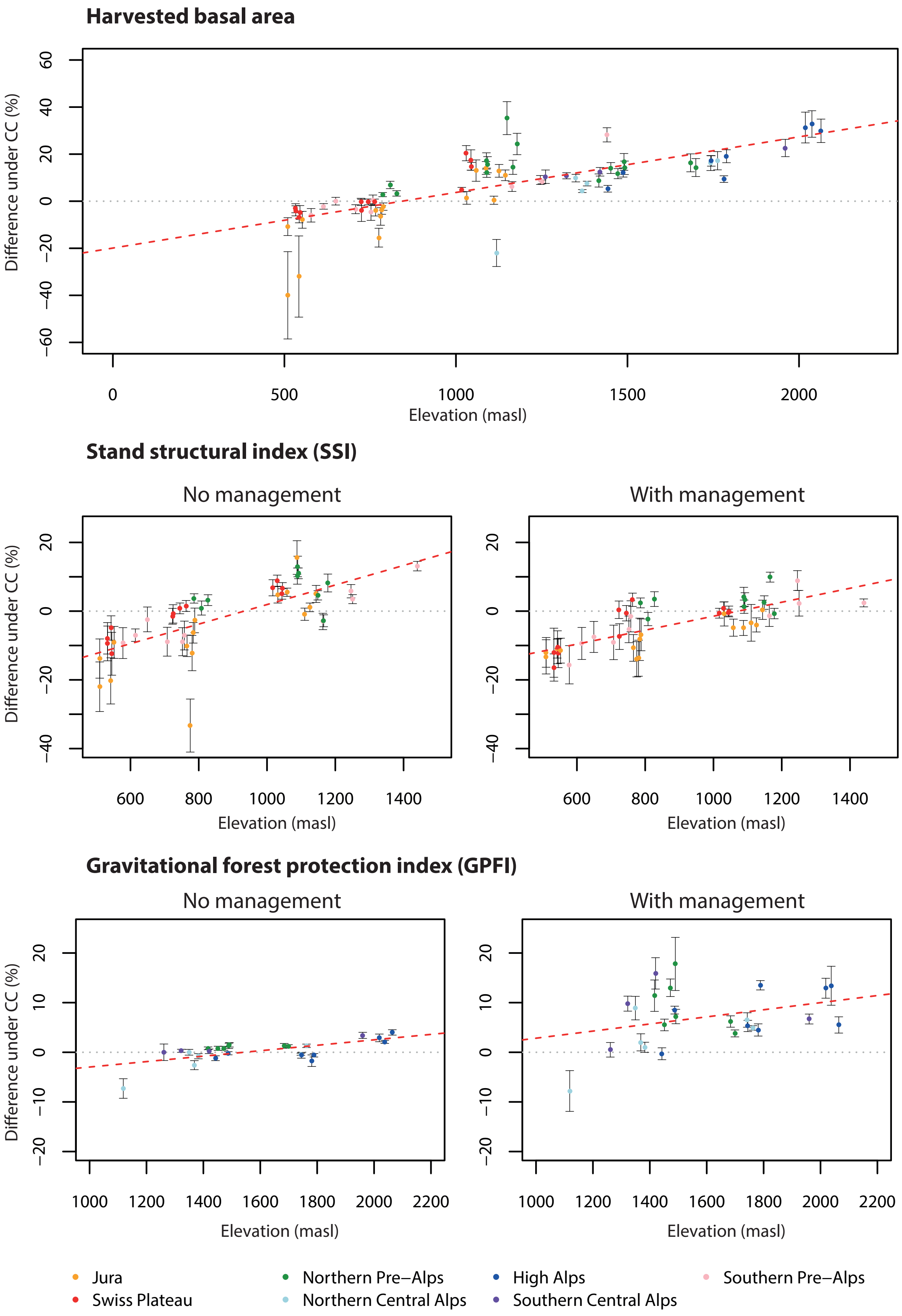


Figure S4.1: Differences between simulated forest ecosystem services (ES) under climate changes (11 scenarios) and current climate for individual forest stands. Median difference and standard deviations are shown for harvested basal area (top), stand structural index (center), and the gravitational forest protection index (bottom). Forest stands are ordered according to average stand elevation (meters above sea level). The median difference was positively correlated with stand elevation for all ES (all $P<0.01$).

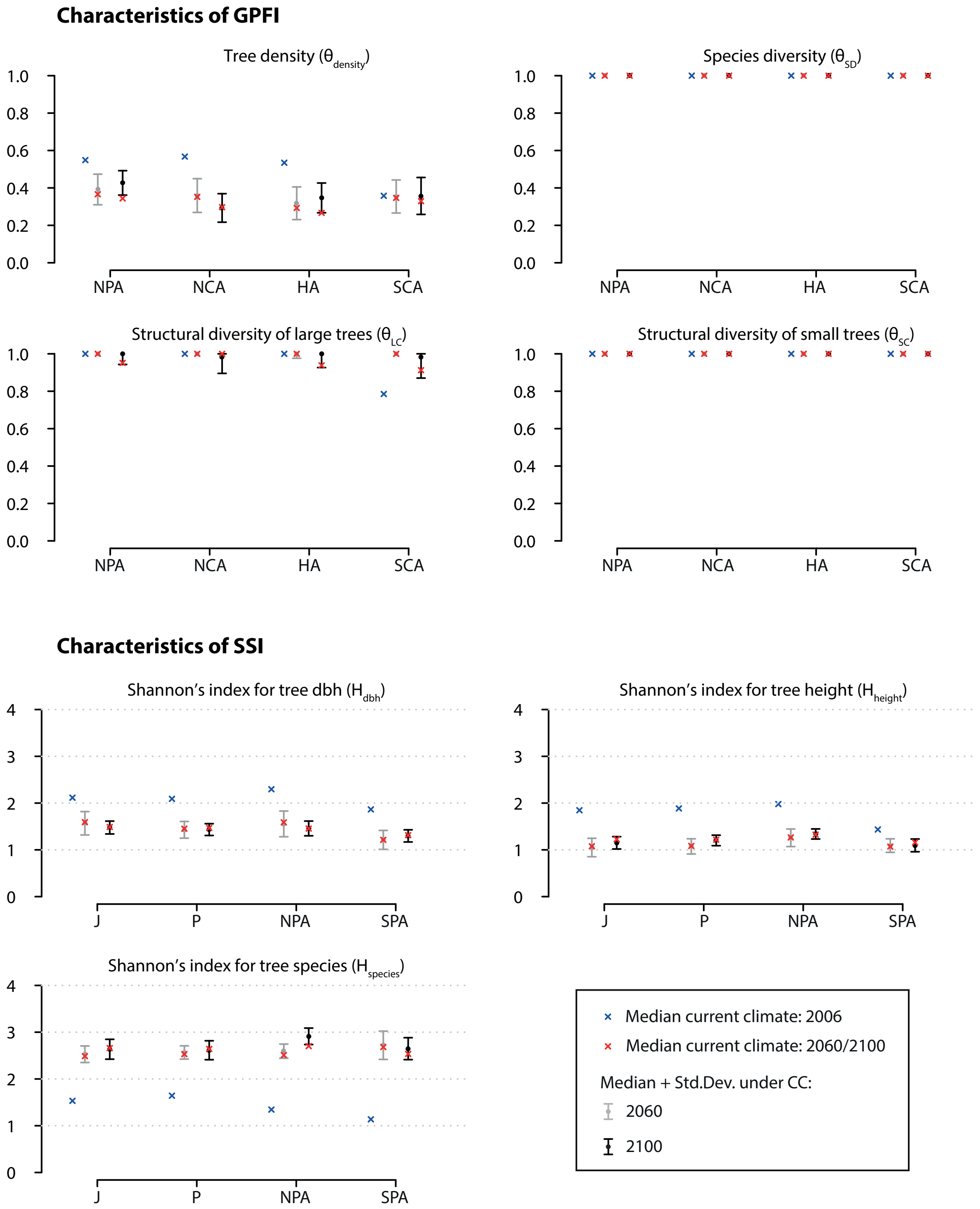


Figure S4.2: Individual compounds of simulated forest ecosystem service metrics. Above: Characteristics of Gravitational Protection Forest Index (GPFI); below: Shannon's stand structural index (SSI). The median is shown for simulations under current climate (years 2006, 2060, and 2100) and the 11 climate change scenarios including standard deviation for the years 2060 and 2100. Simulation results are aggregated according to eco-regions (J = Jura, M = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps).

Table S4.1: Ecosystem Service metrics (median and standard deviation) of harvest, protection (GPFI), and biodiversity/recreation (SSI) simulated by ForClim BC-MAP for each eco-region with forest management. Mean annual harvested basal area ($m^2ha^{-1}yr^{-1}$) was calculated under current climate for two periods (2006-2060, 2061-2100), and the average relative differences (%) due to climate change are listed as well (Diff-CC). For GPFI and SSI, absolute estimates (current climate) are given for the initial state of the forest stand (year 2006) and the years 2060 and 2100. For the latter, the average relative differences due to climate change (Diff-CC) are also indicated.

