Doctoral Thesis

The role of changes in regeneration dynamics for tree species composition and diameter structure in forests

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The role of changes in regeneration dynamics for tree species composition and diameter structure in forests

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presented by
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Summary

Due to the longevity of trees, forests tend to adapt only slowly to environmental changes by means of succession. Therefore tree regeneration plays a significant role in forest development as illustrated in the introductory part 1 of this dissertation. Due to factors such as large spatial heterogeneity and large number of small seedlings and saplings that make measurements of their population difficult, long-term data on tree regeneration are scarce. Increasing disturbance to forest regeneration caused, for example, by insects and, particularly, by ungulates has been found to cause changes to stand structure and species composition. To examine the effect of changes in regeneration dynamics on forest development at the temporal scale of forest succession, i.e., decades and centuries, simulation models need to be used. The overall objective of this research was to contribute to a better understanding of the effect of changes in regeneration patterns on tree species composition and diameter structure in forests. I used ungulate herbivory as a surrogate for processes that affect tree regeneration.

In part 2, I examined the performance of three forest succession models, i.e., two versions of FORCLIM (v2.9.1 and v2.9.3) and PICUS v1.4.1, to represent juvenile tree numbers for regional forest types in the Swiss Alps based on National Forest Inventory data. I found that the models had clear deficiencies in the simulation of successional patterns and of juvenile tree numbers. I concluded that the simulated forest structure is not sufficiently realistic to examine the effects of ungulate herbivory on long-term forest development (part 2.A). In a case study comparing simulation results with long-term forest research data, I was able to clearly identify the overestimation of leaf area in FORCLIM as the cause for the inaccurate representation of juvenile tree numbers (part 2.B).

Based on this knowledge, I improved the representation of the light regime in the FORCLIM model in part 3. I built upon the work by Wehrli et al. (2007) and replaced the static relationship between tree diameter and leaf area of earlier model versions by feedbacks between a) light availability and leaf area per tree, and b) leaf area per tree and diameter growth rate to account for the self-pruning in real stands. The evaluation of the new model, FORCLIM v2.9.5, based on measured data from long-term growth-and-yield research plots and information on the potential natural vegetation along a climate gradient in Europe was encouraging and justified further model application to examine the effect of changes in regeneration dynamics on long-term forest development.
The removal of above-ground biomass through ungulate browsing is a well-known mechanism that affects forest regeneration through seedling and sapling establishment rates and growth. In part 4, I used FORCLIM v2.9.5 to investigate the impacts of three browsing-related phenomena: a) temporal changes in animal densities and thus oscillations in the browsing intensity; b) changes in the importance of browsing as a limiting factor relative to other environmental limitations and thus the fraction of years in which browsing is limiting for ingrowth; and c) changes in the suppression effect of browsing on tree growth and hence different ingrowth rates for slow- vs. fast-growing trees. The results showed that browsing effects differ by site, and that temporal fluctuations in browsing intensity can be more appropriate for guaranteeing the persistence of species that are sensitive to browsing than approaches that aim at maintaining constant animal densities.

In part 5, I examined the combined effects of ungulate herbivory and climate change. For this study, I refined the relationship between browsing pressure and browsing-induced mortality of seedlings and saplings up to 1.27 cm dbh in FORCLIM, which resulted in version 2.9.6. In addition, I revised the species-specific sensitivities to browsing (cf. Appendix III). In simulations along altitudinal gradients in three climatically different regions in Switzerland, I investigated research questions regarding a) altitudinal range shifts in response to climate change, b) the consequences for tree species composition, and c) the combined effect of climate change and ungulate herbivory. The increase in temperature led to an upslope shift of species, but the species responded differently to climate change, which caused a succession to new stand types. Ungulate herbivory changed species composition and reduced both basal area and tree numbers. While climate change partially compensated for reductions in basal area caused by ungulate herbivory, the combined effect of these two agents on the mix of the dominant species and forest type was non-additive.

In conclusion, this dissertation provided new insights into the response of forests to changes in regeneration dynamics. These new insights were discussed in the synthesis (part 6). The investigation of the effect of temporal changes in ingrowth rates on long-term forest development demonstrated that a re-consideration of ungulate management is warranted. Further, I was able to contribute to the development and improvement of forest succession models as crucial tools for fundamental and applied research.
Zusammenfassung


Der Verbiss ist ein viel beobachteter Prozess, der die Baumverjüngung durch Änderungen in der Etablierung und dem Wachstum stark beeinflusst. In Teil 4 wurde das Waldsukzessionsmodell FORCLIM v2.9.5 verwendet, um die Auswirkungen von drei durch Wildverbiss bedingten Mechanismen zu untersuchen: a) zeitliche Schwankungen in Ungulatenbeständen und daher in der Verbissintensität; b) Änderungen in der Bedeutung von Wildverbiss als limitierender Faktor relativ zu anderen Umwelteinflüssen, d.h. der Anteil von Jahren in denen Wildverbiss der limitierende Faktor für die Verjüngung ist; c) Änderungen in der durch Verbiss verursachten Unterdrückung des Wachstums von Baumverjüngung und dadurch bedingten Schwankungen im Einwuchs von langsam- und schnell-wüchsigen Baumarten. Die Ergebnisse zeigten, dass die Auswirkungen von Wildverbiss standortabhängig sind und dass zeitliche Schwankungen in Verbissintensität in bestimmten Fällen geeigneter sind, das Vorkommen von Baumarten, die sensitiv auf Verbiss reagieren, zu sichern, als Ansätze mit konstant gehaltenen Tierbeständen.


Part 1

Introduction

1. Background

Forests cover almost one-third of the earth’s surface (FAO, 2006) and provide a range of important ecological, socio-cultural and economic functions, goods and services (de Groot et al., 2002). However, forests are increasingly exposed to human-caused disturbances including climate change, land use, and air pollution (Millennium Ecosystem Assessment, 2005; Intergovernmental Panel on Climate Change, 2007). This jeopardizes the provision of forest ecosystem functions including climate regulation through carbon sequestration, and goods and services such as timber and non-timber forest products (Millennium Ecosystem Assessment, 2005).

Since trees are long-lived organisms, the adaptation of forest ecosystems to strongly different environmental conditions is a long-term process in which forest regeneration plays a key role (Pacala et al., 1996). Forest regeneration may be delayed or prevented entirely by disturbances such as pathogens and herbivory by rodents, ungulates, and insects (e.g., Castello et al., 1995; Senn, 2000; Price et al., 2001; Kupferschmid Albisetti, 2003; Senn and Suter, 2003; Olofsson et al., 2004). The large-scale and long-term impact of changes in the regeneration process on forest development is difficult to quantify (Weisberg and Bugmann, 2003): observational data are scarce, experiments are limited in scope and duration, and current modeling approaches leave room for improvement as well (Price et al., 2001).

The impact of herbivory by ungulates such as red deer (Cervus elaphus), roe deer (Capreolus capreolus), and chamois (Rupicapra rupicapra) has become a major concern in forests worldwide (e.g., Vila et al., 2003; Palmer et al., 2004; Heuze et al., 2005; Theuerkauf and Rouys, 2008; Ward et al., 2008). Ungulates can alter the tree species composition in forests by selective feeding (Augustine and McNaughton, 1998; Côté et al., 2004), and they can alter the horizontal and vertical distribution of trees (Motta, 1999). The impact of the removal of above-ground biomass by ungulates (hereafter browsing) is particularly severe in mountain forests, where seedling and sapling growth is slow due to harsh environmental conditions (Ott et al., 1997). There is thus a growing concern over the impact of browsing, especially in mountain regions as in the Swiss Alps, where forests often provide protection against rockfall and snow avalanches (Ott et al., 1997; Brang et al., 2001). Ultimately, the aim of this dissertation is to provide a better basis for assessing the long-term impacts of browsing on forest regeneration, using the European Alps as a case study.
2. Research approach

In many studies, the impact of browsing on forest development has been observed (e.g., Casabon and Pothier, 2007; Long et al., 2007; Stroh et al., 2008; Ward et al., 2008) and reproduced in experiments (e.g., Häsl er et al., 2008; Kupferschmid and Bugmann, 2008). Since observational and experimental studies on ungulate-forest interactions generally are short-term only (cf. Gill and Beardall, 2001), the results cannot inform what the long-term implications are. Furthermore, confounding factors such as different site conditions make it difficult to extrapolate experimental results in time or space (Bergström and Edenius, 2003).

Simulation models can be used to examine the combined effects of interacting factors at large spatial and temporal scales, which is hardly possible with field-based (observational or experimental) approaches. Since models are a deliberate simplification of reality, complex processes such as browsing may not be represented explicitly but through proxies because it would be overwhelming to model the behavior of a multitude of plants in the regeneration layer, most of which die due to a host of causes unrelated to the target disturbance. The appropriate development and use of models thus requires a thorough understanding of the behaviour of the system under study to decide which processes must be modeled explicitly and which ones can be captured using simple parameterizations. In return, based on model applications, the understanding of the system can be improved and important processes and research needs be identified. I have selected this route for my dissertation.

2.1. Modeling approaches

Models have been used widely to project ecosystem development at different temporal and spatial scales and levels of detail. Liu and Ashton (1995) distinguished two major model types: stand models (e.g., LANDIS, Mladenoff et al., 1996; 3-PG, Landsberg and Waring, 1997) use aggregated stand level data and operate at a landscape scale, whereas individual-based models, which include gap models (see below) and growth-yield models (e.g., MOSES, Hasenauer et al., 1995; SILVA, Pretzsch et al., 2002) simulate forest development at the level of individual trees and thus operate at the stand scale.

Gap models (or patch models; Shugart and Smith, 1996) are a particular type of individual-based models (Liu and Ashton, 1995) that simulate forest development based on the patch dynamics theory (Watt, 1947; Pickett and White, 1985). In these models, individual trees or cohorts of trees of several tree species are considered, and thus they are particularly suited for investigating species-specific responses to ungulate browsing, as opposed to the approach of stand models that use aggregated stand data such as tree density and total basal area (Liu and Ashton, 1995).
Compared to growth-yield models, which also track individual trees and were developed for applications in planning and management of commercial forests, gap models were formulated for ecological studies of forest dynamics (Liu and Ashton, 1995) with a more explicit focus on tree regeneration and mortality as part of the successional cycle. Moreover, while growth-yield models are typically restricted to a single or few economically relevant tree species, gap models can simulate population dynamics of a large number of species (Liu and Ashton, 1995). For all these reasons, I decided to focus on forest gap models in my dissertation.

2.2. Gap models

Gap models simulate the establishment, growth, and mortality of individual trees on small forest patches (usually 0.01 to 0.1 hectare) based on simple descriptions of biotic (e.g., competition) and abiotic (e.g., soil) processes (Shugart, 1998). The approach used for the first gap model, JABOWA (Botkin et al., 1972), formed the theoretical foundation for many subsequent models of this kind. New tree individuals are generated with a diameter at breast height (dbh) of approximately 1 cm, i.e., as saplings (>1.30 m height to <4 cm dbh). Tree seedlings (<1.30 m height) are not simulated. Environmental filters such as winter temperature, light availability, growing degree days and browsing pressure are implemented as boolean variables that determine whether a specific tree species can establish at a given time step. Height growth of a tree is an allometric function of tree diameter. Optimal growth is limited through factors such as growing degree days, light availability, soil moisture and nitrogen availability. Maximum species age and sub-optimal growth, for example, in response to drought conditions or competition for light, determine tree mortality.

A basic assumption of most “traditional” gap models is the horizontal homogeneity of patches with respect to light conditions and tree distribution. Light interception within the canopy is calculated based on tree height and tree leaf area, whereby tree leaf area often is assumed to be contained in a disc-shaped layer at the top of each tree. Most models also assume unlimited seed availability on a patch to account for seed production and dispersal. Differences between tree species responses to environmental variables such as light availability, winter temperature, or soil moisture are accounted for through species-specific parameters. Conditions for establishment, growth and mortality are, thus, different for every species depending on the characteristics of the site at which forest succession is simulated. Depending on the complexity and approach of a model, the type and number of required species-specific parameters varies strongly, but due to their multi-species nature, parameter estimation usually represents a challenge.
Since JABOWA that had been conceived to study forest succession in New England (Botkin et al., 1972), gap models were developed for a wide range of forest ecosystems and research questions, for example, FORSKA for boreal forests (Leemans, 1991), or FORCLIM for forests in the European Alps (Bugmann, 1994, 1996). To better address forest management concerns, more recent model developments include detailed routines or submodels for harvesting, e.g., FORSKA-M (Lindner et al., 2000), insect infestations, e.g., PICUS ( Lexer and Höninger, 1998), and ungulate grazing, e.g., FORGRA (Jorritsma et al., 1999). As a consequence, a wide array of approaches are available today for capturing various aspects of reality in these model (Bugmann, 2001b).

2.3. Model choice

In the past 25 years, several forest gap models were developed for the conditions of the European Alps, including FORECE (Kienast, 1987), FORSUM (Kräuchi and Kienast, 1993), FORCLIM (Bugmann, 1994, 1996), and PICUS (Lexer and Höninger, 2001). In addition, in a model comparison exercise (Badeck et al., 2001) two models developed for other conditions were applied in the European Alps, i.e., the gap model FORSKA (Leemans, 1991) and the generic vegetation model LPJ-GUESS (Smith et al., 2001). Given this rich experience with model development and application, I decided to build upon one of these models to harness the expertise gained in previous efforts, rather than to start from scratch and develop an entirely new model.

A key challenge I was facing was that tree establishment in gap models is simplified and trees generally establish with a diameter at breast height of approximately 1 cm, corresponding to a tree height that is out of the reach of browsing animals. If tree population dynamics is highly sensitive to regeneration processes, then an explicit, much more detailed modeling of the impact of herbivores on long-term forest succession may be warranted (e.g., Weisberg et al., 2005), whereas otherwise, a slight revision of the formulation of the currently often-employed establishment filters may suffice (cf. Bugmann, 2001b; Price et al., 2001).