	Harvest				**GPFI**					**SSI**				
Region	2006-2060 [m^2/ha.yr]	Diff-CC60 [%]	2061-2100 [m^2/ha.yr]	Diff-CC100 [%]	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]
Jura	0.5 ±0.1	0.5 ±2.8	0.8 ±0.1	-1.5 ±11.9	–	–	–	–	–	2.1 ±0.4	1.0 ±0.4	-1.1 ±4.5	1.5 ±0.2	-6.3 ±8.8
Swiss Plateau	0.6 ±0.1	0.6 ±3.4	0.9 ±0.1	0.0 ±8.7	–	–	–	–	–	2.1 ±0.5	1.0 ±0.4	0.7 ±4.9	1.6 ±0.2	-1.8 ±8.8
Northern Pre-Alps	0.5 ±0.2	1.5 ±2.1	0.6 ±0.2	10.4 ±6.5	77.4 ±8.2	70.2± 3.7	0.8 ±0.6	65.8 ±6.8	8.1 ±3	2.1 ±0.3	1.6 ±0.4	2.3 ±3.5	1.8 ±0.3	3.2 ±5.9
Northern Central Alps	0.5 ±0.1	1.1 ±1.2	0.6 ±0.2	4.2 ±10.5	78.4 ±9.9	71.2 ±5.3	0.5 ±0.7	66.3 ±6.3	3.7 ±5	–	–	–	–	–
High Alps	0.4 ±0.1	1.9 ±3.0	0.4 ±0.2	14.9 ±10.3	76.7 ±10	66.4 ±4.4	0.2 ±0.7	64.7 ±5.5	6.5 ±4.3	–	–	–	–	–
Southern Central Alps	0.3 ±0.2	0.6 ±2.1	0.5 ±0.2	7.8 ±14.8	62 ±20.3	69.6 ±8.3	1.6 ±1.1	66.8 ±11.9	4.9 ±2.2	–	–	–	–	–
Southern Pre-Alps	0.5 ±0.1	0.7 ±2.3	0.7 ±0.1	0.3 ±7.2	–	–	–	–	–	1.2 ±0.6	1.2 ±0.3	-0.2 ±4.9	1.4 ±0.2	-6.4 ±11.1

Table S4.2: Simulated ES metrics protection (GPFI), and biodiversity/recreation (SSI) for model version ForClim v3.3 in simulations without management. Median values and standard deviations are given for each eco-region. Estimates (current climate) are given for the initial state of the forest stand (year 2006) and the years 2060 and 2100, respectively. For the years 2060 and 2100, the average relative differences under climate change (Diff-CC) are also given. Only forest stands from the high montane to upper subalpine zone were considered for the protection index GPFI while for biodiversity/recreation, only forest stands from the colline to upper montane elevation zone were considered.

	GPFI					**SSI**				
Region	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]	2006 [–]	2060 [–]	Diff-CC60 [%]	2100 [–]	Diff-CC100 [%]
Jura	–	–	–	–	–	2.1±0.4	2.1±0.3	0.4±5.6	2.8±0.3	-6±13.1
Swiss Plateau	–	–	–	–	–	2.1±0.5	2.2±0.2	2.8±3	3.1±0.2	0.6±7.1
Northern Pre-Alps	77.4±8.2	79.5±4.6	0.4±0.6	78.6±4	1.2±0.5	2.1±0.3	2.3±0.3	4.2±2.2	3±0.3	4.8±5.1
Northern Central Alps	78.4±9.9	84.6±5.7	0.1±1.3	78.5±5.5	-0.7±3.0	–	–	–	–	–
High Alps	76.7±10	78±6.9	0.3±0.8	74.3±5.5	-0.1±2.1	–	–	–	–	–
Southern Central Alps	62±20.3	75.7±3.1	0.3±1.3	76.9±4.4	0.4±1.9	–	–	–	–	–
Southern Pre-Alps	–	–	–	–	–	1.2±0.6	2.1±0.6	1.3±4.9	2.7±0.7	-4±7.9

Appendix S5: Simulations with ForClim BC-MAP

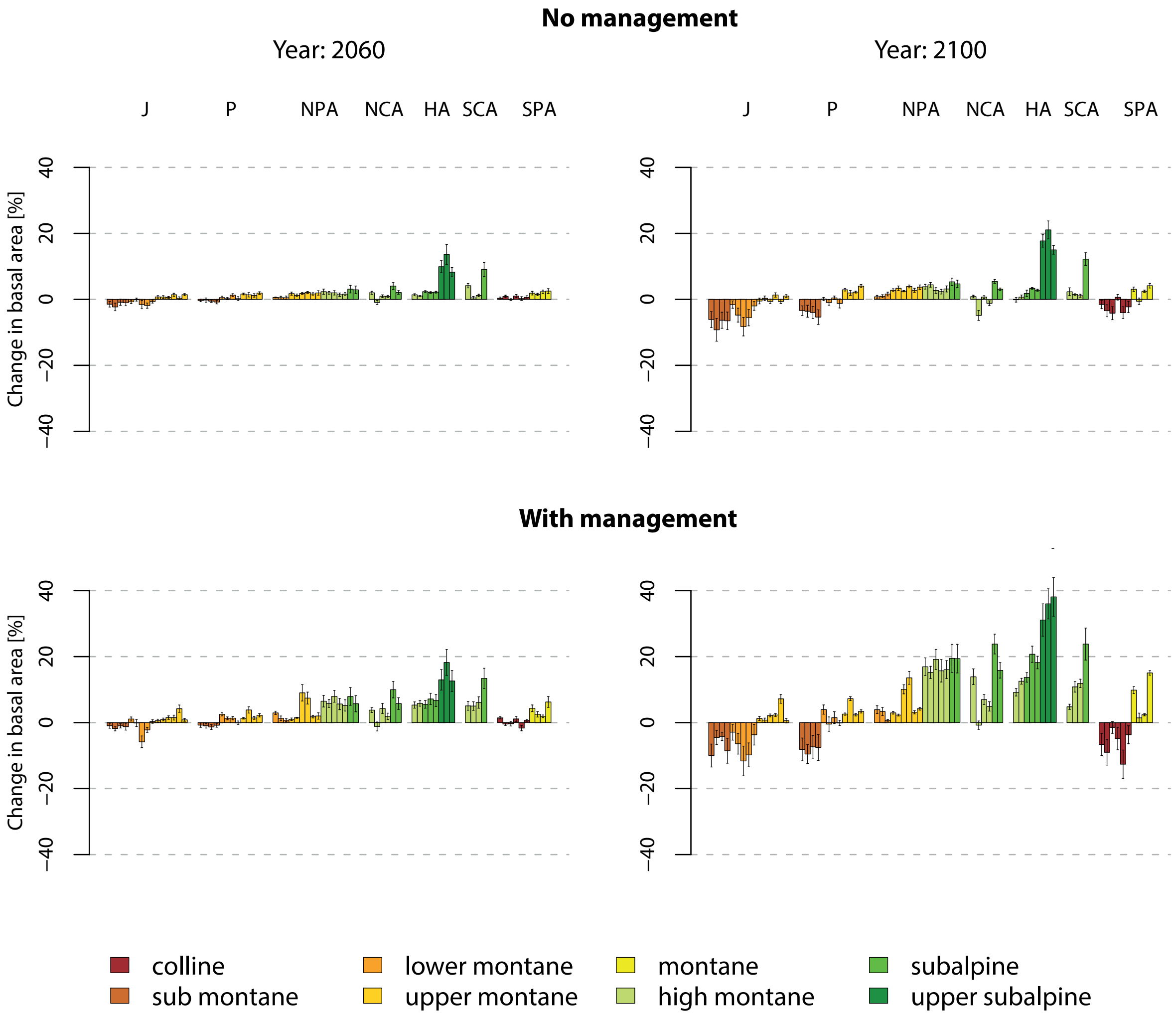


Figure S5.1: Relative difference of basal area (%) for simulations under CC and under current climatic conditions with ForClim BC-MAP for the year 2060 (left panels) and 2100 (right panels) without (upper panels) and with management (lower panels). Each bar represents one forest stratum, ordered by eco-region (J = Jura, M = Swiss Plateau, NPA = Northern Pre-Alps, NCA = Northern Central Alps, HA = High Alps, SCA = Southern Central Alps, and SPA = Southern Pre-Alps) and elevation zones (lowest elevations on the left). The vertical bars are one standard deviation, resulting from the variability of changes in basal area under the 11 CC scenarios.

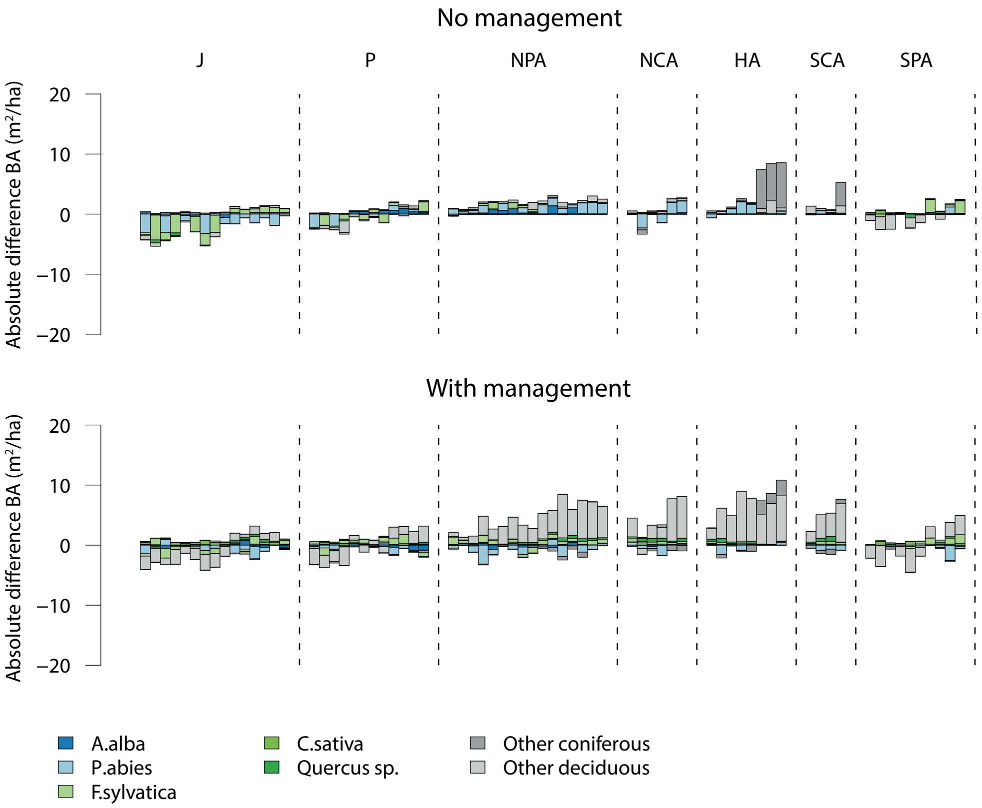


Figure S5.2: Absolute average difference in species-specific basal area between climate change and current climate per forest stand using ForClim BC-MAP. Forest stands are ordered within eco-regions with increasing elevation zone.

Appendix S6: Water holding capacity and simulated drought index

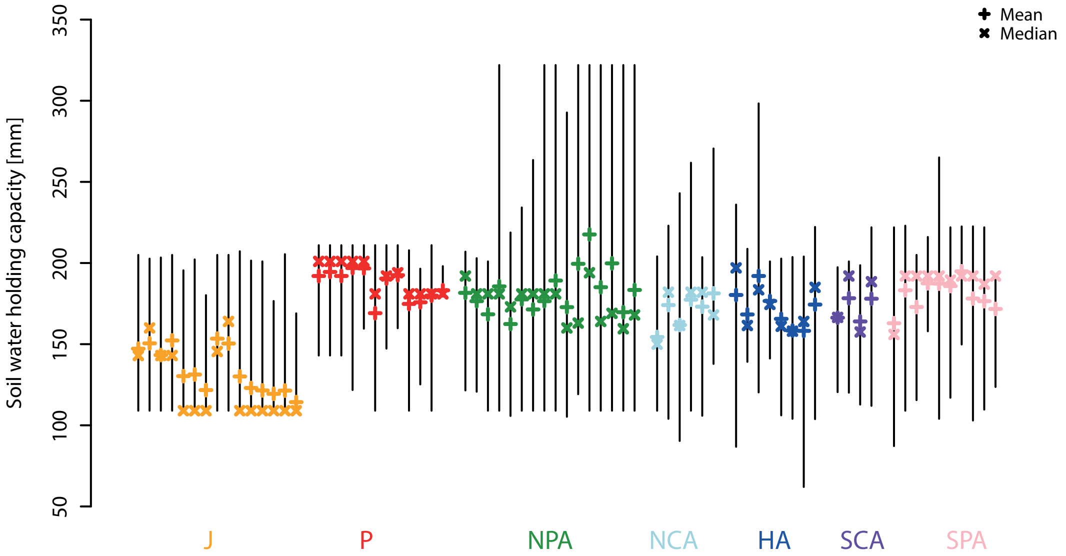


Figure S6.1: Mean and median soil water holding capacity for each stratum. Straight lines indicate the 95%-confidence interval of NFI plots associated to the stratum. Forest strata are ordered within eco-regions with increasing elevation.

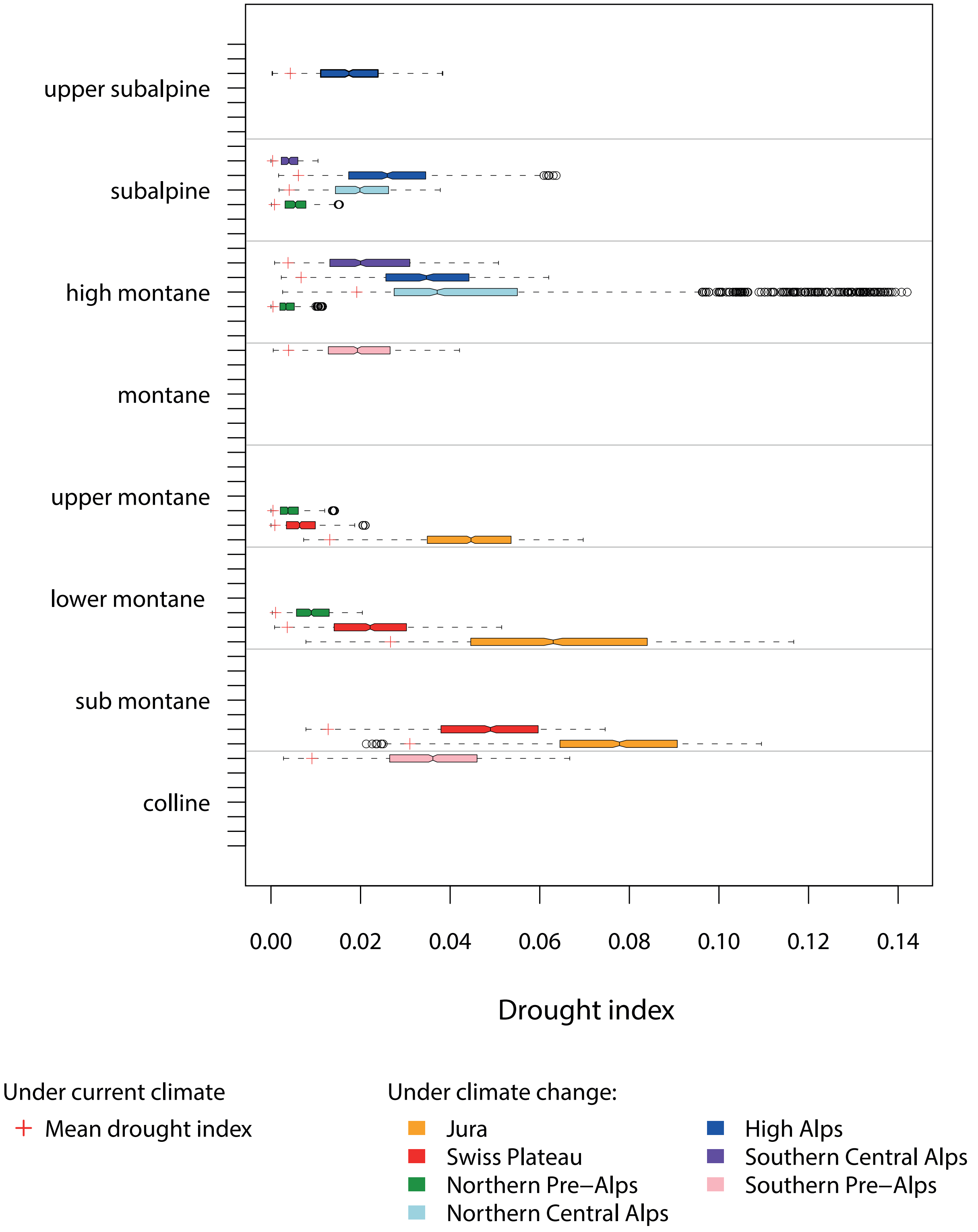


Figure S6.2: Box plots showing the range of simulated drought indices for the years 2086-2100 (i.e., after climate change "ended" in the simulations) including all climate change scenarios. Indices are ordered according to eco-regions (colors) and elevation zones (y-axis). The average drought index for the same period under current climate is shown as well (red crosses).

Synthesis

In this PhD thesis, I aimed to analyze the applicability of empirically derived process formulations in dynamic vegetation models (DVMs). To this end, I tested the behavior and performance of several empirical mortality functions (*Chapters 1* and *2*) in the forest gap model ForClim. Furthermore, I wanted to assess how sensitive common Swiss forest stands will react to climate change. I developed an approach to stratify Swiss forests based on National Forest Inventory (NFI) data (*Chapter 3*) and simulated the future development of these stands under current and future climatic conditions (*Chapter 4*).

The synthesis of these chapters follows the overall structure of the thesis. First, I discuss the findings regarding empirical mortality functions in ForClim and address aspects that I consider to be key for the further development and use of such functions in DVMs. Second, I reflect on the sensitivity of Swiss forests to climate change and on further possible developments of ForClim aimed at producing more accurate simulation results under climate change.

Empirical mortality functions in dynamic vegetation models

General evaluation of results

Only a few empirical mortality functions have been used in dynamic vegetation models (e.g., Larocque *et al.*, 2011), and a comparison of their behavior in DVMs has not been conducted to date. Compared against short-term inventory data from an unmanaged and a managed Norway spruce stand (41 and 72 years, respectively), simulations using empirical mortality functions showed that they are promising alternatives to current mortality formulations, as they provided accurate predictions of stand basal area, total stem numbers, and dbh distribution. However, the identification of a best-fitting mortality model was not possible based on these relatively short time series (<100 yrs), as simulation results were very similar. We were unable to extend the set of sites to include tree species other than Norway spruce, since the tree-ring based mortality function had been calibrated with Norway spruce data only, in contrast to the inventory-based mortality function that had been calibrated for multiple species (using functional types of shade tolerance, see *Chapter 2*).

When simulations for a 400-year period into the future were run under current climate and climate change, a surprising divergence of model behavior was obtained. Due to the lack of empirical reference, validation of such simulation results is not possible, but they still allow us to assess model behavior at longer temporal scales (i.e., centuries) and under changing environmental conditions (cf. Loehle and LeBlanc, 1996), which have the potential to alter tree population dynamics, e.g. by pushing some tree species towards or beyond their physiological limits. Indeed, these long-term simulations revealed considerable differences between the mortality functions, particularly regarding their sensitivity to climate-induced changes in the growth rates. While it had been known that empirical mortality functions can strongly differ in their predictions (e.g., Bigler and Bugmann, 2004a) and the same had been confirmed for theoretical mortality functions among global DVMs (Friend *et al.*, 2014), my results demonstrate that the behavior of empirical functions *within* a DVM is not congruent either. Based on these results, I concluded that it would be premature and irresponsible just to implement any empirical mortality function in a DVM and use that model version for any kind of application (i.e., short-term vs. long-term simulations, with/without stand initialization, etc.).