Another key challenge was to identify one of the existing models as the tool to build upon in my dissertation. Studies with the gap models FORECE (Kienast et al., 1999), FORSKA (Prentice et al., 1993) and FORCLIM (Bugmann and Solomon, 2000) found diverging levels of model sensitivity to changes in tree establishment rates. Simulated biomass and species composition in FORSKA was highly sensitive to changes in the number of newly established trees (Lasch and Lindner, 1995), while in FORCLIM only little sensitivity was observed (Bugmann, unpublished data; Didion, unpublished data). Therefore, before deciding on an approach to extend a model in such a way as to better represent tree regeneration (including browsing), I needed to perform a thorough
analysis of gap model performance and sensitivity with regard to the simulation of tree regeneration. From the gap models that I had identified in the literature review as starting points for my research, I selected for further study two versions of the “traditional” gap model FORCLIM, i.e., v2.9.1 (Bugmann and Solomon, 2000) and v2.9.3 (Risch et al., 2005), and the hybrid model PICUS v1.4.1 (Seidl et al., 2005), which is based on the gap model PICUS v1.2 (Lexer and Hönninger, 2001) with additional physiological detail from the stand model 3-PG (Landsberg and Waring, 1997). In contrast to other candidate models, a) these three models had been applied recently to simulate forest development in my selected study region, the European Alps; b) they were parameterized for all important tree species occurring there; and c) their source code as well as expertise from the original developers were available to me. By including two variants of a “traditional” gap model (FORCLIM) and one “hybrid” model (PICUS), I was also able to evaluate the importance of the different modeling approaches with regard to tree growth (empirical vs. mechanistic) and spatial representation (independent patches vs. a lattice of patches). Two variants of the FORCLIM lineage were chosen because v2.9.1 had been applied successfully in different bioregions (e.g., Bugmann and Solomon, 2000; Badeck et al., 2001; Bugmann, 2001a; Bugmann et al., 2001; Shao et al., 2001), while version 2.9.3 featured the most recent model modifications (Risch et al., 2005) at the time this dissertation was begun.

3. Research aim

The overall objective of this research was to improve our understanding of the long-term effect of changes in regeneration patterns of mountain forests in the European Alps, focusing on the impact of changes in the number of juvenile trees and the effects of browsing on forest development over decades and centuries. An initial goal was to identify the gap model (FORCLIM or PICUS) that is able to best reproduce tree species composition and diameter frequency distribution in different forest types. Based on the outcome of this exercise, I intended to perform a validation in the context of browsing effects and, if required, improve the selected model. In a final step, the mid- and long-term effects of ungulate herbivory on forest development were to be evaluated. With this research I anticipated to answer the following specific questions:

- To what degree do the models allow for an accurate evaluation of ungulate browsing impacts on forest development?
- How sensitive are simulated forest species composition and diameter frequency distribution to changes in tree regeneration?
• What are the probable impacts of ungulate browsing on tree species composition and structure in forests over decades and centuries?

• What are the joint effects of ungulate browsing and climate change on long-term forest succession?

4. Structure of the dissertation

4.1. Evaluating forest gap models

A. Potentials and limitations of using large-scale forest inventory data for evaluating forest succession models

In this part, I evaluated the ability of the two models FORCLIM v2.9.3 and PICUS v1.4 to simulate realistic species composition and numbers of juvenile trees for the range of typical broad forest types of the Swiss Alps. The key objective of this study was to derive recommendations for future improvement of the employed models.

The simulations of forest types in Switzerland as compared against large-scale forest inventory data indicated that the two examined gap models underestimated the number of juvenile trees <12 cm diameter at breast height, in particular of the dominant species. I concluded that the simulated forest structure is not sufficiently realistic to examine the effects of browsing and similar disturbances on long-term forest development. A first hypothesis for the underestimation of juvenile tree numbers was that the models overestimated stress-related mortality due to low growth rates (cf. Wehrli et al., 2005).

In addition to FORCLIM v2.9.3 and PICUS v1.4, I also evaluated an earlier version of FORCLIM in this part of the dissertation. The version history of FORCLIM as used in this PhD dissertation is presented in Appendix I. The results for the simulations with FORCLIM v2.9.1 can be found in Appendix II, showing that FORCLIM v2.9.3 simulated juvenile tree numbers more accurately than v2.9.1.

B. Simulations with FORCLIM v2.9.1, ForClim v2.9.3 and PICUS v1.4 for initialized stands from long-term forest research sites

In order to investigate the hypothesis that stress-related mortality in the models was the main cause for the underestimation of juvenile tree numbers, I changed the resolution of the analysis by initializing the models with long-term forest research data and comparing simulated vs. observed stand attributes for the most recent inventory. The particular objectives of this experiment were a) to evaluate whether the examined models were able to reproduce observed tree numbers and basal area better in simulations using stand-scale forest data compared to large-scale inventory
information (see section A, above), and b) to analyze model sensitivity to changes in
the number of new trees that establish and the consequences thereof for the simulated
medium-term (several decades) development of forest stands.

Since FORCLIM v2.9.1 performed more poorly than v2.9.3 and PICUS, I eliminated it
from the further analysis. In FORCLIM v2.9.3, I was able to identify the overestimation
of leaf area as the cause for the inaccurate representation of juvenile tree numbers. In
PICUS, a combination of several processes was most likely responsible for the
unsatisfactory performance. Due to the lower complexity of the FORCLIM model,
which uses a simple crown structure rather than a 3-dimensional representation as in
the PICUS model, I decided to select FORCLIM v2.9.3 for further study.

4.2. Improving the representation of the simulated light regime in
FORCLIM v2.9.3

Based on the knowledge from the previous part, I improved the representation of
canopy structure in the model. To this end, I built upon research by Wehrli et al. (2007)
in the development of FORCLIM v2.9.4. They had replaced the static relationship
between tree diameter and leaf area of earlier FORCLIM versions by a feedback
between light availability and the amount of leaf area per tree to account for the self-
pruning in real stands. Since their model modifications proved to be unsatisfactory in
long-term simulations of forest development (Didion, unpublished data), I revised their
formulation and introduced an additional feedback between leaf area per tree and
diameter growth rate. I evaluated the performance of the new model, FORCLIM v2.9.5,
 focusing on a) its local accuracy in simulations at three long-term forest research sites
in the Swiss Alps, and b) its generality in simulations of potential natural vegetation
(PNV) at 11 sites along a broad environmental gradient in Central Europe.

The results from the model evaluation were encouraging because the performance of
the model was improved over the previous version with regard to simulating potential
natural vegetation along an extended environmental gradient as well as reproducing
observed forest development at long-term research sites.

4.3. Model sensitivity analysis of browsing impacts

I conducted a sensitivity analysis of FORCLIM v2.9.5 to investigate a) the sensitivity of
forest species composition and diameter frequency distribution to changes in forest
regeneration rates, and b) the potential impacts of ungulate herbivory on forest species
composition and structure over decades and centuries. I examined the following effects
of three browsing-related phenomena: i) temporal changes in animal densities and thus
oscillations in the browsing intensity; ii) changes in the importance of browsing as a
limiting factor relative to other environmental limitations and thus the fraction of years in which browsing is the key limiting factor for ingrowth; and iii) growth suppression by browsing and hence different ingrowth rates for slow vs. fast growing trees. Focusing on these three factors, I performed the analysis for three typical mountain forest sites in Switzerland.

The results showed that browsing can induce profound compositional and structural changes in forest stands and that the practice of maintaining ungulates at constant densities and the consequent constant browsing intensity over time can exacerbate ungulate effects. The impacts were site-specific and depended on the importance of other environmental factors, particularly the length of the growing season and winter temperatures. The low sensitivity of the number of large trees (>51 cm dbh) compared to that of small trees (<12 cm dbh) gave rise to concerns regarding a) a still low sensitivity of the model to changes in regeneration patterns, and b) an underestimated mortality of large trees leading to a poor growth of the smaller trees. The results of this study provided evidence for i) a poor parameterization of species’ sensitivities to browsing (i.e., parameter $k_{Brow}$), and ii) an unrealistic implementation of the relationship between seedling and sapling mortality and browsing pressure as defined in Bugmann (1994, eq. [3.4]). The revision of the parameter of the species sensitivity to browsing (i.e., $k_{Brow}$) and the equation considering the browsing induced species-specific mortality are described in detail in Appendix III (eq. [A-9]).

4.4. Interactions between ungulate browsing and climate change

Since site conditions are expected to change due to global warming, I sought to examine the impact of the joint effects of climate change and ungulate browsing on forest composition and structure in the European Alps. Climate change is expected to lead to a migration of species upslope or poleward. Since ungulate browsing can change species composition of forests, it may therefore be important as a controlling factor for forest succession in response to changes in climate. I selected valleys in three climatically different regions of the Swiss Alps to study these issues at high detail along altitudinal gradients. In these simulations, I investigated a) the impact of different browsing intensities on forest succession, b) the climate change-induced altitudinal range shifts and the effect on species composition of different forest types, and c) the role of ungulate browsing for the response of forests to climate change.

Ungulate browsing changed species composition and reduced both basal area and tree numbers. The increase in temperature led to an upslope shift of species. Species responded differently to the change in climate and did not migrate concurrently, which caused a succession to new stand types. Ungulate browsing delayed forest succession
at the cold tree line, but exacerbated the climate-induced collapse of forests at the dry treeline.

4.5. Synthesis

In the synthesis, the main findings of sections 4.1 to 4.4 were drawn together and their relevance for model development and application as well as for forest management was discussed.

References


Evaluating forest gap models

A. Potentials and limitations of using large-scale forest inventory data for evaluating forest succession models

published as:
Abstract

Forest gap models have been applied widely to examine forest development under natural conditions and to investigate the effect of climate change on forest succession. Due to the complexity and parameter requirements of such models a rigorous evaluation is required to build confidence in the simulation results. However, appropriate data for model assessment are scarce at the large spatial and temporal scales of successional dynamics. In this study, we explore a data source for the evaluation of forest gap models that has been used only little in the past, i.e. large-scale National Forest Inventory data. The key objectives of this study were a) to examine the potentials and limitations of using large-scale forest inventory data for evaluating the performance of forest gap models, and b) to test two particular models as case studies to derive recommendations for their future improvement.

We used data from the first Swiss National Forest Inventory to examine the species basal area and tree numbers in different diameter classes simulated by the gap models FORCLIM (version 2.9.3) and PICUS (version 1.4) for forest types that are typical of mountain forests in Switzerland. The results showed the potential of data from large-scale forest inventories for evaluating model performance. Since this type of data is typically based on a large number of samples across environmental gradients, they are particularly suited for investigations at the general level of the dominant species based on stand basal area. However, the surprisingly small variability of juvenile trees (trees <12 cm diameter at breast height; dbh) indicated limitations of the data used. Insufficient representativeness due to small sample plot size and uncertainty regarding past management limit an evaluation of structural forest aspects such as species diversity, and number of small trees (dbh <12 cm).

The examined models reproduced the observed species composition satisfactorily. However, there were clear model deficiencies in the simulation of successional patterns and of juvenile tree numbers. We identified priorities for future model development.

We conclude that large-scale forest inventory data can be valuable for model evaluation, particularly when they cover large environmental gradients and do not come from intensively managed forests. Due to their limitations, they must, however, be complemented by other data such as from a full cruise.

Keywords: Patch models; FORCLIM; PICUS; forest succession; diameter distribution; mountain forests; Swiss Alps; forest inventory data; gap model; regeneration
1. Introduction

Forest succession models from the family of gap models (Botkin et al., 1972; Shugart, 1984) have been used widely in applied research to examine, for example, the effects of climate change on forest development (e.g., Shugart, 1998; Bugmann et al., 2001; Lasch et al., 2002). Due to the complexity and parameter requirements of these models, a rigorous evaluation is needed to build confidence in the simulation results prior to such applications (Bugmann, 2003). However, the large spatial and temporal extent of forest succession and the lack of appropriate empirical data render the evaluation of gap model simulations a non-trivial task.

A common approach to evaluate forest gap models has been to compare simulated species composition at equilibrium with estimates of potential natural vegetation (PNV; e.g., Lasch et al., 1999; Bugmann and Solomon, 2000; Lindner et al., 2000; Bugmann et al., 2001; Lexer, 2001; Shao et al., 2001). Major problems with this method are a) PNV itself is a model construct that is not based on “hard” data (cf. Ellenberg, 1996); b) since PNV represents the “climax” state of a forest, only the simulated equilibrium species composition can be tested, but not the simulated dynamics, and c) no quantitative assessment is possible (Badeck et al., 2001).

In other studies simulated data were compared with pollen records from paleoecological studies (e.g., Solomon and Webb III, 1985; Lotter and Kienast, 1992; Heiri et al., 2006). Key problems with this approach are a) to obtain climatic data series to drive the model that are independent of the pollen data, and b) the low temporal and sometimes also low taxonomic resolution of the pollen data.

More recently, simulated forest dynamics were compared quantitatively against local time series of stand development (e.g., Lasch et al., 2005; Risch et al., 2005; Seidl et al., 2005; Wehrli et al., 2005). Model evaluation based on this approach is also prone to limitations because a) the legacies of the past such as natural and anthropogenic disturbances that have shaped observed forest stands are uncertain, b) the assumption that the measured data are representative of regional forest dynamics as simulated by succession models may not be correct (cf. Bugmann, 2001b), and c) the measured time series usually span a few decades only, which is exceedingly short compared to the century-long forest dynamics simulated by the models.

In this paper, we explore another data source for the evaluation of forest gap models that has been used only limited in the past (e.g., Rickebusch et al., 2007), i.e., large-scale National Forest Inventory data. These data do not represent “natural” forests but they often span large environmental gradients along which forest properties such as diameter distribution and species composition should be reflected adequately by forest
gap models. Particularly in central European mountain regions (e.g., Switzerland or Austria) where “near-natural” forest management has been prevailing since decades (Gamborg and Larsen, 2003), we can profit from large environmental gradients over short horizontal distances along which the human fingerprint on forest attributes is less pronounced than in more intensively managed low-elevation regions (e.g., Grabherr et al., 1998).

The key objectives of this study are a) to examine the potentials and limitations of using large-scale forest inventory data for evaluating the performance of forest gap models, and b) to test two particular models as case studies and to derive recommendations for their future improvement.

2. Methods

We adopt a novel approach to achieve our objectives. We used data from several thousand forest plots sampled in the first Swiss National Forest Inventory 1982-1986 (NFI1; EAFV and BFL, 1988) to derive “average” forest conditions for 15 regional mountain forest types that can be compared with simulated forest data from two current gap models, FORCLIM v2.9.3 (Risch et al., 2005) and PICUS v1.4 (Seidl et al., 2005).

Most previous model evaluations focused on stand properties such as species-specific biomass or basal area. In our analysis, however, we are seeking to complement the evaluation of stand properties by structural features such as tree numbers, particularly of juvenile trees <12 cm diameter. The numbers of juvenile trees are of particular importance e.g. when succession models are used to assess the impacts of ungulate herbivory (e.g., Jorritsma et al., 1999; Kienast et al., 1999; Seagle and Liang, 2001), but the accuracy of the models in reproducing the numbers of small trees has rarely been scrutinized rigorously.