Instead, further studies are required regarding the detailed behavior of each mortality function, their interaction with other model processes (e.g., growth), and concerning the question how robust model predictions are against parametric uncertainty, which naturally comes with (mortality) functions that were fitted with empirical data.

We subsequently addressed the latter point in *Chapter 2* by inversely recalibrating the inventory-based mortality function (IM; see *Chapter 1*) using Bayesian methods. The use of this statistical approach, which has only recently been extended to process-based DVMs (van Oijen *et al.*, 2005), was novel in the context of ForClim development. It holds high potential for investigating the structural realism of a model using the combined information from a wide variety of data sources with a given model structure (Hartig *et al.*, 2012). Given our specific interest regarding the compatibility of empirical mortality formulations in the context of the ForClim DVM, and for computational reasons, we recalibrated the parameters of the mortality function and one main growth parameter only.

The Bayesian calibration suggested that the general structure of ForClim is appropriate for the integration of empirical mortality functions. Particularly, mortality parameters related to tree size and growth (e.g., *kDBH* and *krelbai*), matched very well with the independently fitted values. Given the observed variability in the sensitivity of mortality functions to annual diameter increment (i.e., the main growth variable of ForClim; *Chapter 1*) , it is important to have further confirmation that tree growth in ForClim is simulated realistically enough such that no larger adjustments are necessary in the mortality function. However, we observed a change of the sign of the effect of $kDBH^2$ on tree survival probability from negative to positive, which is in contrast to studies on empirical tree mortality (e.g., Lorimer and Frelich, 1984; Monserud and Sterba, 1999; Holzwarth *et al.*, 2013). We assume that this change is related to our modification of *relbai* from a factorial to a continuous variable, which I surmise has a similar effect as dbh^2 used to have, i.e., it increases the mortality probability of large trees. Thus, this change most likely represents a methodological artifact. In contrast, shifts of the growth rate parameter imply that the current relationship between tree growth and mortality in the model is not capable of reproducing the patterns evident from the inventory data of natural forest reserves yet. Finally, the parameter shifts of the shade tolerance classes along with their high parametric uncertainty suggest that refinements concerning the balance of the growth-mortality relationship in the model should be approached on the species level (see also “Uncertainties and needs for further research”).

A better performance of ForClim using the recalibrated parameters (BC-MAP) was to be expected at the calibration sites; yet it was encouraging to see that this model version also showed best overall performance for the large number of validation sites. This is an indication that the calibration did not constrain the applicability of the model, at least not at the temporal extent of the data. Differences to the other model versions (ForClim v3.3 and ForClim_IR, respectively) were evident particularly regarding the number of small trees (i.e., stems with a small dbh) and their general applicability. Specifically, although BC-MAP did not perform equally well at each validation site, the risk of a large failure was lower than for any of the other model versions. Although the other model versions did not reach the same performance as BC-MAP, it has to be stated that they still provided acceptable results. This was particularly interesting concerning ForClim_IR. The potential of this model version to provide accurate predictions of forest stand structure when initialized with stand data and run over a few decades was therefore not only confirmed for mono-specific Norway spruce stands (cf. *Chapter 1*) but also for a variety of multi-species stands.

Technically, most empirical algorithms such as the inventory-based mortality function simply represent the output of a specific statistical approach as applied to an empirical data set. Parametric uncertainty (e.g., standard errors) that results from heterogeneity in the data is normally included in such outputs. However, it is not considered afterwards when the average estimates alone are used in a DVM. The application of Bayesian statistics allowed me to assess model robustness (i.e., predictive uncertainty) to such parametric uncertainty. In the case of ForClim, it was informative to see that the uncertainty in total basal area caused by the uncertainty in parameter values was surprisingly low. Highest uncertainties were found for the prediction of stem number in the smallest dbh classes. These results support observations made in *Chapter 1*, where simulated numbers of small trees at the site Scatlè depended highly on the model version used. The consequences of such high sensitivity may be negligible in short-term simulations, but it may strongly affect tree species composition and forest structure in the long term.

Uncertainties and needs for further research on empirical mortality functions

General uncertainties

The results from *Chapter 1* and *2* clearly show that implementing empirical mortality functions in DVMs is encouraging, as these versions satisfactorily reproduced forest inventory data at the decadal time scale. However, it also has become clear in *Chapter 1* that different model behavior may lead to considerably different results when the simulation period extends beyond a few decades. DVMs that have the ambition to reliably portray forest succession across several generations of trees (i.e., several centuries) or aim to project forest dynamics under climate change need to be capable of extrapolating beyond the time horizon of the empirical data sets.

In *Chapter 1* (p.38*)*, I argued that "empirical formulations are directly derived from measured data and hence, their structure and parameter values are not subject to speculation". However, we cannot ignore that we are facing an increasing number of empirical tree mortality equations (cf. Chapter1, Hawkes, 2000; Allen *et al.*, 2010; Holzwarth *et al.*, 2013), which differ considerably in their structure and parameter values. On the one hand, tree mortality is a complex ecological process (Franklin *et al.*, 1987) with high spatial and temporal variability (e.g., Hurst *et al.*, 2011; Holzwarth *et al.*, 2013) that can lead to highly heterogeneous signals in the empirical data. On the other hand, the choice of the methodological approach that is used to analyze the empirical data (i.e., data selection, statistical analysis and evaluation) can strongly influence the ecological interpretation. Wunder et al. (2008; p. 827) conclude that there is no "simple universal growth-mortality relationship".

From a vegetation modeler's perspective, this has unpleasant consequences: First, as one is forced to choose between different mortality functions, applying an empirical process is far from being free of speculation. Since this choice will considerably influence model behavior and simulation results (see *Chapter 1*), the question whether the "right" function was chosen does certainly not contribute to a reduction of uncertainty in model projections. Second, as mortality rates and processes can differ depending on the empirical data, the predictive power of DVMs containing such a formulation is limited to the spatial and temporal extent of the data set. That is, projections beyond these scales must be carried out with greatest caution (see also *Chapter 2*).

Recommendations for further development

Model behavior in long-term simulations was addressed in *Chapter 1*, but validation was constrained by the lack of sufficiently long empirical data series. An approach that was not discussed in *Chapters 1* and *2* is the simulation of Potential Natural Vegetation (PNV) at sites where we have some qualitative or even semi-quantitative knowledge on the tree species composition expected in a pseudo-equilibrium state in the absence of human influences (Ellenberg and Klötzli, 1972; Frehner *et al.*, 2005; Ellenberg and Leuschner, 2010). Despite the fact that PNV itself is a contended concept that defies exact quantification, it may still provide insights on model plausibility in long-term simulations. Since PNV information has not been used anywhere in this thesis to structure the model, to determine process formulations, or to estimate model parameters (cf. Shugart, 1984) , it is highly illustrative to use a range of model formulations to examine their capability of simulating "reasonable" PNV data for sites along an extended climatic gradient in Central Europe (cf. Bugmann and Solomon, 2000; Figure 1).

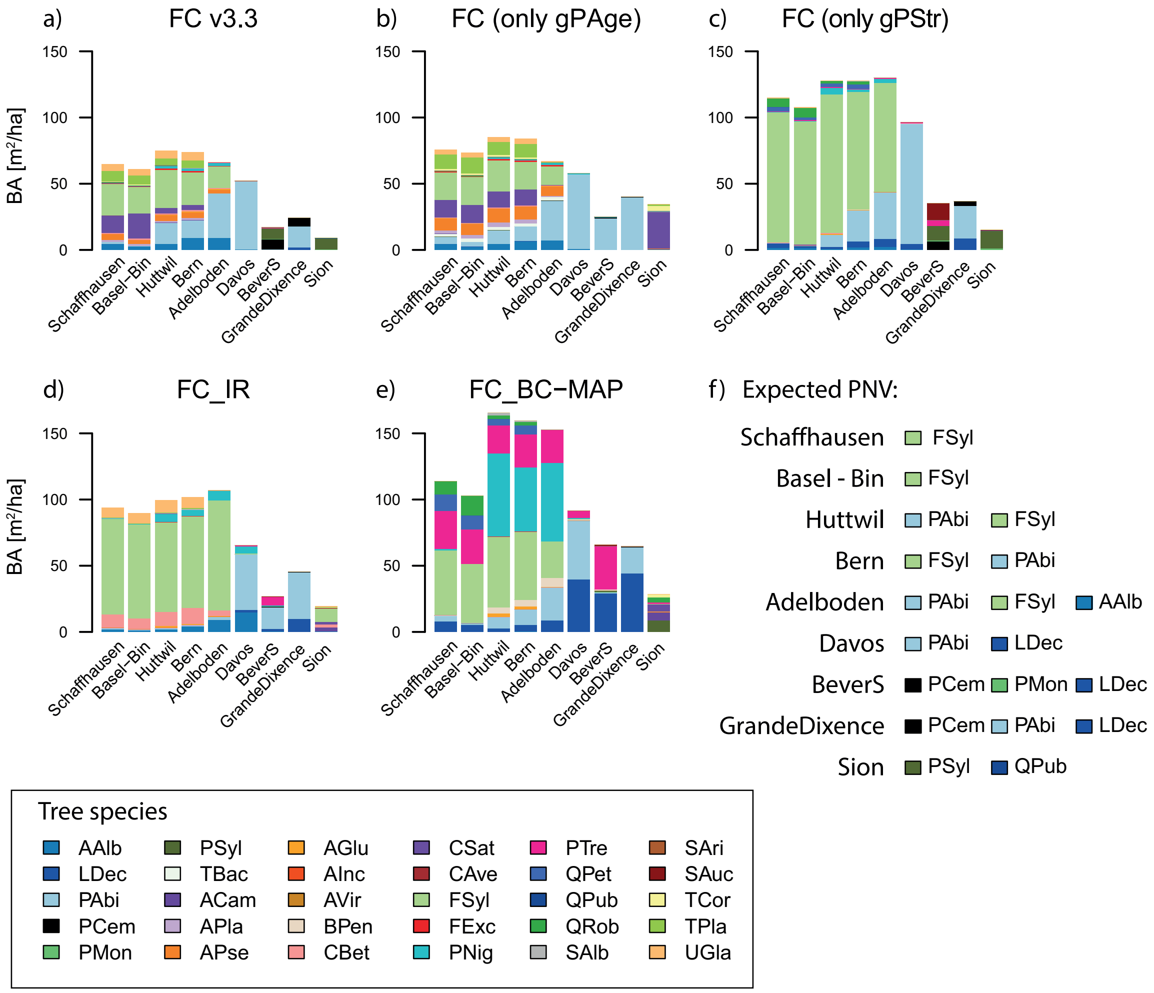


Figure 1: Potential natural vegetation (Basal Area per species) at the end of a 1500-yr simulation using different ForClim (FC) versions at sites located along a bioclimatic gradient across Switzerland. Results are shown for a) the current ForClim version (v3.3) containing a theoretical mortality function, whose two components were also tested separately by activating b) only the age-related mortality component (gPAge), or c) only the stress-induced mortality (gPStr). PNV simulated by the inventory-based mortality function with independently fitted parameters (d; ForClim_IR) and inversely calibrated parameters (e; BC-MAP) are shown as well. In f), expected PNV is shown for each site according to Rasche *et al.* (2012). Simulations were run from bare ground. Note that ForClim_IR had been named "IM_randNr" in Chapter 1.

Improve validity of empirical functions along time axis

Reflecting our results from *Chapters 1* and *2*, I have come to the conclusion that inventory-based data have the potential to provide reliable information on forest dynamics on a short-term scale. This is confirmed by the fact that ForClim_IR and BC-MAP (to a lesser degree) reflect what is labeled 'stress-induced' mortality in ForClim v3.3 (cf. Figure 1-d and 1-e with 1-c). That is, shade- and also drought-tolerant tree species that are expected to be better capable of handling stress due to limited light availability or soil moisture (e.g. at dry sites like Sion) dominated in the PNV simulations. We find a larger amount of little and moderately shade-tolerant tree species in BC-MAP (Figure 1-e), as their parameters (*kShadeLow* and *kShadeIntm*, respectively) were shifted in the Bayesian calibration. However, extrapolating a function based on short-term data to predict forest dynamics over centuries is an ambitious endeavor (cf. Hawkes, 2000), to say the least. In particular, long-term simulations seem to be driven by different factors than only stress (compare Figure 1-a and 1-c). Of course, one may argue that we do not know exactly what PNV would look like at those gradient sites. However I am confident that most readers would agree that the pattern produced by ForClim v3.3 (Figure 1-a), if compared with expected PNV (Figure 1-f), is much more realistic than what we see with ForClim_IR (Figure 1-d) or BC-MAP (Figure 1-e). This is particularly so because where the other models produce more "realistic" dominance of, for example, European beech (e.g., sites Basel, Bern, Huttwil), the total basal area simulated by those models is far too high (cf. Hobi *et al.*, 2015). If it is true that ForClim v3.3 provides the best representation of PNV, one is inclined to conclude that the data used to fit the mortality functions of the latter two model versions are unlikely to capture all factors that are required to explain long-term forest succession.

Interestingly, Gutiérrez *et al.* (2015) made similar experiences when considering spatial scales. Species parameters that had been derived for predicting the large-scale species distribution in the Pacific Northwest of North America failed to accurately portray species composition at the local scale (i.e., along a transect across the mountains of Oregon). Vice versa, parameters that were locally accurate turned out to be unsuitable for reproducing species distribution ranges. Apparently, local and regional forest dynamics are not driven by the same (bioclimatic) factors and/or one data source alone does not comprise all information that is needed to achieve general model applicability across spatial scales.

Thus, I conclude that forest inventory data should be combined with other data sources that cover longer time periods, such as tree-ring or even pollen data (Henne *et al.*, 2013). Tree-ring data have their own limits (see *Chapter 1*), but the annual resolution of diameter increment over a tree's entire life would allow for assessing, for example, the consequences of long-lasting low-level growth rates.

However, not all causes of tree mortality are related to growth. Holzwarth *et al.* (2013) tested different "modes" of tree mortality, of which only one ('standing dead') was significantly correlated with diameter increment. Other "modes" were found to be related to tree size (see section below: "Integration of the thinning stage"), but most of them were best explained by an intercept only (i.e., a constant value). Although the concept of constant background mortality in forest gap models has been heavily criticized (Keane *et al.*, 2001), tree mortality seems to be at least partly driven by stochastic processes (e.g., Franklin *et al.*, 1987; Hurst *et al.*, 2011), and an entirely deterministic approach may fail by definition. In fact, Larson and Franklin (2010; p. 2100) found that physical processes (e.g., uprooting, stem breakage etc.) are a "chronic background source of mortality" that was responsible for around 40% of the mortality events of trees ≥15 cm dbh, which even increased in importance with succession. Based on these findings, I would not reject stochastic mortality events as pure "nonsense" in a DVM; rather, I could imagine to have them integrated, for example, in the form of constant mortality rates that express different modes/causes of mortality, as found by Holzwarth *et al.* (2013).

Finer resolution regarding species-specific growth-mortality relationships

Generally, I advocate for an enhanced consideration of species-specific growth-mortality relationships in dynamic vegetation models. First, it has been shown that trees feature species-specific growth-mortality relationships (e.g., Wunder *et al.*, 2008; Ireland *et al.*, 2014). Second, dividing tree species into broad groups of shade-tolerance is highly subjective and a considerable source of uncertainty. For instance, Bugmann (1994) assumed the uncertainty of the shade tolerance parameter *kLa* in ForClim (nine classes: [1...9]) to be ±2 classes. Given that the three shade tolerance classes in the inventory-based mortality function were based on this classification (high = *kLa* classes 1-3, intermediate = 4-6, and low = 7-9, respectively), the probability is high for a species attributed a *kLa* of 3 (e.g., *Carpinus betulus*) or *kLa* of 7 (e.g., *Quercus petraea*) to represent the wrong shade tolerance class in the calibration process. Consequently, we forced the likelihood function to find one suitable parameter estimate for each of a wide variety of species within one specific shade tolerance class. The final best combination of estimates (e.g., maximum *a posteriori* value, MAP) may accurately reproduce tree species composition in short-term simulations when the model is initialized with stand data. However, the chance that shade tolerance of a majority of tree species would be better reflected by another value is high, given the large parametric uncertainty that we found. The consequence of the species aggregation into coarse groups appears to be strongly limiting the projection accuracy of species that were marginal in the calibration data (e.g., *C. betulus* and *Ulmus glabra* in Figure 1-d and *Populus tremula* and *Populus nigra* in Figure 1-e, respectively), so that they erroneously come to dominance in the PNV simulations.

Species-specific growth-mortality relationships in DVMs have been successfully tested for mono-specific (ForClim; *Chapter 1*) and mixed-species systems (ZELIG; Larocque *et al.*, 2011). With a view towards ongoing and possible future research on species-specific growth-mortality relationships for the main tree species of Central Europe (e.g., PhD projects of Lisa Hülsmann and Marco Vanoni), I strongly recommend to implement and test such algorithms in mixed-species forests with ForClim.

For species where data are too scarce to derive a specific growth-mortality relationship, I would recommend one of the following approaches: 1) These species are excluded from calibration, but their parameters are adjusted based on the results of the calibration for more dominant species, carefully taking into account their functional traits (e.g., Rasche *et al.*, 2012). 2) These species are integrated in the calibration, but the number of shade tolerance classes is increased (i.e., > 3).

Integration of the thinning stage

The need of including the smallest trees into model calibration has already been discussed in *Chapter 1*. In *Chapter 2,* I have found further support for this need, as 1) stem numbers of small trees were more accurately predicted after Bayesian calibration when data from trees with a dbh ≥4 cm were available, and 2) predictive uncertainty of the model was particularly high in the smallest dbh classes. For these reasons, I strongly recommend the inclusion of small tree data (i.e., dbh <12 cm) when fitting empirical growth-mortality functions. If such data are not available or the statistical performance of a function is not satisfactory across all size classes, a further option would be to partition tree mortality into several functions that reflect the different stages of tree life (e.g., saplings/juvenile trees vs. large/canopy trees). Partitioning tree mortality is not necessarily limited to the growth-mortality relationship, but could be extended to other causes of mortality such as physical processes whose importance varies along the life-history stages of trees (cf. Larson and Franklin, 2010; Holzwarth *et al.*, 2013).

Integrating more accurate mortality formulations for small trees is very important for another reason: Seed dispersal is not limited in ForClim. That is, each species can establish at every site given that environmental conditions are favorable. Afterwards, species not able to cope with site conditions in the long term are quickly ‘removed’ due to high mortality rates after two consecutive years of low growth (growth-related mortality). That is, high mortality rates are compensating for a rather simple regeneration mechanism. This ‘correction’ effect is missing if mortality functions are applied that are based on data of trees beyond the thinning stage only, where mortality rates are generally lower. As a consequence, sapling of such ‘unsuitable’ species can remain in the stand and contribute to low light availability at the forest floor impeding the establishment of better-adapted but more light-demanding species (e.g. Scots pine). In this context, although tree regeneration is a highly stochastic process, it would be worth to think about a more sophisticated formulation of tree establishment (e.g., consideration of seedling banks and pools, Cailleret *et al.*, 2014).