2.1. Gap models

Gap models are individual-tree based models that simulate forest development based on the patch dynamics theory (Watt, 1947; Pickett and White, 1985). Establishment, growth and mortality of individual trees on independent, small patches of land (size 0.01-0.1 ha) are simulated as a function of biotic (competition) and abiotic factors (climate). Succession is driven by the mortality of large, dominating trees that produce gaps in the forest, leading to increased tree recruitment rates and a growth release of suppressed trees. Tree growth and properties such as height and leaf area are calculated using species-specific allometric functions based on tree diameter at breast height.
We selected the gap models FORCLIM v2.9.3 (Risch et al., 2005) and PICUS v1.4 (Seidl et al., 2005) for our analysis because these two models represent strongly different lines of development of this large class of models (Bugmann, 2001b) with FORCLIM being closer to a “traditional” gap model (sensu Botkin et al., 1972; Shugart, 1984) and PICUS being a “hybrid” model that incorporates elements of physiology-based forest growth models.

2.1.1. FORCLIM

FORCLIM has maintained the traditional approach of forest gap models, with multiple new formulations to better reflect climatic influences on tree population dynamics. Rather than tracking each individual tree, the fate of cohorts of trees of the same age is modeled (Bugmann, 1996; Bugmann and Solomon, 2000). Tree growth is specified as a species-specific maximum that is reduced to a realized growth rate by taking into account key limiting factors (temperature, drought, light availability, and nitrogen availability). Tree establishment consists of the recruitment of saplings with a diameter at breast height (dbh) of 1.27 cm. This process is simulated as a function of species-specific responses to winter temperature, light availability, growing degree-days and browsing pressure. FORCLIM performed well in several studies compared to local, site-specific forest data and to PNV in various mountain regions under large temperature and precipitation gradients (cf. Bugmann and Solomon, 2000; Badeck et al., 2001; Bugmann, 2001a; Bugmann et al., 2001; Shao et al., 2001). As input the model requires monthly means and standard deviations of temperature and precipitation as well as their cross-correlation (Bugmann, 1994).

2.1.2. PICUS

As opposed to the traditional approach of horizontal independence between patches, the hybrid model PICUS accounts for horizontal interactions. For a more mechanistic description of tree growth, the gap model PICUS v1.2 ( Lexer and Hönninger, 2001) and the stand-level forest productivity model 3-PG (Landsberg and Waring, 1997) were hybridized resulting in PICUS v1.3 (Seidl et al., 2005). A radiation submodel is used to simulate horizontal and vertical changes in the light regime between patches and crown cells (Lexer and Hönninger, 1998a). In the simulation of tree growth temperature, radiation, vapour pressure deficit, soil water and nutrient supply are considered as environmental factors (Seidl et al., 2005).

In model version 1.4 the recruitment approach of traditional gap models has been replaced by a more detailed regeneration submodel. Based on four height classes (0-10 cm, 10-30 cm, 30-80 cm, 80-130 cm) seedling establishment and development are simulated as a function of the species-specific height growth potential and stress.
tolerance in conjunction with patch-specific light availability and the effects of environmental factors (Woltjer et al., 2008). Outgrowth from the regeneration submodel is initialized as saplings with approx. 1.0 cm dbh (Woltjer et al., 2008). PICUS v1.4 also includes a process-oriented soil submodel that tracks belowground C storage and site nutrient status (Seidl et al., 2007). The model requires monthly climate input data for temperature, precipitation, radiation and vapor pressure deficit.

PICUS was used successfully in several studies to simulate site-specific forest development in the Austrian Alps and PNV, e.g., PICUS v1.0 to v1.2 ( Lexer and Hönninger, 1998a; 1998b; Lexer et al., 2000a; 2000b; Lexer, 2001; Lexer and Hönninger, 2001; Lexer et al., 2002), and PICUS v1.3 (Seidl et al., 2005). So far, PICUS v1.4 has mainly been applied to managed forests (e.g., Seidl et al., 2005; Seidl et al., 2007; Seidl et al., 2008).

For the present study, we employed PICUS v1.4 with the dynamic soil submodel turned off since the required data were not available for our study area. Disabling the soil submodel and assuming static soil nutrient conditions created analogous conditions to FORCLIM as used in previous studies (e.g., Risch et al., 2005) and minimized unintentional effects due to inconsistent data. The effect of turning off the soil submodel was tested for several sites with known soil data and was found to be acceptable (data not shown).

2.2. Data

2.2.1. National Forest Inventory data

For our case study, we used data from the First Swiss National Forest Inventory 1982-1986 (NFI1), which was sampled on a 1-km grid (EAFV and BFL, 1988). From the NFI1, we obtained data for 12 main species or species groups (EAFV and BFL, 1988) on a total of 7543 sampling plots. For the model evaluation we used data for species basal area (trees >12 cm dbh sampled on 0.02 ha plots and trees >36 cm dbh on 0.05 ha plots, respectively) and juvenile tree numbers (130 cm height (i.e., a dbh >0 cm) to <4 cm dbh, 4 ≤ dbh <8 cm, 8 ≤ dbh <12 cm dbh, all sampled on randomly selected 28.3 m$^2$ sub-plots within the sampling plots; cf. Zingg and Bachofen, 1988).

Following the altitudinal zonation of mountain forests in Switzerland (e.g., Ott et al., 1997) we stratified the NFI1 data according to the montane (approx. 700 to 1500 m a.s.l. depending on region, cf. Table 1) and subalpine (approx. 1300 to 1900 m a.s.l., cf. Table 1) zones. The majority of Swiss forests are older than 60 years and most stands are between 90 and 150 years old (BUWAL and WSL, 2005). To reproduce this pattern and to eliminate the very early-successional stages, we removed all plots that had a dominant dbh (i.e., average dbh of the largest 100 trees) <12 cm, and focused on
stands in the pole stage (biomass accumulation/competitive exclusion phase of Franklin et al., 2002) and older. Low-elevation forests on the Swiss Plateau (colline zone) were not considered here because, among other reasons, they are managed more intensively than mountain forest stands (Brassel and Brändli, 1999).

We used the site classification by Frehner et al. (2005) to further stratify the NFI1 plots into five major forest types based on the measured species-specific basal area and elevation data: 1) subalpine spruce, 2) high montane fir, 3) montane spruce, 4) montane fir-beech-spruce (including the subtypes fir-beech and fir-spruce), and 5) montane beech (Table 2). These types were further separated into four bioclimatic regions (Fig. 1) based on the NFI1 “production regions” (cf. EAFV and BFL, 1988): 1) Western Central Alps (Alpen according to NFI nomenclature; dry and warm continental climate); 2) Southern Alps (Südalpen; insubrian climate, warm and moist); 3) Northern Pre-Alps (Voralpen; moist and cool oceanic climate); and 4) Eastern Central Alps (Alpen; high montane and subalpine, with moist and cold continental climate). Overall, fifteen regional forest types were distinguished (Table 1) comprising a total of 2010 NFI1 plots, each of which was assigned to a regional forest type based on location and elevation.

In order to assess the correctness of the aggregation and to obtain an additional variable to evaluate the within-stratum variability of forest attributes, we calculated the quartiles of the observed elevation distribution of the plots describing each forest type (Table 1). This showed that observed variables were relatively uniform within strata except for the montane fir-beech-spruce forest type in the Northern Pre-Alps. We thus subdivided the NFI1 sampling locations of this forest type into fir-spruce and fir-beech forests, respectively. The species basal area composition of plots between 950 and 1200 m a.s.l. corresponded to fir-spruce forests and that of plots between 800 and 1000 m a.s.l. to fir-beech forests (data not shown).

Most forests in the European Alps have been shaped to some extent by human activities. The NFI1 data reflect these legacies and may over-represent the amount of *Picea abies* Karst in particular and under-represent species such as *Abies alba* Mill., *Fagus sylvatica* L. and *Sorbus aucuparia* L. compared to unmanaged conditions (Ott et al., 1997). By merging data of all NFI1 sampling locations representing a regional forest type we expected to dampen local legacy effects.

### 2.2.2. Climate data

For each of the 15 regional forest types two to four climate stations were selected from the climate database of the Swiss Meteorological Agency to represent the temporal and spatial variability in the climate prevalent for a forest type in the last century (Fig. 1 and Table 1), whereby one climate station was sometimes used to describe the climate
in more than one forest type per region. For each climate station we obtained from the available time series daily mean values of temperature, precipitation, vapor pressure and relative humidity as well as the daily sum of sunshine hours.

Table 1. Forest type and climate station details; climate station with elevation (meters a.s.l.), low (25%ile) and high (75%ile) elevation of NFI sampling locations in the regional forest types (meters a.s.l.) and corresponding temperature adjustments (°C; NA = no adjustment); N = number of aggregated NFI plots for regional forest types.

<table>
<thead>
<tr>
<th>Forest Type</th>
<th>Southern Alps (S Alps)</th>
<th>Western Central Alps (W Cen Alps)</th>
<th>Northern Pre-Alps (N Pre-Alps)</th>
<th>Eastern Central Alps (E Cen Alps)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Climate station</td>
<td>Elevation</td>
<td>N</td>
<td>Climate station</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>High</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Sub-alpine spruce</td>
<td>1581m</td>
<td>1769m</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>San Bernardino</td>
<td>NA</td>
<td>-1°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arosa, 1149m</td>
<td>-2°C</td>
<td>-3°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rodeli, 1808m</td>
<td>+1.5°C</td>
<td>+0.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High montane fir</td>
<td>1544m</td>
<td>1635m</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>San Bernardino</td>
<td>NA</td>
<td>+0.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arosa, 1149m</td>
<td>-0.5°C</td>
<td>-1.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rodeli, 1808m</td>
<td>+2°C</td>
<td>+1.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montane spruce</td>
<td>1237m</td>
<td>1434m</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td>San Bernardino</td>
<td>+2.5°C</td>
<td>+1°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arosa, 1149m</td>
<td>+0.5°C</td>
<td>-1.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rodeli, 1808m</td>
<td>+4°C</td>
<td>+2.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montane fir-beech-spruce</td>
<td>1088m</td>
<td>1420m</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>San Bernardino</td>
<td>+2.5°C</td>
<td>+1°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arosa, 1149m</td>
<td>+0.5°C</td>
<td>-1.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rodeli, 1808m</td>
<td>+4°C</td>
<td>+2.5°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montane beech</td>
<td>907m</td>
<td>1064m</td>
<td>63</td>
<td></td>
</tr>
<tr>
<td>Cinetta, 1572m</td>
<td>+4°C</td>
<td>+3°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stabio, 353m</td>
<td>-2.5°C</td>
<td>-3.5°C</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

From these data we derived the inputs for FORCLIM, i.e., monthly means and standard deviations of temperature and precipitation plus the cross-correlation between these variables. From these statistics, random weather data are generated by FORCLIM for each year of the 1000-year simulations.

For PICUS we calculated the monthly means for temperature, precipitation as well as solar radiation and vapor pressure deficit from the available climate data time series. We used the Angström equation to estimate solar radiation from actual observed and maximum possible sunshine hours (Duffie and Beckman, 1991). Vapor pressure
deficit \((v_{pd})\) was calculated based on an established relationship with relative humidity \((r_H)\) and vapor pressure \((v_p)\; \text{van Eimen and Häckel, 1979}):

\[
v_{pd} = \frac{v_p}{100 \cdot r_H}
\]  

As input for PICUS we randomly recycled the annual data, i.e., annual sets of 12 monthly means, to obtain a time series sufficient to run simulations over 1000 years.

We adjusted the temperature means for each climate station using a lapse rate of 0.5 °C per 100 m to represent the elevation quartiles of the NFI1 sampling locations. This yielded a low-elevation scenario (i.e., 25%ile) and a high-elevation scenario (i.e., 75%ile) for each climate station (cf. Table 1 for temperature adjustments). Although other climate variables such as precipitation and solar radiation also change with altitude, we assumed that the use of this single proxy would be sufficient since temperature is a key variable in the model formulations of species establishment and growth, and also in real mountain topography (Barry, 1992).

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Region</th>
<th>Min. species fraction in stand basal area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subalpine spruce</td>
<td>Southern Alps, Western Central Alps, Northern Pre-Alps, Eastern Central Alps</td>
<td>Picea abies &gt;85%</td>
</tr>
<tr>
<td>High montane fir</td>
<td>Southern Alps, Western Central Alps</td>
<td>Abies alba &gt;40%, Picea abies &lt;5%, Larix decidua &gt;5%, Fagus sylvatica and Acer pseudoplatanus &lt;60%</td>
</tr>
<tr>
<td>Montane spruce</td>
<td>Southern Alps, Western Central Alps, Eastern Central Alps</td>
<td>Picea abies &gt;40% and &gt; BA Pinus spp., Larix decidua &gt;5%, Abies alba &lt;10%, Pinus spp. &gt;5%</td>
</tr>
<tr>
<td>Montane beech</td>
<td>Southern Alps, Northern Pre-Alps</td>
<td>Fagus sylvatica &gt;40%, Abies alba and other deciduous &gt;40%, Picea abies &lt;40%</td>
</tr>
<tr>
<td>Montane fir-beech-spruce, incl. subtypes in Northern Pre-Alps:</td>
<td>Southern Alps, Western Central Alps, Northern Pre-Alps, Eastern Central Alps</td>
<td>Abies alba &gt;10%, Fagus sylvatica &gt;10%, Abies alba and Fagus sylvatica and other deciduous &gt;40%, Picea abies &lt;40%</td>
</tr>
<tr>
<td>Montane fir-beech</td>
<td>Abies alba &gt;30%, Picea abies &gt;25%, Fagus sylvatica &lt;10%</td>
<td></td>
</tr>
<tr>
<td>Montane fir-spruce</td>
<td>Abies alba &gt;15%, Fagus sylvatica &gt;30%, Picea abies &lt;30%</td>
<td></td>
</tr>
</tbody>
</table>
2.3. Simulation experiments

Based on the climate data representing the 15 regional forest types (cf. Table 1), we simulated forest development with FORCLIM v2.9.3 and PICUS v1.4 over 1000 years starting from bare ground. We did this separately for the climate stations representing the conditions within one forest type. For example, the simulations for montane beech forests in the Southern Alps included four simulations, i.e., lower elevation based on the stations Cimetta and Stabio, plus the higher elevation again for Cimetta and Stabio (cf. Table 1).