Sensitivity of Swiss forests under climate change

General evaluation of results

The stratification (*Chapter 3*) resulted in a remarkably high number of forest strata (71) although only four criteria were applied to group the NFI plots (but note the number of classes per criteria!). In my eyes, this high number is reasonable, as it reflects the high diversity of forest types in Switzerland (see also *General introduction*). However, the proportion of NFI plots represented in the strata (~25%) ended up being relatively low. Although already discussed in *Chapter 3*, it is important to stress the point that we were not focusing on representing the highest possible number of NFI plots in the stratification, but we aimed at capturing those stands that are characteristic of the different regions and altitudinal vegetation zones, and that provide a sufficiently large number of sample plots (“patches” in the ForClim jargon) for the quantitative estimation of the properties of the associated “typical” forest stands.

The criteria chosen for the stratification were intended to be well established among forest practitioners, thus allowing them to have an accurate mental picture of a forest stand based on the stand attributes. This aim was accomplished: The eco-regions and altitudinal vegetation zones represent basic components of current Swiss forest management strategies (cf. Frehner *et al.*, 2005), while both the developmental stage and the vertical structure are key attributes to describe a forest’s state and structure. Given the high species diversity between NFI plots, it was necessary to implement thresholds in terms of species abundance to split plots into more strata to increase their uniformity. Although this step was based on expert knowledge and thus arbitrary to some extent, I am convinced that we obtained more realistic forest stand structure and composition than if we had applied rigorous statistical clustering methods. Importantly, the applicability of these strata has already been tested successfully in field workshops of the research program “Forests and Climate Change”, where forest practitioners were easily able to establish the link between a stratum of my analysis and a “real” forest stand in their district, thus greatly supporting the application of the findings of my thesis as elements of decision support in practical forestry.

Most European forests, including those in Switzerland, are growing under conditions that are far from natural or in equilibrium due to past forest management practices, other land-use regimes (Bürgi, 1998; Bürgi *et al.*, 2013), and ongoing environmental changes such as nitrogen deposition (e.g., De Vries *et al.*, 2006), CO_2 enhancement of the atmosphere (e.g., Bellassen *et al.*, 2011), and temperature increase (e.g., Allen *et al.*, 2010), among others.

Since land-use history considerably influences future forest development (Kulakowski *et al.*, 2011; Temperli *et al.*, 2012), it is crucial to initialize simulation studies based upon such data to realistically reflect the sensitivity of *current* (rather than some hypothetical) forests to climate change. NFI data have the advantage that they capture the current state of a forest. However, initializing ForClim with single-tree data of aggregated NFI plots was a novel approach. It could not be taken for granted that ForClim would cope well with such initialization data. The sampling area for the single-tree data of the NFI plots was rather small (500 m^2; Keller, 2011), certainly causing variation between plots even if their stand attributes (which were assessed on a 2500 m^2 square!) were similar. The high heterogeneity in initialization data and thus between ForClim patches could have led to artifacts in the simulations. In earlier studies conducted in the Forest Ecology group, partly drastic crashes of basal area or other obvious, dramatic artifacts were observed when the model was initialized with empirical data (all this work is unpublished, of course). To my surprise and satisfaction, such artifacts were not observed in any of the 3’408 simulation runs that I conducted in *Chapter 4*. On the one hand, this suggests that the robustness of the ForClim model has increased considerably over the past few years; on the other hand, some artifacts inherent in the NFI plot data and/or in the process representation in ForClim may have been masked in the simulations because variation between plot attributes may have been mitigated by averaging the simulation results across all ForClim patches.

Deriving forest management regimes that realistically reflect current Swiss forestry practice but are still applicable to 71 strata in a plausible and efficient way was a further challenge for *Chapter 4* of my thesis. Based on a stakeholder dialogue, I defined one predominant management practice for every combination of elevation zone and forest type (even-aged vs. uneven-aged) and applied it across all the strata included. Such an “average approach” can be questioned from a forester’s perspective regarding its relation to local stand reality. The applied management was not capable to keep forest ecosystem services (ES) such as protection against gravitational hazards or biodiversity at initial levels (*Chapter 4*). For forest protection, harvest intensity for trees with dbh >24 cm was possibly too high. For biodiversity, both high harvest intensity and the unspecific management (i.e., all species were harvested without exceptions) might have contributed to the simulated forest ES decrease over time. This suggests that site-specific conditions were still not sufficiently taken into consideration and thus, such criticism is justified to a certain degree. However, we developed forest management without the ambition to optimize a specific ES but to evaluate a management regime that forest practitioners would agree to be generally valid in the region in which they work. To assess the impact of forest management on forest sensitivity to climate change, I would argue that it was more important to have the general effects of management integrated in the simulations than achieving highest plausibility at the individual stratum.

From the simulations in *Chapter 4*, I have learnt that most forests in Switzerland will respond sensitively to climate change under an A2 greenhouse gas emission scenario, but only in the years after 2060. While forests at lower elevations are expected to experience a loss of basal area under climate change due to increased drought, a positive effect was predicted for high-elevation sites. Well, this news alone does not make my study exceptional, as shifts in tree species composition at dry forest sites have already been observed (e.g., Rigling *et al.*, 2013) and drastic future shifts in Swiss forest ecosystems have been projected for quite some time (Bugmann, 1997; Elkin *et al.*, 2013b; Rasche *et al.*, 2013; Bugmann *et al.*, 2014). However, our study is a big step forward to discuss the impacts of climate change on current Swiss forests at much higher resolution and on a much finer spatial scale while it maintains a comprehensive (i.e., national) perspective. That is, in contrast to other model-based assessments of climate change impacts on forest ecosystems, my study excels in several respects.

First, it does not view Switzerland only as a cluster of a few mountain pixels (cf. Morales *et al.*, 2007; Hanewinkel *et al.*, 2013) but includes the responses of 71 different forest strata that represent the high spatial heterogeneity of Switzerland and the variety of forest types and structures that are found across different eco-regions and elevation zones.

Second, the findings of this study are not restricted to a specific region such as two catchments in the Swiss Alps (cf. Elkin *et al.*, 2013b), but based on the stratification, I provide results from which forest practitioners can not only gain a perspective on future forest development at the national scale (i.e., across all strata) but also at the forest stand scale (i.e. for one particular stratum).

Third, the results allow one to derive realistic implications for forest management, as the current state of the forests is considered by empirical data and not by a highly theoretical "spin-up" process, as commonly done in many ecological climate impact studies (cf. Rasche *et al.*, 2013).

Although most forests in lower elevation zones were found to be negatively affected by climate change, the response varies considerably between eco-regions. For example at same elevation, the impact of climate change on forests in the Jura region was more severe than in the Swiss Plateau, possibly due to differences in soil water holding capacity. Norway spruce is expected to suffer under future climate, not only at lower elevations but also in dry inner-alpine regions (e.g., Northern Central Alps, High Alps). However, my study also shows that cold-wet regions (e.g., Northern Pre-Alps) may serve as a refuge, which underlines the need to assess the fate of tree species at national, regional and local scales. Furthermore, steep elevation gradients lead to very heterogeneous responses of forest stands within the same region.

Surprisingly at first sight, current forest management mainly has a positive effect on forest basal area under climate change, although it has become evident that site- and service-specific, tailored management regimes would be necessary to more effectively counteract adverse impacts of climate change at the local scale; this is a resolution that I was not able to achieve in my study.

Our results clearly underline the importance to reflect factors that drive forest sensitivity to climate change such as topography, elevation, climate, and forest management, at the local and/or regional scale (where I regard "regional" as a landscape- rather than continental-oriented dimension; cf. Pearson and Dawson, 2003). Unfortunately, model-based studies on climate change impacts that meet the requirements to discuss implications at these scales are still scarce (Lindner *et al.*, 2010) due to coarse model resolution (Hickler *et al.*, 2012), high degree of landscape aggregation (Elkin *et al.*, 2013a), and/or neglecting biotic interactions (Pearson and Dawson, 2003), among other reasons. However, it is crucial to evaluate possible impacts at such small scales to accurately evaluate the future of forest ES (e.g., Elkin *et al.*, 2013b) and to develop adaptive management practices (e.g., Füssel and Klein, 2006; Rasche, 2014). My thesis shows that ForClim, and forest gap models in general, are useful for such a purpose as they are capable to provide sufficient spatial resolution and to integrate essential processes such as competition and forest management. Therefore, I am convinced that they are highly suitable to assess forest development under climate change, and they should be further considered as support tools in decision-making on future forest management.

Uncertainties and further research needs

Purves and Pacala (2008, p. 1452) suggested that forest dynamics are "one of the greatest sources of uncertainty in predicting future climate", as projections can vary considerably among models (Moorcroft, 2006). The general agreement between the model versions used in *Chapter 4* strengthens my confidence in the projections of the development of Swiss forest stands under novel climatic conditions as expected for the coming decades. However, even these two versions of the same model differed in the projected magnitude of changes of certain tree species and the point in time when they will occur.

A substantial source of uncertainty comes from the climate projections, which is quite large even within a single greenhouse gas scenario. As seen in *Chapter 4*, the response of forests to climate change depends strongly on the climate scenario that is applied. On the one hand, all DVM applications are confronted with this uncertainty and have to accept it. On the other hand, however, we now normally have the computational power to consider uncertainties in climate change projections by running a large number of simulations that accommodate different climate scenarios. The 11 scenario chains that I applied in *Chapter 4* are a first step towards this end, but it is certainly true that more sophisticated designs could and should be elaborated to further evaluate the importance of climatic scenario assumptions on simulated forest dynamics.

A key question that DVM developers should be concerned about, is whether their model is actually capable to reliably portray climate-induced changes of forest dynamics under different scenarios. The two model versions that I applied in *Chapter 4* contained different mortality functions that reacted with different sensitivity to changes of the growth rate. The decision which function to use is largely subjective, unfortunately. However, even if functions are used that are designed for capturing tree population dynamics in equilibrium and/or under the current climate, they may lose validity if the environment is changing rapidly (e.g., Hawkes, 2000; Keane *et al.*, 2001). Similarly, parameters of tree species derived from the literature and/or empirical sources normally reflect the knowledge for current climatic conditions, but possibly miss a tree species' plasticity, which would be of high importance for simulations including climate change (Pearson and Dawson, 2003). In summary, DVM developers need to be aware that they apply current knowledge on forest dynamics and species behavior to project forest development but they cannot be sure whether this knowledge will still be valid in a future climate.

For these reasons, among others, it is crucial to further increase our understanding of model behavior and to test simulations under conditions of climate change for their plausibility. Model behavior can, for instance, be assessed by sensitivity analysis, inverse calibration methods (i.e., Bayesian statistics), and/or by comparing simulation results against inventory or even paleoecological data. Evaluating simulation results that include strong climatic change is quite difficult as we lack empirical reference that would allow us to determine model accuracy. A multi-model design is one possible approach to compare and evaluate such projections. Applied models may complement each other regarding 1) ecological processes (e.g., biogeochemical fluxes; Hlasny *et al.*, 2014), 2) spatial resolution (e.g., stand (ForClim) vs. landscape scale (LandClim, LPJ-Guess); Elkin *et al.*, 2013b), 3) and/or formulations of an ecological process. In *Chapter 4*, I used ForClim with two formulations of tree mortality, which allowed me to examine the consistency in simulated patterns of forest response to climate change. This comparison was extremely useful to discuss possible projection uncertainties in the context of differences in model behavior but also model limitations.

I would like to conclude this chapter by addressing some aspects of ForClim that I consider as pitfalls or limitations when running climate change impact simulations:

1. The conversion of maximum tree height from a parameter to a site-dependent variable has increased the accuracy of ForClim simulations under current climate (cf. Rasche *et al.*, 2012). As trees approach maximum height (in reality or in ForClim), their height growth ceases rapidly, and – in ForClim – this also reduces diameter growth very strongly. This is linked to a strong increase of the tree's mortality probability in the model ('growth-related' mortality). Under climate change, maximum tree height may react quite sensitively to increased drought, which results in rapid decreases of maximum height, irrespective of current height of the canopy trees. For some species such as spruce, this has been a driver of the simulated mortality events in the second half of the century. The consideration of a dynamic maximum tree height variable is certainly desirable in general terms (Rasche *et al.*, 2012), however I am not convinced that the currently simulated rates and magnitudes of changes in maximum tree height under climate change are realistic. Therefore, I recommend that they are investigated carefully, which should include:

    - Comparing empirical tree height data with maximum tree height values calculated by ForClim, preferable at a range of sites where tree species are known to already reach their physiological limits (e.g., Scots pine in Sion).

    - Assessing whether the current linear relationship between site conditions (degree-day sum, soil moisture) and the reduction of maximum tree height is adequate.

    - Assessing the plausibility (and generality) of the species-specific maximum height parameter (*kRedMax*) regarding that it was derived from yield plots.

2. Natural disturbance regimes are expected to change rapidly under climate change (Turner, 2010) and are important to be considered in assessments of climate change impacts (Seidl *et al.*, 2014). However, their current implicit consideration in ForClim (in the background mortality function and/or in the intercept of empirical mortality functions, respectively) does not allow for a dynamic reflection of changes in occurrence and intensity. On the one hand, trying to implement more sophisticated formulations for large-scale disturbances such as fire or wind in ForClim seems not expedient to me, due to their usually instantaneous and annihilating effect at the stand level, resembling a clear-cut intervention. In cases where such events should be taken into consideration, I regard a multi-model approach to be promising, for example by adding a model operating at the landscape level such as LandClim (Schumacher *et al.*, 2004; Elkin *et al.*, 2012) to the assessment (e.g., Elkin *et al.*, 2013b). On the other hand, outbreaks of pathogens in a forest stand could be included by additional functions or external modules (e.g., Seidl *et al.*, 2008). The probability of a bark beetle infestation, for instance, can be assessed for individual patches (Seidl *et al.*, 2007); yet the spatial implicit model structure of ForClim would pose a challenge for identifying centers of bare beetle spots and defining its outreach.
3. Simulations for the lower elevation zones and dry inner-alpine regions of Switzerland imply substantial difficulties in guaranteeing sustainable tree establishment in the future (*Chapter 4*). At the same, Mediterranean species (e.g., *Quercus ilex*, *Pinus pinaster, Pinus pinea* etc.) and other drought-tolerant European species (e.g., *Pinus nigra*) are likely to expand their range as they are becoming less constrained by cold

winters and are more competitive thanks to better adaptation to drought. Thus, their potential, for example to replace current species at sites that are expected to experience severe drought in the future, should be taken into consideration. At the moment, only Q. *ilex* is parameterized in ForClim.

4. Similarly, there are clear signs that climate change is positively affecting the invasion of alien plant species into new areas (Dukes and Mooney, 1999; Walther *et al.*, 2009). In Switzerland, a number of non-native species (e.g., *Ailanthus altissima*, *Cinnamomum glandulifera*, *Robinia pseudacacia*, *Trachycarpus fortunei*) has already gained 'invasive' status in southern parts of the country (Conedera and Schoenenberger, 2014; Küffer *et al.*, 2014). The risks (and opportunities) of invasive tree species should be considered in assessments of stand development under climate change to evaluate their impacts on stand structure and the provision of forest ES.

5. In simulations under climate change, species might react too quickly to changing environmental conditions, as there are no limits to seed dispersal in ForClim. Thus, species are able to establish immediately, while in reality it may take them decades to reach a given site. Thus, climate-induced shifts in tree species distributions along latitudinal gradients are likely to be projected to happen too rapidly in ForClim (cf. Gutiérrez *et al.*, 2015). Fortunately, consequences of this model limitation seem to be of less relevance along altitudinal gradients (cf. Jump *et al.*, 2009). Still, I think it is an important point to keep in mind particularly when simulation results are presented to forest practitioners in mountain areas.

6. ForClim is lacking temporal autocorrelation in simulated tree growth. This hampers the application of empirical functions (e.g., tree-ring based mortality functions; Bigler and Bugmann, 2004b) that rely on reliable growth trend estimates. The integration of surplus carbon and nutrient storage pools (e.g., Misson *et al.*, 2004) or thresholds for maximum changes in annual diameter increment may be possible approaches to remedy this problem.

Conclusion

This thesis has shown that empirical mortality functions have the potential to replace current theoretical concepts in dynamic vegetation models. In spite of the need to improve the balance between different processes in ForClim, the current model structure was found to be realistic enough to allow for integrating such empirically based functions. However, different behavior of the mortality functions particularly in long-term simulations showed that 1) the choice of the function has considerably influence on the simulations results and 2) one function alone respectively its empirical data set might not be sufficient to capture all factors that are required to explain long-term forest succession. Therefore, to assume a general applicability of such functions would be premature at this point. Further research and development should focus in particular on obtaining mortality algorithms that are robust beyond the calibration data set.

The stratification of Swiss forest area based on NFI data has resulted in a large number of strata that give credit to the high diversity of forest types in Switzerland. The aggregation of single-tree data from different plots to one stratum created forest stand structures that 1) forest practitioners were able to link to real forest stands, 2) could be initialized in ForClim, and thus, 3) allowed the consideration of current forest states. According to simulations of these strata with ForClim, current Swiss forests are expected 1) to show high sensitivity to climate change and 2) to experience clear changes towards the end of the 21st century. However, this thesis has demonstrated that assessments of climate change impacts on forest ecosystems need to carefully consider forest conditions and processes at the local and regional scale. Forest gap models bring the necessary prerequisites for such assessments and thus are valuable tools to support the decision-making process regarding future forest management. The use of these models should, however, not end with unquestioned application but with the scrutiny of uncertainties, open debate and further improvement of limitations.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

Bellassen, V., Viovy, N., Luyssaert, S., Le Maire, G., Schelhaas, M.J., Ciais, P., 2011. Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. Global Change Biol. 17, 3274-3292.

Bigler, C., Bugmann, H., 2004a. Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. Ecol. Model. 174, 225-239.

Bigler, C., Bugmann, H., 2004b. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14, 902-914.

Bugmann, H., 1994. On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study. Ph.D. Thesis No. 10638, Swiss Federal Institute of Technology Zurich, Switzerland, 258 p.

Bugmann, H., 1997. Sensitivity of forests in the European Alps to future climatic change. Clim. Res. 8, 35-44.

Bugmann, H., Brang, P., Elkin, C., Henne, P., Jakoby, O., Lévesque, M., Lischke, H., Psomas, A., Rigling, A., Wermelinger, B., Zimmermann, N.E., 2014. Climate change impacts on tree species, forest properties, and ecosystem services. In: CH2014-Impacts (2014) (Ed.), Toward Quantitative Scenarios of Climate Change Impacts in Switzerland. OCCR, FOEN, MeteoSwiss, C2SM, Agroscope, and ProClim, Bern, Switzerland, pp. 79-89.