For the forest types montane fir-beech-spruce and montane beech, we assumed favorable soil conditions and thus set the water-holding capacity in the simulations to an ample 150 mm. We used a water holding capacity of 100 mm for the simulations of subalpine spruce, high montane fir and montane spruce forests.

With FORCLIM, we simulated 200 patches of 800 m$^2$ to represent stand-scale forest development (cf. Section 2.1). In PICUS, a forest stand consisted of 100 (10 by 10) patches of 100 m$^2$ (10 by 10 m) representing an area of one hectare. The models were generally used without adjustments to their default parameters, but to simplify the comparison of model performance and to remove artifacts, we made the following assumptions:

- Nitrogen is not limiting, i.e., soil N availability was set to 100 kg/ha.
- Soil pH is near optimal for most species, i.e. pH = 4.2.
2.4. Data Analysis

2.4.1. Basal area

We calculated the species-specific absolute basal area (i.e., m²/ha⁻¹; hereafter BA) and the fraction of the total basal area (i.e., %; hereafter %BA) as the average over all NFI1 sampling locations representing one regional forest type (Table 2) in order to examine whether the models are able to reproduce observed basal area data.

The observed BA was from trees >12 cm whereas simulated BA was based on trees >1.27 cm dbh in FORCLIM and approx. >1 cm dbh in PICUS; a completely analogous sampling from both models was not possible due to technical constraints. Since we used %BA for most of our analyses, this difference was negligible. We derived the simulated BA and %BA for each of the 15 regional forest types as the mean over all scenarios representing one regional forest type (cf. Table 1). In analogy to the observed data, simulated BA and %BA of fir-spruce and fir-beech forests were distinguished in the montane fir-beech-spruce forests of the Northern Pre-Alps.

We used a percentage similarity coefficient (PS; eq. 2) to compare observed %BA with simulated %BA for every 50th year of the 1000 years of simulated data:

\[
PS = 1 - \frac{\sum_{i=1}^{n} |x_i - y_i|}{\sum_{i=1}^{n} (x_i + y_i)}
\]

where \(x_i\) is the value for species \((i)\) in the simulated data, \(y_i\) is the value for species \((i)\) in the observed data, and \(0 \leq PS \leq 1\) (Bugmann, 1997).

2.4.2. Tree numbers <12 cm dbh

We compared species-specific tree numbers for three dbh classes in the juvenile stage (class 1: saplings <4 cm dbh; class 2: 4 \(\leq\) dbh <8 cm; class 3: 8 \(\leq\) dbh <12 cm). The lower limit in class 1 depended in the NFI1 on the measurement cut-off of 130 cm tree height (i.e., a dbh >0 cm) and in the models on the tree dbh at establishment (~1 cm in PICUS; 1.27 cm in FORCLIM), which is a consequence of the use of tree dbh as a state variable in the models. These differences could not be removed, but the effects were taken into account in the interpretation of the results.

We compared simulated and observed data for the dominant species and for the totals over all 12 species or species groups per regional forest type. We evaluated observed data against simulated tree numbers in a time window between 200 and 400 years of the simulation to ensure that the simulations from bare ground reached a mid-successional stage similar to the observed data. We also used a second time window
between 800 and 1000 years of the simulation as FORCLIM simulations reach an equilibrium after 700 to 800 years (Bugmann et al., 1996); we assumed that PICUS simulations have similar properties in this regard.

Because the size of the plots varied between observed and simulated data, i.e., 28.3 m$^2$ in the NFI1, 100 m$^2$ in PICUS, and 800 m$^2$ in FORCLIM, we adopted the following protocol for comparing tree numbers over an area equivalent to the smallest common multiple of the sample plot sizes in our data, i.e., 800 m$^2$: For each of the 15 regional forest types we derived a frequency distribution of tree numbers by repeating the following procedures 200 times:

- **NFI1**: Summing the number of trees from 28 NFI1 plots sampled randomly with replacement (i.e., $28 \times 28.3$ m$^2 \approx 800$ m$^2$) per regional forest type (sampling with replacement was necessary here due to the limited number of plots, cf. Table 1);

- **PICUS**: Summing the number of trees from eight (out of 100; cf. Section 2.3) contiguous 100 m$^2$ PICUS patches (i.e., $8 \times 100$ m$^2 = 800$ m$^2$) sampled randomly without replacement at one point in the 200 year time window simulated for the two elevation scenarios of each climate station representing a regional forest type. In contrast to the analysis of basal area we did not make separate analyses for the two elevation scenarios;

- **FORCLIM**: Obtaining the number of trees on one (out of 200; cf. Section 2.3) 800 m$^2$ FORCLIM patch randomly sampled without replacement for one point in the 200 year time window simulated for the two elevation scenarios of each climate station representing a regional forest type.

### 3. Results

#### 3.1. Basal area

Our stratification of the NFI1 data represented forest types typical for mountain regions in the Swiss Alps, although in some cases with relatively few plots per forest type (Table 1). The majority of the observed plots were dominated by *P. abies* (Table 1) reflecting the species’ naturally broad range and its preference by past forest management (Brändli, 1996). Since the measured BA data were based on trees >12 cm dbh, rare species and typical understory species such as *S. aucuparia* are likely to be underrepresented in the forest inventory (Brändli, 1996).

FORCLIM v2.9.3 and PICUS v1.4 generally simulated the dominant species for a regional forest type correctly, as reflected by the PS coefficients (Fig. 2). The temporal pattern of the PS differed between the two models: max. PS in PICUS after ca. 200-400 and in FORCLIM after >800 simulation years (Fig. 2).
While the results of FORCLIM varied little with the elevation gradient, i.e., adjusted temperatures for the low and high elevations of one climate station, PICUS was more sensitive to changes in temperature within regions (Fig. 3). We thus analyzed PICUS
results for BA and $\%$BA of each forest type separately for the low- and high-elevation scenarios, but averaged the results for the analysis of FORCLIM.

For the montane fir-beech-spruce forests of the Northern Pre-Alps, NFI1 data showed that the dominant species changed with elevation from *F. sylvatica* to *P. abies* (cf. NFI1 BA for this forest type in Fig. 3). This pattern was reproduced by PICUS (Fig. 3), but it was missed by FORCLIM (detailed results not shown).

In the drier montane spruce forest type of the Western Central Alps species such as *Pinus montana* Mill. are expected (~5% of the BA; cf. NFI1 BA for this forest type in Fig. 3). FORCLIM simulated *Pinus cembra* L. and *Pinus* spp. (i.e., *Pinus sylvestris* L. and *P. montana*; Fig. 3). In the PICUS simulations *Pinus* spp. occurred only in the first 50 years of the low-elevation scenario and with a very low fraction of total BA (<1%; Fig. 3). Generally, FORCLIM overestimated BA and species diversity, while PICUS underestimated these properties (Fig. 3). FORCLIM typically produced a large fraction of deciduous species including *Quercus* spp. and even *Castanea sativa* L. in the montane fir-beech-spruce forests of the Northern Pre-Alps (Fig. 3), which were rare or
absent in the measured data. Across all forest types PICUS simulated only five
dominant species, i.e., Larix decidua Mill., P. abies, A. alba and, depending on
elevation, P. cembra or F. sylvatica (Fig. 3). Mostly absent in PICUS simulations were
common broadleaved deciduous species such as S. aucuparia and Betula pendula
Roth, which are typical for early-successional forests in the European Alps. Such
species appeared in the measured data (~2% “other Deciduous” in the NFI1 data; Fig.
3) and were simulated by FORCLIM, although overestimated in their abundance (Fig.
3). In PICUS L. decidua was simulated as the main pioneer species, often representing
more than 50% of BA in the first few hundred simulation years (Fig. 3). Early-
successional forests simulated by PICUS often contained uncharacteristic species such
as A. alba in the montane spruce forests of the Western Central Alps (a fraction of
approx. 15% in the low-elevation scenario, and approx. 10% in the high-elevation
scenario; Fig. 3).

3.2. Tree numbers <12 cm dbh

In most forest types measured and simulated tree numbers differed greatly with a
larger deviation for the dominant species (i.e., up to one order of magnitude) than for
all species (Fig. 4). In the NFI1 data, median tree numbers varied with forest type and
generally decreased with elevation (Fig. 4). This pattern was also apparent in the
simulated data (Fig. 4). Only little difference existed between the two time windows,
with larger differences in PICUS simulations than in FORCLIM (Figs. 5 and 6).

In natural forests, stem diameter distributions over larger areas tend to decline
monotonically (Rubin et al., 2006). Measured tree numbers in the NFI1 showed a
similar trend for the median tree numbers of all species and for the dominant species
(Fig. 4). This pattern was reproduced qualitatively by FORCLIM, typically for all
species (Figs. 4-6), but in most PICUS simulations tree numbers of the dominant as
well as of all species peaked in dbh class 2 (Figs. 4-6), which is likely to reflect a
technical problem (cf. Section 4).

To check for possible skewness of the distributions, we also evaluated the difference
between median and average values of tree numbers (Figs. 5 and 6). The simulated
mean number of trees was consistently higher than the median, reflecting the large
number of very small values and the relatively few very large simulated values. Still,
the general trends in tree numbers per dbh class mentioned above were also evident in
the means (Figs. 5 and 6).

Variability in simulated tree numbers was high in both models with a wide range for
the outliers (Figs. 5 and 6), particularly for the dominant species. This was illustrated
by difference between simulated median and mean tree numbers with many median
values of 0 and means that in some cases approached or even exceeded the observed
Figure 4. Medians of tree numbers in 3 dbh classes (<4 cm, 4-8 cm, 8-12 cm) for 15 regional forest types, simulation time window 200 to 400 years. Open symbols and dashed lines represent the dominant species, filled symbols and solid lines for all species. The values for the 3 dominant species in the montane fir-beech-spruce forests were averaged. NB the log y-scale with a constant value of 1 added to the number of trees. Lower right hand corner: Ratio of simulated to observed medians of tree numbers calculated as the average of all 15 regional forest types for time window 200 to 400 years.
mean (cf. Figs. 5 and 6). Variability in the NFII data was lower than in the simulations (Figs. 5 and 6), even for forest types with a low number of sampling plots such as Southern Alps high montane fir forests (i.e., 13 plots, cf. Table 1).

![Figure 5. Montane spruce forests of the Eastern Central Alps - boxplots showing median, lower and upper quartiles, 5%ile and 95%ile, and outliers of the number of trees in 3 dbh classes (<4 cm, 4-8 cm, 8-12 cm) in observed and simulated data for the dominant (here *Picea abies*) and for all species for simulation time windows 200 to 400 years and 800 to 1000 years. Note: The log y-scale with a constant value of 1 added to the number of trees. The mean tree number is symbolized with an 'x'.](image)

4. Discussion

4.1. Use of large-scale forest inventory data for evaluating forest gap models

4.1.1. Potentials

Large-scale forest inventories cover large environmental gradients, particularly so in mountain regions. Therefore, such extensive inventory data allow for a much more rigorous evaluation of a) model generality and particularly b) the simulation of vegetation gradients than, for example, descriptions of potential natural vegetation (PNV; e.g., Lindner et al., 1997; Bugmann and Solomon, 2000).
Figure 6. Montane fir-beech spruce forests of the Southern Alps - boxplots showing median, lower and upper quartiles, 5%ile and 95%ile, and outliers of the number of trees in 3 dbh classes (<4 cm, 4-8 cm, 8-12 cm) in observed and simulated data for the three dominant (here Abies alba, Fagus sylvatica, Picea abies) and for all species for time window 200 to 400 years and 800 to 1000 years. Note: The log y-scale with a constant value of 1 added to the number of trees. The mean tree number is symbolized with an ‘x’.
In addition, the large number of samples in forest inventories allows compiling forest properties in the form of frequency distributions. Therefore, a more robust evaluation is possible that is based on the simulated frequency distributions of forest properties by gap models, rather than on averages as was done in most other assessments (e.g., Busing et al., 2007).

Lastly, the standardized nature of forest inventory data provides a consistent data set for a range of variables that can be compared with simulation results. This facilitates the analysis particularly for comparisons across a wide range of sites. In other studies, data compatibility across sites and regions has often been a considerable problem (e.g., Bugmann and Solomon, 2000).

### 4.1.2. Limitations

Due to the spatial extent of national forest inventories, the natural and anthropogenic disturbance history that has shaped the measured variables is not known, at least not for the entire area of the inventory. Due to this uncertainty it is difficult to identify a plausible extent of deviation between simulated and measured variables, which may be caused by an inappropriate setup of the simulation experiments or erroneous comparisons. By averaging data over many sampling plots, as done here, the influence of “extreme” situations and events has certainly been reduced, but it is still present in the data set. This problem is intimately tied to the nature of inventory data and is unlikely to be resolved easily (cf. Bürgi, 1999; Bürgi and Russell, 2001).

While we are confident that the dominant forest features based on trees >12 cm dbh are represented adequately by sampling data on 0.02 and 0.05 ha plots, it was surprising to note that simulated variability for the sapling and juvenile stages was larger than the variability derived from the inventory regardless of the number of inventory plots in one forest type. As plot size increases, between-plot variance decreases (Scott, 1998), and the largest variability was thus expected in the inventory data measured on 28.3 m² plots compared to 100 m² in PICUS and 800 m² in FORCLIM. In addition, the comparison of this type of measured data from particularly small sampling plots with simulated data that are characteristic of larger spatial scales is compromised because of a) the requirement for different sampling schemes to derive data for the comparison, and b) the small plot size that may not have been sufficient to capture the variability of a stand. Although these issues may be evaded by employing a large spatial dataset, a robust evaluation of simulated stand diameter structure may not be possible at the scale used in this study, but only at the stand scale and based on data from a full cruise.

Finally, information from several consecutive inventories would greatly assist in the interpretation and would improve the strength of the analysis. However, large-scale
forest inventories do not have a long history and it is well known that changes in space are not a perfect analogue for changes in time (e.g., Finegan, 1984).

4.2. Model evaluation

Most Swiss forests are managed or have been managed until recently (EAFV and BFL, 1988), whereas the simulated data refer to unmanaged stands (Bugmann, 2001b), thus rendering comparisons difficult. We attempted to reduce this problem by focusing on mountain forests, which often are less intensively managed than low-elevation stands (e.g., Grabherr et al., 1998; Brassel and Brändli, 1999).