Bugmann, H.K.M., Solomon, A.M., 2000. Explaining Forest Composition and Biomass across Multiple Biogeographical Regions. Ecol. Appl. 10, 95-114.

Bürgi, M., 1998. Habitat alterations caused by long-term changes in forest use in northeastern Switzerland. In: Kirby, K., Watkins, C. (Eds.), The ecological history of European forests: based on presentations given at the International conference on advances in forest and woodland history, held at the University of Nottingham in September 1996. CAB INTERNATIONAL, pp. 203-211.

Bürgi, M., Gimmi, U., Stuber, M., 2013. Assessing traditional knowledge on forest uses to understand forest ecosystem dynamics. For. Ecol. Manage. 289, 115-122.

Cailleret, M., Heurich, M., Bugmann, H., 2014. Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. For. Ecol. Manage. 328, 179-192.

Conedera, M., Schoenenberger, N., 2014. When do non-native species become invasive? A methodological approach. Schweizerische Zeitschrift für Forstwesen 165, 158-165.

De Vries, W., Reinds, G.J., Gundersen, P., Sterba, H., 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Global Change Biol. 12, 1151-1173.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. 14, 135-139.

Elkin, C., Cailleret, M., Bugmann, H., 2013a. Climate change impacts on forest ecosystem services at local and landscape scale: the challenge of creating representative regional projections. Impacts World 2013 Conference Proceedings, Potsdam: Potsdam Institute for Climate Impact Research, pp. 637-647.

Elkin, C., Gutiérrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., Bugmann, H., 2013b. A 2 °C warmer world is not safe for ecosystem services in the European Alps. Global Change Biol. 19, 1827-1840.

Elkin, C., Reineking, B., Bigler, C., Bugmann, H., 2012. Do small-grain processes matter for landscape scale questions? Sensitivity of a forest landscape model to the formulation of tree growth rate. Landscape Ecol. 27, 697-711.

Ellenberg, H., Klötzli, F., 1972. Waldgesellschaften der Schweiz. Mitt. Schweiz. Anst. forstl. Versuchsw 48, 930.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht. Verlag Eugen Ulmer, Stuttgart.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550-556.

Frehner, M., Wasser, B., Schwitter, R., 2005. Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion, Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., Woodward, F.I., 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Acad. Sci. U.S.A. 111, 3280-3285.

Füssel, H.M., Klein, R.J.T., 2006. Climate change vulnerability assessments: An evolution of conceptual thinking. Clim. Change 75, 301-329.

Gutiérrez, A.G., Snell, R., Bugmann, H., 2015. Using a dynamic forest model to predict tree species distributions. Global Ecol. Biogeogr., under revision.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.J., Nabuurs, G.J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203-207.

Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O'Hara, R.B., Scheiter, S., Huth, A., 2012. Connecting dynamic vegetation models to data – an inverse perspective. J. Biogeogr. 39, 2240-2252.

Hawkes, C., 2000. Woody plant mortality algorithms: description, problems and progress. Ecol. Model. 126, 225-248.

Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., Tinner, W., 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. Landscape Ecol. 28, 819-833.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kuhn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecol. Biogeogr. 21, 50-63.

Hlasny, T., Barcza, Z., Barka, I., Merganicova, K., Sedmak, R., Kern, A., Pajtik, J., Balazs, B., Fabrika, M., Churkina, G., 2014. Future carbon cycle in mountain spruce forests of Central Europe: Modelling framework and ecological inferences. For. Ecol. Manage. 328, 55-68.

Hobi, M.L., Commarmot, B., Bugmann, H., 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). J. Veg. Sci. 26, 323-336.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. J. Ecol. 101, 220-230.

Hurst, J.M., Allen, R.B., Coomes, D.A., Duncan, R.P., 2011. Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane Nothofagus forest. Plos One 6.

Ireland, K.B., Moore, M.M., Fule, P.Z., Zegler, T.J., Keane, R.E., 2014. Slow lifelong growth predisposes Populus tremuloides trees to mortality. Oecologia 175, 847-859.

Jump, A.S., Mátyás, C., Peñuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24, 694-701.

Keane, R., Austin, M., Field, C., Huth, A., Lexer, M., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree Mortality in Gap Models: Application to Climate Change. Clim. Change 51, 509-540.

Küffer, C., Bugmann, H., Conedera, M., 2014. Invasive non-native species in forests: key concepts and scientific foundations. Schweizerische Zeitschrift für Forstwesen 165, 124-131.

Kulakowski, D., Bebi, P., Rixen, C., 2011. The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120, 216-225.

Larocque, G.R., Archambault, L., Delisle, C., 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecol. Model. 222, 2570-2583.

Larson, A.J., Franklin, J.F., 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. Can J Forest Res 40, 2091-2103.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698-709.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model. 90, 1-31.

Lorimer, C.G., Frelich, L.E., 1984. A simulation of equilibrium diameter distributions of sugar maple (Acer saccharum). Bulletin of the Torrey Botanical Club 111, 193-199.

Misson, L., Rathgeber, C., Guiot, J., 2004. Dendroecological analysis of climatic effects on Quercus petraea and Pinus halepensis radial growth using the process-based MAIDEN model. Can. J. For. Res. 34, 888-898.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109-123.

Moorcroft, P.R., 2006. How close are we to a predictive science of the biosphere? Trends Ecol. Evol. 21, 400-407.

Morales, P., Hickler, T., Rowell, D.P., Smith, B., T Sykes, M., 2007. Changes in European ecosystem productivity and carbon balance driven by regional climate model output. Global Change Biol. 13, 108-122.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecol. Biogeogr. 12, 361-371.

Purves, D., Pacala, S., 2008. Predictive models of forest dynamics. Science 320, 1452-1453.

Rasche, L., 2014. The importance of climate variability changes for future levels of tree-based forest ecosystem services. International Journal of Biodiversity Science Ecosystem Services & Management 10, 187-197.

Rasche, L., Fahse, L., Bugmann, H., 2013. Key factors affecting the future provision of tree-based forest ecosystem goods and services. Clim. Change 118, 579-593.

Rasche, L., Fahse, L., Zingg, A., Bugmann, H., 2012. Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. Ecol. Model. 232, 133-143.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Global Change Biol. 19, 229-240.

Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol. Model. 180, 175-194.

Seidl, R., Baier, P., Rammer, W., Schopf, A., Lexer, M.J., 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. Ecol. Model. 206, 383-399.

Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (Ips typographus L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. For. Ecol. Manage. 256, 209-220.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nature Clim. Change 4, 806-810.

Shugart, H.H., 1984. A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. The Blackburn Press, New Jersey.

Temperli, C., Bugmann, H., Elkin, C., 2012. Adaptive management for competing forest goods and services under climate change. Ecol. Appl. 22, 2065-2077.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833-2849.

van Oijen, M., Rougier, J., Smith, R., 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiology 25, 915-927.

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24, 686-693.

Wunder, J., Brzeziecki, B., Zybura, H., Reineking, B., Bigler, C., Bugmann, H., 2008. Growth-mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. Oikos 117, 815-828.

Acknowledgments

During my PhD project, I could rely on the support of a great number of people, without whom this thesis would not have been possible. I would like to express my gratitude to all of them, especially:

Harald Bugmann: for his great dedication to people entrusted to him; for always making me feel being welcome when walking into his office; for his endless energy, interest and encouraging advice that always made me leaving his office with renewed enthusiasm and confidence

Maxime Cailleret: for always keeping my project in mind even in stressful times; for his patience and iron will to get my work into a better shape; for the countless discussions, shared ideas and a pint of Guinness after work

Florian Hartig: for introducing me into the world of Bayes and inviting me to Freiburg i. Br.

Monika Frehner and Peter Rotach: for taking their time to explain a vegetation modeler how forests really grow

the Forest Ecology group: for being amazing people, where everyone’s door is open for the questions and needs of others. In particular, my office mates Marco and Martin for sharing depressions, interests and joys each day; the “seniors” Christof, Ché, Dario, Rebecca, and Jan for sharing their knowledge and experience; the PhD office “at the other end of the corridor” with Laura, Tim, Matthias and Marco, for forcing me to have a “PhTea” once in a while; Dominic, our IT wizard who did some magic things in the ForClim code; Lisa “behind the mountains” for interesting chitchats on what statistics to use for killing trees; Corina and Veronique for expanding my horizon beyond the “Limes”

the model ForClim: for giving me riddles, headaches and sometimes, quite plausible results

all my friends that shared my life outside of ETH: for notoriously asking questions about how the PhD is going, how many manuscripts are already submitted and when the defense is taking place

my family: who has always believed in me

Melanie: for her love and understanding that gave me the energy to overcome each and every hurdle

Curriculum Vitae

Nicolas Bircher
Born September 8, 1985
Citizen of Küttigen (AG), Switzerland

2011 – 2015	Ph.D. thesis in the Forest Ecology Group, Department of Environmental Systems Science at Swiss Federal Institute of Technology Zurich (ETH Zurich): *'To die or not to die: Forest dynamics in Switzerland under climate change'* under the supervision of Prof. Dr. Harald Bugmann and Dr. Maxime Cailleret (both ETH Zurich)
2009 – 2011	Master Studies in Environmental Sciences at ETH Zurich Master thesis: *'Silvicultural measures for the conservation of the Capercaillie in the special forest reserve of Amden – A first assessment of effectiveness'* under the supervision of Dr. Kurt Bollman (Swiss Federal Institute for Forest, Snow and Landscape Research WSL) and Prof. Dr. Harald Bugmann (ETH Zurich)
2005 – 2008	Bachelor Studies in Environmental Sciences at ETH Zurich
1998 – 2004	Matura, Kantonsschule Zürcher Oberland