4.2.1. Basal area

The differences in the two models regarding the temporal PS patterns between simulated and observed %BA (cf. Fig. 2) can be attributed to the contrasting species diversity produced by PICUS and FORCLIM. In FORCLIM, succession to equilibrium with only a few dominant species appears to be delayed by the large share of pioneer species that persist throughout several centuries of forest development. In PICUS, the dominant late-successional species emerged faster and commonly had more than 10% of total BA after only 50 simulation years (cf. Fig. 3). The speed of succession and the simulated species diversity in the models thus require further investigation (also cf. Weber et al., 2008). In FORCLIM the assumption of unlimited seed supply and the simple calculation of the light regime may lead to exaggerated competitiveness of shade-intolerant species (Wehrli et al., 2007), or underestimated mortality.

In PICUS, seed availability depends on a low background seed supply of all species plus the presence of mature potential seed trees of a species in the stand. Besides natural individual tree mortality, no disturbances were included in the simulations, which favors shade-tolerant late-successional species over light demanding pioneer species. This may be the mechanism that, together with parameterization problems in the regeneration module (see below), causes the low species diversity and partly unrealistic successional pattern with a dominant role of *A. alba* and *P. abies* in the early succession (cf. Fig. 3). Since the focus in the development of the current PICUS regeneration module was on managed forests, parameter estimation focused on late-successional species, applying only lumped parameters for pioneers (Woltjer et al., 2008). Thus, simulating natural forest development with PICUS is likely to result in an underestimation of pioneer species abundance, which in turn may have the effect that their successional niches are filled by other tree species, resulting in unrealistic successional patterns.

The interpretation of the simulated data is not easy due to the often multiple, counter-acting effects of management on forest features. For example, it appears that *Fagus*
sylvatica-dominated forests of Eastern Europe are characterized by very few tree species (e.g., Korpel’, 1995; Commarmot et al., 2005), and that after the cessation of management species numbers have declined in some Swiss forest reserves (Heiri et al., 2009), indicating that management has favored early-successional species by reducing competition for light. Thus, simulated species diversity should be lower than measured diversity (a pattern that was evident from PICUS but not from FORCLIM in the present study). However, past management often favored a single, commercially attractive species, such that diversity in managed stands should be lower than in the simulations. The net effect of these impacts is exceedingly hard to evaluate, particularly at fairly large spatial scales as those studied here.

4.2.2. **Number of trees <12 cm dbh**

The results for tree numbers with dbh <12 cm gave rise to two major concerns: a) the underestimation of measured tree numbers by the models, particularly the high number of zero values for the median tree number of the dominant species (Fig. 4), and b) the large difference in the variability between simulated and measured data (Figs. 5 and 6).

Although the reliability of the measured data may be limited (see above), we feel that the strong underestimation of tree numbers by both models (cf. Figs. 4 to 6) is likely to represent a model problem rather than a data problem.

In FORCLIM the overly strong decline in the simulated tree numbers with increasing dbh indicates deficiencies in the simulation of tree mortality. This has been reported already for an earlier FORCLIM version, where it was attributed to a leaf area overestimation due to a fixed relationship between tree diameter and leaf area, which results in overly dark stands where understory trees have very low chances of survival (cf. Wehrli et al., 2005). Mortality of small trees in FORCLIM may be amplified further by the overestimated species diversity and the resulting strong competition between small trees. Furthermore, in some phases of simulated forest development, the underestimation of light availability at the forest floor prevents tree establishment (Wehrli et al., 2007), which is partly responsible for the large number of zero median values of tree numbers (cf. Fig. 4).

The pattern observed in PICUS, with median and mean tree numbers being highest in dbh class 2 (cf. Figs. 4 to 6), may indicate that trees grow too fast through the smaller diameter classes. This leads us to surmise that tree growth may be too rapid and mortality consequently too low as light conditions are more favorable with fewer trees on a patch. Also, the lateral shading effect that is included in the spatially explicit PICUS model may be underestimated leading to light conditions that overestimate sapling growth. In PICUS version 1.4, biomass (and thus leaf area) is estimated
differently for juvenile and older trees, leading to a discontinuity in simulating the light environment. For trees with <130 cm height, total biomass is estimated for a representative tree per height class independent of density (cf. Woltjer et al., 2008), but outgrowth from the juvenile stage is treated as individuals and their biomass compartments are estimated using allometric equations that differ from those employed for smaller trees. These inconsistencies are smoothed out in the course of the simulated succession and are evident only if one focuses explicitly on tree regeneration, as done here.

4.3. Implications for model development

The magnitude of the underestimation of observed tree numbers was similar for both models, which is surprising because the models simulated rather different basal area values per forest type (cf. Fig. 2 and 3). For example, FORCLIM simulated a total basal area in the Western Central Alps montane spruce forests that was twice as high as the one produced by PICUS (cf. Fig. 3), with only little difference in simulated spruce tree numbers <4 cm dbh (cf. Fig. 5). While in FORCLIM the underestimation of tree numbers in the dbh class <4 cm can be attributed to the overestimation of leaf area mentioned above, the cause for this result in PICUS is more difficult to identify given the more complex representation of the tree canopy. Future efforts in model development should address this issue; it is disconcerting when models achieve realistic basal area values (i.e., “the right answer”) based on unrealistic tree numbers (i.e., “the wrong reason”).

Another significant finding was the difference in model sensitivity to changes in environmental drivers, with PICUS being more sensitive to changes in temperature than FORCLIM within some forest types. PICUS results were clearly closer to the inventory data (cf. Fig 3), suggesting a higher realism of this model. Thus, future model evaluations should emphasize the appropriateness of the response of a model to changes in environmental driving variables, beyond what we did in the analysis of regional forest types. A key factor appears to be temperature and particularly its effects on tree growth (cf. Rickebusch et al., 2007).

5. Conclusion

To overcome some shortcomings of previous model evaluation studies, we explored the suitability of large-scale forest inventory data for the evaluation of gap models. The results of our study indicate that such data can be valuable for investigating model performance at the level of the dominant species using basal area data. However, large-scale forest inventory data lack in the detail required for an evaluation whether a
model is able to reproduce structural forest aspects such as species diversity, successional patterns, and tree numbers in the low diameter classes (e.g., <12 cm dbh in this study).

Therefore, we conclude that large-scale forest inventory data can be valuable for model evaluation, particularly when they cover large environmental gradients and do not come from intensively managed forests. Due to their limitations, they must, however, be complemented by other materials such as data from a full cruise and regeneration measurements. A combination of approaches is needed for model evaluation, and inventory data are likely to play an important role in this task, in spite of the several limitations of this data source.

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References


Evaluating forest gap models

B. Simulations with FORCLIM v2.9.1, v2.9.3 and PICUS v1.4 for data from long-term forest research sites

Abstract

Didion et al. (2009) found that the models PICUS v1.4.1 and FORCLIM v2.9.3 underestimated observed juvenile tree numbers of, particularly the dominant species in simulations based on large-scale data from the First Swiss National Forest inventory. In further investigations this deficiency was also found in FORCLIM v2.9.1. In order to investigate the hypothesis that stress-related mortality in the models was the main cause for this underestimation, I performed a case study based on long-term forest research data, which allowed a comparison between observed and simulated forest development. The particular objectives of this experiment were a) to evaluate whether the examined models could reproduce observed tree numbers and basal area better in simulations using stand-scale forest data, and b) to analyze model sensitivity to changes in the number of new trees that establish and the consequences thereof for the medium-term (several decades) simulated forest.

In FORCLIM v2.9.3, I was able to attribute the overestimation of leaf area as the cause for the inaccurate representation of juvenile tree numbers. In PICUS several processes were responsible for the unsatisfactory performance. Since FORCLIM v2.9.1 performed poorer than v2.9.3 and PICUS, I eliminated it from the further analysis. Due to the lower complexity of the FORCLIM model, which uses a simple crown structure rather than a 3-dimensional representation as in PICUS, I selected FORCLIM v2.9.3 for further study.
1. Introduction

The results from the comparison with large scale data from the First Swiss National Forest Inventory (Didion et al., 2009; Appendix II) indicated that the examined gap models PICUS v1.4, FORCLIM v2.9.1 and v2.9.3 had deficiencies in the simulation of the number of trees <12 cm diameter at breast height (dbh). Compared with observed patterns, the decline in total tree numbers with increasing dbh was too strong and tree numbers of the dominant species were strongly underestimated. Since the models simulated the share of the dominant species with respect to basal area acceptably, this unsatisfactory representation of tree numbers was not expected.

Based on results for PICUS v1.4 and FORCLIM v2.9.3 from simulations at the stand-scale based on data from a full cruise (e.g., Risch et al., 2005; Seidl et al., 2005), a second experiment was initiated to evaluate the simulation of structural forest attributes such as basal area, tree numbers, and dbh distribution in such simulations. To this end, I decided to conduct simulations with all three models (PICUS v1.4, FORCLIM v2.9.1 and v2.9.3) using data from long-term forest research sites. I performed a small pilot study with simple simulations to test the procedure for initializing stands in the models with measured data and to gain first insights in model performance with regards to the simulation of tree numbers, before carrying out in-depth simulations at more sites. I used data from forest research sites (Versuchsflächen der Waldwachstumsforschung; WSL 2002). These comprise long-term forest inventory data of trees >8 cm diameter at breast height from different sites across Switzerland.

In this study, I placed particular attention on corroborating the hypothesis that the formulation of the stress-related mortality in the models was the main cause for the overestimated decline in tree numbers with increasing dbh as found in Didion et al. (2009). The specific objectives of this experiment were a) to evaluate whether the models were able to reproduce observed tree numbers and basal area better in simulations with initialized stands than in simulations from bare ground (i.e., clear cut conditions), and b) to analyze model sensitivity to changes in the number of new trees that establish and the consequences thereof for medium-term (several decades) simulations. I expected better model performance with regards to these attributes in simulations with initialized stands than in simulations from bare ground because stand structure, including the number of trees of the dominant species was strongly prescribed through the initialization and was not an emergent feature in a stochastic process in simulations from bare ground.
2. Pilot study

As a first test, a pilot study was conducted at 3 sites in Switzerland with the two models used in Didion et al. (2009) - i.e., PICUS v1.4 and FORCLIM v2.9.3 - and additionally with the model FORCLIM v2.9.1. The results of this pilot study were intended for

- establishing a procedure to create a stand initialization file as input for the models that closely resembled the observed stand data; and

- identifying important variables that are responsible for the poor model performance with regards to the simulation of numbers of tree regeneration.

I formulated several working hypothesis for the pilot study:

- In simulations with model regeneration (cf. section 2.1.3), I expected that simulated tree numbers are higher than observed numbers because a) harvesting was not simulated and b) simulation results included trees >1.27 cm dbh in FORCLIM and > approx. 1 cm in PICUS (cf. section 2.1.1), respectively, as opposed to the observed data with trees >8 cm only (cf. section 2.1.2).

- In simulations without model regeneration, I expected that simulated tree numbers are similar to the observed data as no or only little ingrowth had occurred in the measured stands.

- In simulations with and without model regeneration, I expected a good match between simulated and observed basal area, since small trees <8 cm dbh contribute only little to the total basal area.

2.1. Methods

2.1.1. Models

PICUS

As opposed to the traditional approach of horizontal independence between patches, the hybrid model PICUS accounts for horizontal interactions between patches. For example, PICUS assumes that species that are present in a stand (in the simulated patches) have an increased probability of establishment (Seidl et al., 2005). For a more mechanistic description of tree growth, the gap model PICUS v1.2 ( Lexer and Hönninger, 2001) and the stand-level forest productivity model 3-PG (Landsberg and Waring, 1997) were hybridized resulting in PICUS v1.3 (Seidl et al., 2005). In the current model version 1.4, the recruitment approach of traditional gap models has been replaced by a more detailed regeneration submodel, which employs a size-class approach with four height classes (0-10 cm, 10-30 cm, 30-80 cm, 80-130 cm) to
simulate seedling establishment and development dependent on species-specific height growth potential and stress tolerance in conjunction with patch-specific light availability and the effects of environmental factors (Woltjer et al., 2007).

PICUS uses a “pre-run” to establish stand light conditions (R. Seidl, pers. com.). The pre-run is used to determine the crown length of each tree based on stand density. This may lead to mortality of individual trees, if their crown length is below a minimum that is necessary for growth (“light compensation point”). Other than mortality in the pre-run, trees can die from intrinsic causes or from stress due to unfavourable environmental conditions (Seidl et al., 2005).

FORCLIM

In FORCLIM (Bugmann, 1996; Bugmann and Solomon, 2000), trees are established as saplings with a dbh of 1.27 cm as a function of species-specific responses to winter temperature, light availability, growing degree-days and browsing pressure. FORCLIM assumes unlimited seed availability of all species in each patch (i.e., there are no patch interactions as in PICUS). In this study two model versions were used: FORCLIM v2.9.1 (Bugmann and Solomon, 2000) and FORCLIM v2.9.3 (Risch et al., 2005; for the differences between the two model versions see Appendix I). As in other gap models, FORCLIM simulates intrinsic and stress-related mortality (Bugmann, 1996). The risk of stress-related mortality depends on the mortality rate of slow growing trees ($k_{\text{SlowGrP}}$), the number of consecutive years a tree has experienced stress ($k_{\text{SGr}}$), and the number of consecutive years $k_{\text{SGrT}}$ ($k_{\text{SGrYrs}}$ in Bugmann, 1994, Table 3.4) a tree can experience stress (i.e., minimal growth) without increased risk of mortality (Bugmann, 1996).

2.1.2. Study area

Simulations were run for three sites with different forest types (Table 1; Fig. 1), which were obtained from the database of forest research sites (Versuchsflächen der Waldwachstumsforschung; WSL 2002). The three sites were selected because only little management in form of tree removal occurred over the observation period.

2.1.3. Model initialization

The three models were initialized based on the stand information from the respective first observation year. For the sake of simplicity, all observed trees were grouped into dbh classes of 2 cm width and in the initialization a random dbh out of the respective dbh class was assigned to each tree. Based on the plot area, the trees were randomly distributed on a number of model patches, which was calculated as plot area / model patch size. In the spatially explicit PICUS, a forest consists of multiple 100 m$^2$ patches
with interactions between patches regarding light regime and seed dispersal. The initialized PICUS forest thus consisted of a number of 100 m² patches to match the site area. The spatially not explicit FORCLIM requires the simulation of a minimum number of patches to reduce the stochastic noise in the simulation results (Bugmann, 1996). Therefore, the procedure from Wehrli et al. (2005) was used to create multiple 800 m² patches that were then replicated sacral times in order to obtain the required number of patches.

Table 1. Site description (WSL, unpublished data) for forests stands used to initialize simulations in the pilot study.

<table>
<thead>
<tr>
<th>Site</th>
<th>Hospental, UR</th>
<th>Niederhünigen, BE</th>
<th>Wiesen, GR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>1512 m a.s.l., Central Alps</td>
<td>931 m a.s.l., Northern Pre-Alps</td>
<td>1330 m a.s.l., Eastern Central Alps</td>
</tr>
<tr>
<td>Stand type</td>
<td>high montane, even-aged Norway spruce forest; estimated stand age in 1985: 106 years; the stand originated from spruce plantation and was managed as high standard forest (“Hochwald”)</td>
<td>montane, uneven-aged Norway spruce-silver fir forest; managed as single-tree selection forest (“Plenterwald”)</td>
<td>high-montane, even-aged European larch forest; estimated stand age in 1996: 176 years; used as forest pasture</td>
</tr>
<tr>
<td>Inventory</td>
<td>13 observations between 1898 and 1985. In the first measurement at this site in 1898, all trees higher than 130 cm were recorded and their dbh measured in the following observations; in later observations, new trees were only recorded if their dbh was &gt; 8 cm. With the exception of the time between the first and second observation, with the continuing closure of the young stand no ingrowth of trees &gt; 8 cm dbh was observed until the last inventory in 1985.</td>
<td>18 observations between 1905 and 2005. The measurement dbh threshold was 8 cm. Only little ingrowth of new trees &gt; 8 cm dbh was observed at the site over the inventory period.</td>
<td>10 observations between 1921 and 1996. The measurement dbh threshold was 8 cm. Due to the use as pasture no ingrowth of trees &gt; 8 cm dbh was observed at the site and tree numbers remained almost constant over the observation period.</td>
</tr>
</tbody>
</table>
2.1.4. Simulation scenarios

In order to evaluate the regeneration in the models, two sets of simulations were carried out:

1. The regeneration in the three models was turned on and it was assumed that all 30 parameterized species in the three models could establish if environmental conditions (e.g., winter temperature, degree days) were suitable for a species’ establishment. This was consistent with the assumption of unlimited seed supply in these models.

2. The regeneration in the three models was turned off, i.e., there was no ingrowth of young trees during the simulations.

The forest stands at each of the three sites were simulated with all three models for 100 years. The irregular harvesting of a few single trees at the sites was not simulated due to technical constraints. The simulation results were compared with the stand data over the respective observation periods. While, with the exception of the site at Hospental, the observed number of trees was calculated based on trees larger than 8 cm dbh, in the simulation scenarios with model regeneration trees established with a dbh of approx. 1 cm in PICUS, and 1.27 cm in FORCLIM, respectively. Thus an overestimation of the number of small trees by the models was expected.

The default parameter settings and assumptions for both models were: medium soil moisture conditions (i.e., FORCLIM bucket size was 10 cm, PICUS water holding capacity was 100 mm), Nitrogen and pH were not limiting (i.e., available N
[kg/(ha·yr)] was 100, pH was 4.2), and the forest stand was assumed to be on an even surface.

The required climate information for the models (Didion et al., 2009) was acquired for each site from the nearest climate station maintained by the Swiss Meteorological Agency whereby a temperature lapse rate of 0.5°C per 100 m elevation change was used to account for differences in the altitude of the site and the climate station. Precipitation was not adjusted. The climate stations used for the three sites were:

- Wiesen: Arosa with 46 years of data from 1959 to 2005.

2.2. Results

2.2.1. Hospental

For the three models, the number of trees declined sharply below observed numbers in the first three decades of the simulation regardless of the scenario with or without model regeneration (Fig. 2a-f), suggesting an overestimated mortality. In both scenarios, the basal area simulated by PICUS was only half of the observed basal area, but closer to the observed data than the basal area simulated by the two FORCLIM versions (Fig. 2g-l).

In the scenario with model regeneration, besides the dominant Norway spruce no other species established in PICUS simulations (Fig. 2a), which was likely due to the fact that in PICUS, species that are present in a stand have an increased establishment probability (cf. section 2.1.1). In both FORCLIM models the stand remained dominated by Norway spruce, although deciduous species such as *Quercus spp.* and *Populus spp.* started to establish from the start of the simulation and *Abies alba* after approx. 10 simulation years (Fig. 2c and e).
Figure 2. (a-f) Annual species-specific tree numbers (ha) and (g-l) annual species-specific basal area (m²·ha⁻¹) for 100-year simulations with three models for Hospental as bars and observed total tree number of *Picea abies* as solid line for 13 observations between 1898 and 1985.
2.2.2. Niederhünigen

As opposed to Hospental, where the scenarios with and without model regeneration produced similar results, regeneration was abundant at Niederhünigen in the scenarios with model regeneration in all models (Fig. 3a-f). This was apparent in the data on species tree numbers (Fig. 3a, c, e) but not in the species basal area data (Fig. 3g, i, k). The trees could establish but did not survive to grow into larger dbh classes and thus could not contribute to stand basal area.

In all three models, a sharp decline in tree numbers of the two observed species, Norway spruce and silver fir occurred in both scenarios with and without model regeneration (Fig. 3a-f). Simulated basal area (Fig. 3g-l) was strongly overestimated by PICUS, and slightly underestimated by the two FORCLIM versions.

Few beech (*Fagus silvatica*) trees were observed at the site, and were included in the model initialization. These trees were not present in the stand at simulation start in PICUS (cf. Figs. 3a, b, g, h) because of the model setup with a pre-run that, based on the light environment calculated by the model, removes trees if conditions are considered unfavorable (cf. section 2.1.1).

2.2.3. Wiesen

The stand in Wiesen was relatively open due to its continuous use as pasture (Table 1; unpublished data, WSL). The grazing limited natural tree regeneration to a large extent and no ingrowth was observed over the observation period (Fig. 4). In the simulations without model regeneration, the three models overestimated mortality and tree numbers in the simulations declined faster than in the observed stand (Fig. 4b, d, f). The simulated increase in basal area slightly overestimated the observed increase (Fig. 4h, j, l). While both FORCLIM versions simulated a steady increase in basal area (Fig. 4j, l), basal area in PICUS declined to the end of the simulation period (Fig. 4h), which was more consistent with the observed data. As observed in the simulations for Niederhünigen, PICUS removed trees found in the stand during the pre-run. Few *Pinus montana* trees that appear in both FORCLIM versions (Figs. 4d, f, j, l) did thus not appear in the PICUS simulations (Figs. 4b, h).

In the scenarios with model regeneration, tree establishment was quite abundant because of the openness of the stand (Fig. 4a, c, e) and, as opposed to the simulations for Niederhünigen, trees survived and grew into larger dbh classes, which was evident by their contribution to the simulated basal area (Fig. 4g, i, k). Simulated tree numbers and basal area in the scenarios with model regeneration were thus strongly overestimated, particularly by FORCLIM v2.9.3. Whereas in PICUS simulations only trees of the dominant European larch established (Figs. 4a and g), in both FORCLIM versions almost all species included in the model established (Figs. 4c, e, i, k).
Figure 3. (a-f) Annual species-specific tree numbers (ha) and (g-l) annual species-specific basal area (m$^2$·ha$^{-1}$) for 100-year simulations with three models for Niederhünigen as bars and observed total tree number over all species as solid line for 13 observations between 1905 and 2005.
Figure 4. (a-f) Annual species-specific tree numbers (ha) and (g-l) annual species-specific basal area (m²·ha⁻¹) for 100-year simulations with three models for Wiesen as bars and observed total tree number over all species as solid line for 13 observations between 1921 and 1996.
2.3. Discussion and conclusion

The fact that PICUS tends to simulate species poor forests with only few species such as Norway spruce and beech that dominate and without pioneer species was already observed as a limitation of the model in Didion et al. (2009).

The sharp decline in tree numbers from dbh class <4 cm to dbh class 8 to <12 cm (cf. Didion et al., 2009) was also evident in the simulations with initialized stands of this pilot study. This suggested a deficiency in the models with respect to an overestimation of mortality. The stepwise pattern of tree mortality, observed in both FORCLIM versions, pointed toward stress-related mortality as the underlying cause. This was corroborated by changes in the relevant parameter $k_{SGrT}$, which resulted in a change in the length of the stepwise mortality pattern (cf. section 2.1.1; results not shown).

Therefore, I expected that detailed simulations for one site with two ingrowth scenarios would be sufficient to further evaluate the hypothesis that the stress-related mortality was the main cause for the sharp decline in total tree numbers with increasing dbh and the consequent underestimation of tree numbers in dbh class 8 to <12 cm found above and in Didion et al. (2009).

Since the results from Didion et al. (2009) and from the pilot study (Figs. 2-4) showed that FORCLIM v2.9.3 performed better than FORCLIM v2.9.1 with regard to simulated tree numbers, I decided to continue only with the former.

3. Detailed simulations at Oberhünigen

The purpose of this study was to evaluate the sensitivity of the two models, PICUS v1.4. and FORCLIM v2.9.3, to changes in the number of trees that regenerate. To control the number of ingrowing trees in a model, they had to be “planted”. The results from simulations with different planting scenarios were then compared with the observed differences between two inventories. Due to technical constraints with planting in FORCLIM, comparisons were made for only two consecutive inventories. The site Oberhünigen was selected because no harvesting had occurred over the observation period from 1993 to 2001.

3.1. Methods

3.1.1. Study area

The site in Oberhünigen, BE is located in central Switzerland, in the Northern Pre-Alps at an elevation of 1050 m asl (Fig. 1). All trees >8 cm dbh on an area of 0.4 hectare were measured in the even aged Norway spruce-silver fir stand. In 1993, the
estimated stand age was 149 years, the stand was composed of more than 100 trees with dbh >50 cm and a basal area of approximately 60 m²ha⁻¹. The spacing of the trees allowed for relatively full crowns that are untypical for an even-aged stand of this age (pers. com. A. Zingg). Few scattered beech and European larch individuals completed the stand.

### 3.1.2. Input data

The nearest climate station of the Swiss Meteorological Agency was Heiligenschwendi with 10 years, from 1961 to 1970, for which the required data for the models were available. Figure 5 shows the monthly averages of temperature and precipitation for the 10 year period. The climate data was processed as described in Didion et al. (2009).

Based on a stand description, available soil nitrogen was set to 80 kg/ha⁻¹ yr⁻¹, water holding capacity to 150 mm (in FORCLIM: bucket size), and soil pH in PICUS to 4.2. For the simulations no slope adjustments were used which conformed to the conditions at the site. In FORCLIM a medium background browsing impact was assumed (i.e., the browsing pressure was set to the default of 5; cf. Didion et al., 2009).

![Figure 5. Monthly averages of temperature and precipitation over the period from 1961 to 1970 for Heiligenschwendi.](image)

### 3.1.3. Stand initialization

The stand data from the inventory in 1993 were used to initialize the stand for the simulations. Based on the simulated patch sizes of 800 m² in FORCLIM and 100 m² in PICUS, all observed trees on the 0.4 hectare study site were randomly distributed on 5 patches in FORCLIM (i.e., 5 x 800 m²) and on 40 patches in PICUS (i.e., 40 x 100 m², which were arranged as 8 patches in length and 5 patches in width). To be consistent
with the modeling approach in FORCLIM which requires a certain number of repetitions, 10 replicates of the 5 original patches were used to obtain a total number of 50 patches. This procedure to initialize stands was successfully used by Wehrli et al. (2005). All trees were initialized with their observed dbh.

3.1.4. Simulation scenarios

A small sensitivity analysis with different scenarios was set up for

- evaluating the behavior of the two models in response to changes in the number of trees that establish, and
- corroborating the assumption that the stress-related mortality was the main cause for the sharp decline in simulated tree numbers observed in Didion et al. (2009).

The observed ingrowth between the last inventory before 1993 (i.e., 1985) was used to establish the ingrowth scenarios. A total of four ingrowth scenarios was simulated for 50 years:

- observed ingrowth (hereafter scenario 1);
- twice the observed ingrowth (hereafter scenario 2);
- observed ingrowth, but no stress-related mortality (hereafter scenario 3);
- twice the observed ingrowth, but no stress-related mortality (hereafter scenario 4).

I assumed that using twice the observed ingrowth as alternative simulation scenario allows to discern the effect of the stress-related mortality due to competition for light. For all four scenarios that were simulated with both models, the ingrowth was “planted” and tree regeneration in the models was turned off.

3.2. Results

At initialization, PICUS v1.4 and FORCLIM v2.9.3 slightly underestimated the observed basal area from 1993 in scenarios 1 and 3 (Fig. 6a). In scenarios 2 and 4 with twice the observed ingrowth, the observed basal area was overestimated by PICUS as expected due to the increased ingrowth but it was underestimated by FORCLIM (Fig. 6a). A visual comparison of the data on the species-specific number of trees in 12 dbh classes from the inventory in 1993 (Fig. 7a) and the initialized stand in the models showed a very good match (Fig. 7c, g, k, o) disregarding the number of trees <18 cm dbh in the scenarios with twice the observed ingrowth (Fig. 7e, i, m, q). Since PICUS and FORCLIM estimate tree height based on tree dbh, tree height in the initialized stand varied from the observed data. These variations were minimal and considered
negligible for the comparison between observed and simulated forest development (data not shown).

The simulated forest after 8 years of simulation was compared with the stand data from observation year 2001 (Fig. 6b for the basal area and Fig. 7b, d, f, h, j, l, n, p, r for the dbh distribution). While the observed basal area increased from 1993 to 2001 by approx. 5% (Fig. 8), the observed total number of trees decreased by approx. 2% (Fig. 9). In the first 8 years of the simulation scenarios with observed ingrowth (i.e., scenarios 1 and 3), the increase in the observed basal area was reproduced only in the PICUS simulation for scenario 3 without stress-related mortality (Fig. 8). The total number of trees in PICUS scenario 3, however, decreased more strongly than in the measured stand (Fig. 9). In FORCLIM scenario 3 without stress-related mortality, basal area decreased minimally (<5%) (Fig. 8) but the total number of trees was closer to the observed data than in the PICUS simulation for scenario 3 (Fig. 9). In scenario 1 with the observed ingrowth and stress-related mortality, both models simulated a stronger decline in the total basal area and in the total number of trees than in scenario 3 without stress-related mortality (Figs. 8 and 9).

The basal area simulated was not sensitive to doubling the observed ingrowth in simulations with FORCLIM (i.e, an average deviance of 1% over 10 samples after initialization) and little sensitive in simulations with PICUS (i.e, an average deviance of 9% over 10 samples after initialization; Fig. 8 scenarios 1 vs. 2 and 3 vs. 4). This was due to the fact that small trees, i.e., those in the ingrowth contributed only very little to basal area. While observed and simulated tree numbers differed at the start of
Figure 7. Diameter distribution for observed data in 1993 and 2001 and for the initialized stand and the simulated stand after 8 years in PICUS and FORCLIM for 4 scenarios. The dbh classes were as follows: 1: <10 cm dbh, 2: 10-14, 3: 14-18, 4: 18-22, 5: 22-26, 6: 26-30, 7: 30-34, 8: 34-38, 9: 38-42, 10: 42-46, 11: >50.

the simulation by the number of trees in the ingrowth, tree numbers in scenario 2 (stress-related mortality and doubled ingrowth) dropped soon to levels similar to
Part 2

scenario 1 (stress-related mortality and observed ingrowth; Fig. 9). This was the case particularly for FORCLIM scenario 2 where tree numbers dropped sharply and after 10 simulation years were already close to tree numbers in scenario 1 (Fig. 9). In PICUS scenario 2, tree numbers did not decline as sharply as in FORCLIM, but with increasing simulation length they approached the numbers from scenario 1 (Fig. 9). Therefore, stress related mortality was higher in FORCLIM than in PICUS (Fig. 8 and 9).

![Figure 8. Total basal area for the observed data from 1993 and 2001 and for 50-year simulations with PICUS and FORCLIM for four scenarios.](image)

![Figure 9. Total number of trees for the observed data from 1993 and 2001 and for 50-year simulations with PICUS and FORCLIM for four scenarios.](image)
In scenario 4 (no stress-related mortality and doubled ingrowth), total tree numbers remained high since trees died only of intrinsic causes, i.e., age-related mortality. Age-related mortality was higher in PICUS than in FORCLIM and the total number of trees in the FORCLIM simulation was consequently higher than in PICUS (Fig. 9).

3.3. Implications for the further model evaluation process

The results of the simulations for Oberhünigen confirmed that the overestimation of stress-related tree mortality is the main cause for the decline in tree numbers with increasing dbh of juvenile trees found in Didion et al. (2009) for FORCLIM v2.9.3 and by Wehrli et al. 2005 for FORCLIM v2.9.1.

In FORCLIM v2.9.3, the cause for the overestimated stress-related mortality can be attributed to the overestimation of the leaf area in the simulated stand which leads to an underestimation of the available light in the patch. One consequence of low light conditions is a reduction in diameter growth and, consequently, an increase in the resulting stress factor $SGr$ (cf. Bugmann, 1994, eq. [3.32]) that is used to determine stress-related mortality (cf. section 2.1.1). In FORCLIM, leaf area is calculated based on the assumption of idealized trees, i.e., maximum crown extent, and because the model does not account for self-pruning, crown volume and thus leaf area is overestimated (cf. Wehrli et al., 2007). Thus in FORCLIM, the source for the deficiency to reproduce observed tree numbers realistically can be assigned with a high degree of confidence to the overestimated crown volume.

The results suggest that in PICUS v1.4 also an overly strong stress-related mortality is responsible for the faster than observed decline in tree numbers. In PICUS v1.4, particularly the simulation of the light regime is more complex (i.e., including a 3-dimensional tree crown) than in FORCLIM v2.9.3, and further analyses would be required to identify the underlying causes for the underestimation of tree numbers. Due to the higher model complexity in PICUS v1.4, more factors may play a role than is the case in FORCLIM v2.9.3.

To achieve the goal of my dissertation project to develop a modeling approach that is suitable to evaluate the impact of ungulate browsing on medium- and long-term forest development I, therefore, decided to use FORCLIM v2.9.3 in further experiments. However, since the current implementation of FORCLIM v2.9.3 is not able to reproduce observed tree number patterns, modifications of the simulation of the light regime based on idealized trees with full crowns are required (cf. Wehrli et al., 2007). The deficiencies of PICUS have been addressed in research by its developers.
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References


Improving the representation of the simulated light regime in FORCLIM v2.9.3

Gaining local accuracy while not losing generality – Extending the range of gap model applications

published as:
Abstract

For the study of long-term processes in forests, gap models generally sacrifice accuracy (i.e., simulating system behavior in a quantitatively accurate manner) for generality (i.e., representing a broad range of systems’ behaviors with the same model). We selected the gap model FORCLIM to evaluate whether the local accuracy of forest succession models can be increased based on a parsimonious modeling approach that avoids the additional complexity of a 3-D crown model, thus keeping parameter requirements low.

We improved the representation of tree crowns by introducing feedbacks between a) light availability and leaf area per tree, and b) leaf area per tree and diameter growth rate to account for the self-pruning in real stands. The local accuracy of the new model, FORCLIM v2.9.5, was significantly improved in simulations at three long-term forest research sites in the Swiss Alps, while its generality was maintained as shown in simulations of potential natural vegetation along a broad environmental gradient in Central Europe.

We conclude that the predictive ability of a model does not depend on its complexity, but on the reproduction of patterns. Most importantly, model complexity should be consistent with the objectives of the study and the level of system understanding.

Keywords: patch model; FORCLIM; validation; forest succession model; management support tool; self-pruning; diameter growth
1. Introduction

Simulation models are commonly used to improve our understanding of the processes and patterns that drive forest dynamics (e.g., Shugart 1998; Didion et al. 2007; Wehrli et al. 2007). Forest gap models have often been applied to study long-term processes in near-natural forests at the stand scale (Shugart 1984). This scale of application is particularly relevant for guiding management decisions in an era of rapidly and strongly changing environmental conditions (Bugmann et al. 2001). However, many forest gap models have been found to have relatively low local accuracy (Badeck et al. 2001).

Levins (1966) argued that models of ecological processes always represent an optimization between the qualities of generality, realism, and “precision” (note that we prefer the term accuracy, cf. Botkin 1993), which is dictated by the scientific question at hand. Although there has been considerable debate about the appropriateness of Levins’ triangle (Odenbaugh 2006), its fundamental message is applicable: a model is a deliberate simplification of a real system, and as such it must sacrifice certain details of the system under study. Models thus face a fundamental trade-off between realism (simulating system behavior based on a qualitatively realistic model structure), accuracy (simulating system behavior in a quantitatively accurate manner), and generality (representing a broad range of systems’ behaviors with the same model; after Costanza 1996). In this sense, most forest gap models are probably realistic in their structure (Bugmann et al. 2001) but limited in either their generality (i.e., representing forests along broad environmental gradients) or their accuracy (i.e., representing site-specific structural features such as diameter distributions).

Recognizing the limitation of gap models to accurately reproduce measured data, various approaches have been pursued, typically involving more detailed formulation of certain parts of the model (e.g., Martin 1992; Friend et al. 1997; Lexer and Höninger 2001; Smith et al. 2001; Wullschleger et al. 2003; Lasch et al. 2005), often leading to highly complex models that are difficult to parameterize, time-demanding to run, and often cumbersome to analyze in terms of the causes of simulated behavior. In this paper, we explore whether the local accuracy of gap models can be improved by simple, parsimonious changes of the model structure that maintain the general applicability of the model. Parsimony, i.e., the preference for the least complex explanation for an observation using the minimal amount of parameters (see, for example, Astrup et al. 2008 and references therein), plays an important role regarding the accuracy of a model but also our ability to understand model forecasts (cf. Astrup et al. 2008; Kimmins 2008; Kimmins et al. 2008).
As a case study, we used the FORCLIM model, which was developed with the aim of a wide range of applicability without requiring any parameter tuning, i.e., modification of the model and parameters for site-specific applications except local climate data. The generality of the model was established in studies for a wide range of forests (e.g., Bugmann and Cramer 1998; Bugmann and Solomon 2000; Shao et al. 2001; Busing et al. 2007). In simulations for various forest types of the Swiss Alps, FORCLIM v2.9.3 showed a good degree of generality, whereas it lacked in accuracy to reproduce measured tree numbers in the diameter classes <12 cm from the Swiss National Forest Inventory (Didion et al. 2009). A major reason for this underestimation was the highly simplified representation of tree crowns as discs at the top of the stem (cf. Bugmann 2001) and the assumption of a static relationship between diameter at breast height and leaf area per tree (cf. Wehrli et al. 2007).

Several approaches to represent the light regime have been implemented in gap models to improve the original, simplifying assumption of disc-shaped tree crowns introduced by Botkin et al. (1972), as reviewed by Bugmann (2001). The increased accuracy of more complex 2-D (e.g., Leemans 1991) and 3-D (e.g., Pacala and Canham 1993) models of tree crowns comes, however, at the expense of model generality because of the considerably increased model complexity and parameter requirements (Bugmann 2001).

The challenge we are addressing in this study is twofold. First, can we improve the local accuracy of the gap model FORCLIM by including tree crown dynamics without requiring a full 2-D or 3-D crown model? Second, can we maintain the model’s generality of representing forest composition and biomass along a broad gradient of climatic and soil conditions ranging from the cold to the dry treeline in central Europe without requiring model and parameter modifications except for site-specific data for temperature and precipitation to represent local climate? A gap model with a high degree of generality and local accuracy would present a widely applicable and reliable research and decision support tool for investigating, for example, climate change effects on forests and the ecosystem services they provide.

2. Methods

2.1. Model description

The FORCLIM model was developed for simulations over a wide range of environmental conditions without the necessity of any parameter tuning. To this end, the model is based on a minimum number of ecological assumptions to reduce model parameter requirements (Bugmann 1996).
Following the standard approach of gap models (e.g., Botkin 1977), FORCLIM simulates the establishment, growth, and mortality of trees on multiple forest patches to derive regional-scale stand dynamics (Bugmann 1996). Trees are established as saplings with a diameter at breast height (dbh) of 1.27 cm as a function of species-specific responses to winter temperature, light availability, growing degree-days and a simplified formulation of browsing pressure (Bugmann 1994). Similarly to tree establishment, growth is regulated by growing degree-days and light availability, and additionally by soil moisture and nitrogen status. Most of these factors depend on the abiotic environment, which is represented by the mean monthly temperatures and the precipitation sums, as well as soil water holding capacity and nitrogen availability (Risch et al. 2005). Trees grow as a function of species-specific constraints such as maximum growth rate or maximum tree height. Mortality has a random and a growth-related component, the latter being an integral proxy for stress conditions (tree vigor; Bugmann 1996). A more detailed description of the model and its development over time can be found in Bugmann (1996, v2.4), Bugmann and Solomon (2000, v2.9.1), Risch et al. (2005, v2.9.3) and Wehrli et al. (2007, v2.9.4).

2.2. A simple model of light effects on tree morphology and growth

The modifications to achieve the intended improvements of the FORCLIM model required several steps as detailed below.

2.2.1. Implementing a dynamic crown structure

Based on the observed self-pruning of trees, Wehrli et al. (2007) argued that the development of leaf area and thus of tree crowns follows a dynamic process that is regulated by light conditions in the stand (Mäkinen 1999). This mechanism has been taken into account in other gap models by modeling crown length explicitly (e.g., Leemans 1991). Rather than introducing the complexity of an explicit crown model, Wehrli et al. (2007) proposed that the self-pruning mechanism can be approximated simply by modifying the original static relationship (Bugmann 1994, eq. [3.21]) between foliage fresh weight ($g_{FolW}$ [kg]) and diameter at breast height ($dbh$ [cm]). Using the original equation

$$g_{FolW} = kC_1 \cdot kA_1 \cdot dbh^{kA_2}$$

[1]

where $kA_1$, $kA_2$, and $kC_1$ were allometric parameters, Wehrli et al. (2007) modified the dbh-leaf area relationship of an individual tree by turning the parameter $kA_1$ of eq. [1] into an auxiliary variable, $gA_1$ that can be interpreted as an indirect linear measure for crown length:
\[ gA_i = kA_{i,max} - (kA_{i,max} - kA_{i,min}) \cdot gLAI_{mod} \]  \[2\]

Here \( kA_{i,max} \) and \( kA_{i,min} \) are the maximum and minimum envelope of the relationship between foliage fresh weight and dbh, respectively, derived from readily available field data (cf. Wehrli et al. 2007). The leaf area index (LAI) factor \( gLAI'_{mod} \) (\( gkLAI \) in Wehrli et al. 2007, eq. [2]) ranges from 0 (no canopy shading) to 1 (full canopy shading), and was calculated by Wehrli et al. (2007, eq. [3]) as follows:

\[ gLAI'_{mod} = \text{MIN} \left( \frac{gLAI_0}{kLAI_{max}}, 1 \right) \]  \[3\]

where \( gLAI_0 \) is cumulative LAI down to the forest floor (height = 0) as calculated by FORCLIM, and \( kLAI_{max} \) is the maximum value of double-sided LAI in a patch resulting from the light compensation point (cf. Bugmann 1994, eq. [3.22] and [3.23]) of the most shade-tolerant species (i.e., \( kLAI_{max} = 11.98 \), based on data for Abies alba Mill. and Fagus sylvatica L.).

As the approach by Wehrli et al. (2007) contained weaknesses, we modified it in two ways: First, to account for the fact that dominant trees experience less shading than smaller trees in the lower canopy (Leemans 1991), we implemented the change in tree leaf area based on the LAI experienced at the top of that tree \( (gLAI_h) \) rather than the LAI at the forest floor \( (gLAI_0) \). Second, because self-pruning increases with stand density and crown width is inversely related to the square root of stand density (Jack and Long 1991), we applied the square to the ratio of \( gLAI_h \) and \( kLAI_{max} \) to obtain the final LAI factor:

\[ gLAI_{mod} = \text{MIN} \left( \left[ \frac{gLAI_h}{kLAI_{max}} \right]^2, 1 \right) \]  \[4\]

Due to the dynamic leaf area-dbh relationship (eq. [2] and [4]), the same stand has a lower LAI than when using a static leaf area-dbh relationship (as in former FORCLIM versions) for otherwise equal parameter values. Since more light is now penetrating the canopy, more trees can establish and growth rates of the remaining trees will increase up to the point where diameter growth approaches its maximum when foliage approaches its minimum, which is clearly not realistic. Indeed, we found that this model modification alone produced ecologically implausible basal area estimates in long-term simulations in the Swiss Alps (e.g., after 250 years: 128 m²/ha (measured: 74 m²/ha) at the Stotzigwald site used by Wehrli et al. (2007) and 107 m²/ha (measured: 35-45 m²/ha) in subalpine Picea abies Karst forests). This motivated a further important improvement in the model, as described below.
2.2.2. **Crown feedback to tree growth**

The strong overestimation of stand basal area is attributable to a missing explicit feedback between crown length to tree growth. In reality, a decrease in the leaf area (at a given diameter and height) of a tree results in a lower growth rate (Mitscherlich and von Gadow 1968); this was not taken into account in the approach by Wehrli et al. (2007). Therefore, we implemented a feedback between the amount of leaf area per tree and its diameter growth based on empirical data from pruning experiments in North America and Europe (Mitscherlich and von Gadow 1968). These experimental data showed a clear relationship between remaining crown length (i.e., leaf area reduction) and diameter growth (Fig. 1), suggesting that a certain degree of crown removal does not usually hamper tree growth (plateau at the top left in Fig. 1) and may even be conducive to growth, i.e., when branches with negative net assimilation rates are shed (cf. secondary y-axis in Fig. 1). With increasing degree of crown removal, tree growth decreases more or less linearly (Fig. 1), although the large amount of scatter in the data precludes any firm statement about the exact form of the relationship. However, other studies reported similar results (e.g., Spiecker 1986; Spathelf 2003). Spiecker (1986) found a nearly linear relationship between crown reduction and diameter increment for *P. abies* and *A. alba* in selection forests of the Black Forest in Germany.

Forest gap models including FORCLIM simulate optimal tree growth, which is then modified based on environmental conditions such as temperature and the availability of light, nutrients and moisture (cf. Section 2.1). To be consistent with this approach, we took the maximum observed diameter increment in the Mitscherlich and von Gadow data as representing optimal growth and assumed that diameter growth would come to a halt when the entire tree crown is removed (rescaled primary y-axis in Fig. 1). Because in the data maximum diameter increment was observed at 75% remaining crown length (Fig. 1), we assumed no effect of changes in tree crown losses up to this value, i.e., we capped the growth regulation at 1. For remaining crown lengths of less than 75%, we used the linear relationship obtained from the empirical data (cf. line in Fig. 1). The resulting “crown length growth factor” (*gCLGF’*) thus ranges from 0 to 1:

\[
gCLGF' = \text{MIN}(a \cdot \frac{gA_1}{kA_{1,max}}, 1)
\]

where \( a = \frac{4}{3} \), \( kA_{1,max} \) is the upper envelope of the relationship between foliage fresh weight and dbh, and \( gA_1 \) is the current value of the auxiliary variable to calculate this relationship (cf. eq. [2]). *gCLGF’* is used to modify crown length in the model based on the proportional relationship to foliage weight (cf. eq. [2]).
Figure 1. Derivation of the growth regulation based on pruning experiments by Mitscherlich and von Gadow (1968). Represented are data points from all experiments, the observed relationship between remaining crown length and diameter increment compared to control trees, and the obtained growth regulation (solid line) with a slope factor of \(\frac{4}{3}\) and a maximum of 1. Note: The x-axis represents the decrease in crown length relative to control conditions, i.e., a reduction in the value of \(gA_i\) (cf. eq. [5]). The primary y-axis is rescaled to represent 100% diameter increment as the optimal growth observed for the maximum diameter increment in the data.

Neither the data used by Wehrli et al. (2007) for calibrating the crown regulation nor those in Mitscherlich and von Gadow (1968), which we used for the growth regulation, included information on the light environment in the observed stands. However, it is plausible to assume that for the same change in crown length a shade-tolerant tree experiences a different growth regulation than a shade-intolerant tree (Spathelf 2003). All species in the review by Mitscherlich and von Gadow (1968) were of intermediate shade-tolerance; thus we adjusted the growth regulation using the species’ shade-tolerances as represented by the species-specific light compensation points \(k_{LCP}\) to obtain the final crown length growth factor:

\[
g_{CLGF} = \text{MIN} \left( a \cdot \frac{gA_i}{kA_{i,\text{max}}} \cdot \frac{k_{LCP}}{k_{LCP_{\text{mean}}}} , 1 \right) \tag{6}\]
Here $kLCP_{\text{mean}}$ is the mean light compensation point of all 30 species parameterized for European conditions (all parameter values as in Bugmann, 1994 except for $kA_{1,\text{max}}$ and $kA_{1,\text{min}}$ that were taken from Wehrli et al., 2007). The crown regulation is thus not as strong for shade-tolerant species compared to shade-intolerant species.

The crown length growth factor was used as a multiplier to modify the otherwise unmodified calculation of diameter growth in previous model versions (cf. Risch et al. 2005):

$$\frac{dD}{dt} = gD \cdot \left( \frac{1 - \frac{H}{H_{\text{max}}}}{2H_{\text{max}} - be^{cD}(cD + 2)} \right) \cdot f(e) \cdot gCLGF$$

where $g$ is maximum growth rate (cm/year), $D$ is tree diameter at breast height (i.e., at 137 cm), $H$ is tree height (cm), $H_{\text{max}}$ is maximum tree height (cm), $b$ is $H_{\text{max}} - 137$ cm, $c$ is $-s/b$ where $s$ is a parameter denoting the initial height growth relative to diameter growth (Risch et al. 2005), and $f(e)$ is a function to reduce maximum diameter growth based on environmental conditions (cf. Section 2.1).

### 2.2.3. Drought establishment filter

As the implemented changes resulted in shorter tree crowns, light availability for tree establishment increased, particularly so at sites with naturally open stands such as towards cold or dry treelines. Towards the cold treeline, it is ultimately the minimum winter temperature and the sum of growing degree-days that determine whether tree establishment is possible in the model. However, near dry treeline there was no mechanism other than available light to limit tree establishment in FORCLIM. Thus, we introduced a multiplicative, binary drought establishment filter as commonly used in other, similar models (Shugart 2002). We applied the same species’ drought tolerances as those used for tree growth in previous FORCLIM versions (Bugmann 1996).

### 2.3. Simulation experiments

#### 2.3.1. Evaluating local model accuracy using long-term forest research plots

Data from long-term forest research plots were obtained for three locations in the Swiss Alps (Zingg et al. 1999). The stands were inventoried at 5 to 10 year intervals starting around 1920 (Table 1). In each inventory, the species and dbh of all trees >8 cm dbh were recorded. All three stands were managed as uneven-aged selection (or “plenter”) forests (Zingg et al. 1999). The objective in a plenter (selection) forest is to maintain forest structure over time by removing mainly dominating individuals and thereby enhancing regeneration (Schütz 2006). At small spatial scale management interventions in plenter forests resemble gap-phase dynamics, which are the
underlying principle of forest gap models. It is thus plausible to assume that observed and simulated stand structure should be broadly comparable over the selected periods of 41 to 54 years, as long as no large-scale disturbances such as windthrow occur, a condition that was fulfilled in the three stands.

The three stands are located along an elevation gradient from the subalpine site St. Moritz (eastern central Alps; 1810 m a.s.l.) across the high montane site Rougemont (western Pre-Alps; 1294 m a.s.l.) to the montane site Niederhünigen (central Pre-Alps; 931 m a.s.l.; cf Table 1), which allowed us to examine the local accuracy of model results compared to observations under diverse environmental conditions.

Table 1. Long-term research sites used in the present study, their location, area, altitude, main species, and species association (cf. Zingg et al. 1999) and simulation details on estimated bucket size (BS) or water holding capacity, available nitrogen (N), nearest climate station with altitude and approximate distance to site, simulation period, and number of observations (n) available for the comparison.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area (ha)</th>
<th>Alt. (m a.s.l.)</th>
<th>Main species</th>
<th>Species association</th>
<th>BS (cm)</th>
<th>N ( \left(\frac{\text{kg}}{\text{ha} \cdot \text{yr}}\right))</th>
<th>Climate station (Alt. (m a.s.l.), distance (km))</th>
<th>Simulation period (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. Moritz (ID1033)</td>
<td>1.0</td>
<td>1810</td>
<td>P. abies, P. cembra, L. decidua</td>
<td>Larici-Pinetum cembrae</td>
<td>10</td>
<td>60</td>
<td>St. Moritz (1825,1.3)</td>
<td>1932 – 1979 (6)</td>
</tr>
<tr>
<td>(46.5, 9.9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rougemont (ID1041)</td>
<td>1.5</td>
<td>1294</td>
<td>P. abies, A. alba (F. sylvatica)</td>
<td>Aceri-Fagetum</td>
<td>15</td>
<td>80</td>
<td>Saanen (1008, 3.4)</td>
<td>1928 – 1969 (9)</td>
</tr>
<tr>
<td>(46.5, 7.2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Niederhünigen (ID1015002)</td>
<td>1.2</td>
<td>931</td>
<td>P. abies, A. alba (F. sylvatica)</td>
<td>Abieti-Fagetum typicum, Bazzanio-Abietetum</td>
<td>15</td>
<td>80</td>
<td>Heiligen-schwendi (1125, 12.5)</td>
<td>1923 – 1977 (11)</td>
</tr>
<tr>
<td>(46.9, 7.7,)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

Tree species and dbh data from the first of the consecutive observations at each site were used to initialize the model’s state variables based on the method described in Wehrli et al. (2005). The site area was divided by the default patch size of 800 m² used in FORCLIM and, if necessary, rounded up to the next integer, resulting in 13, 19 and 16 patches for St. Moritz, Rougemont and Niederhünigen, respectively. If rounding up was required, we ensured to obtain a similar density as found in the stand by randomly
selecting additional trees. The trees were allocated randomly to the patches. In order to obtain a minimum of 50 patches for each site (cf. Wehrli et al. 2005), we copied the information of the initial sets of 13, 19 and 16 patches, respectively, 4, 3, and 4 times.

In the model, new trees establish with a dbh of 1.27 cm and, depending on environmental conditions, may require years to decades before reaching the callipering limit of 8 cm dbh. In the observed stands, an unknown number of trees <8 cm dbh was present (but not measured; A. Zingg, pers. obs.) in the first inventory that were potentially able to grow to more than 8 cm dbh much faster than the trees that established in the model during the simulation and needed to grow from 1.27 cm to 8 cm. Therefore, our initialization with data for trees >8 cm dbh caused an artificial lag between observed and simulated future ingrowth, thus distorting the comparison of the observed and simulated tree numbers in the low diameter classes.

The observed stands were simulated for 250 years under current climatic conditions, starting from the first inventory. The goal of these long-term simulations was to make sure that no artifacts were simulated beyond the measured period, such as crashes of the stand or unrealistically high basal area values. We assumed that only species present in the stand at the initial inventory can establish, based on the fact that during the time of the observation no other species appeared. The climate data, i.e., long-term monthly means and standard deviations for temperature and precipitation for each site were derived from climate stations nearby (Table 1). Values for bucket size and nitrogen availability were estimated based on site descriptions (Table 1). All other parameters were set to their default values. The same simulations were also performed with FORCLIM v2.9.1 (Bugmann and Solomon 2000) to evaluate to what extent the local accuracy of the new model version had improved.

We used a percentage similarity coefficient (PS) to compare observed and simulated dbh distribution in 11 dbh classes for every observation year:

$$PS = 1 - \frac{\sum_{i=1}^{n} |x_i - y_i|}{\sum_{i=1}^{n} (x_i + y_i)}$$  \[8\]

where $x_i$ is the value for tree numbers in dbh class $i$ in the simulated data, $y_i$ is the value for tree numbers in dbh class $i$ in the observed data, and $0 \leq PS \leq 1$ (Bugmann 1997).
2.3.2. **Evaluating model generality using potential natural vegetation along an environmental gradient**

We selected 11 sites along a broad elevation and drought gradient in Europe (Table 2). All sites except Grande Dixence had been used in previous modeling studies (e.g., Lasch et al. 1999; Bugmann and Solomon 2000), allowing for a comprehensive evaluation of the generality of the new model version over a range of environmentally different sites. Although Potential Natural Vegetation (PNV) constitutes a model representation of vegetation communities in the absence of human influence (Ellenberg 1996), it is based on profound expert knowledge and thus provides a good indicator of model performance under a range of environmental conditions.

**Table 2. European PNV sites used in the present study, their location, altitude, long-term annual mean temperature (T), long-term annual precipitation sum (P), observation period of T and P, bucket size (BS) and available nitrogen (N) used in the models FORCLIM v2.9.1 and v2.9.5, and dominating tree species of the potential natural vegetation (PNV) according to Ellenberg and Klötzli (1972), Krausch (1992), and Ellenberg (1996). For the sites Bever and Sion, we assumed a south-facing slope.**

<table>
<thead>
<tr>
<th>Site (abbr.)</th>
<th>Lat. (°N)</th>
<th>Long. (°E)</th>
<th>Alt. (m a.s.l.)</th>
<th>T (°C)</th>
<th>P (mm)</th>
<th>Observation period (MM.YYYY)</th>
<th>BS (cm)</th>
<th>N (kg ha⁻¹ yr⁻¹)</th>
<th>PNV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bever (Bev)</td>
<td>46.6</td>
<td>9.9</td>
<td>1712</td>
<td>1.5</td>
<td>841</td>
<td>01.1901-12.1982</td>
<td>10</td>
<td>60</td>
<td>P. cembra, P. montana, L. decidua</td>
</tr>
<tr>
<td>Grande Dixence (G. Dix)</td>
<td>46.1</td>
<td>7.4</td>
<td>2166</td>
<td>1.2</td>
<td>1016</td>
<td>01.1965-12.1984</td>
<td>10</td>
<td>60</td>
<td>P. cembra, P. abies, L. decidua</td>
</tr>
<tr>
<td>Davos</td>
<td>46.8</td>
<td>9.8</td>
<td>1590</td>
<td>3.0</td>
<td>1007</td>
<td>01.1867-12.2003</td>
<td>10</td>
<td>60</td>
<td>P. abies, L. decidua</td>
</tr>
<tr>
<td>Adelboden (A’boden)</td>
<td>46.5</td>
<td>7.6</td>
<td>1325</td>
<td>5.5</td>
<td>1351</td>
<td>01.1959-12.2005</td>
<td>15</td>
<td>80</td>
<td>P. abies, F. sylvatica, A. alba</td>
</tr>
<tr>
<td>Huttwil (H’wil)</td>
<td>47.1</td>
<td>7.88</td>
<td>638</td>
<td>8.1</td>
<td>1290</td>
<td>01.1972-12.1995</td>
<td>20</td>
<td>100</td>
<td>P. abies, F. sylvatica, (A. alba)</td>
</tr>
<tr>
<td>Bern</td>
<td>46.9</td>
<td>7.4</td>
<td>570</td>
<td>8.4</td>
<td>1006</td>
<td>01.1864-12.2003</td>
<td>20</td>
<td>100</td>
<td>F. sylvatica, (P. abies)</td>
</tr>
<tr>
<td>Schaffhausen (S’hausen)</td>
<td>47.7</td>
<td>8.6</td>
<td>400</td>
<td>8.6</td>
<td>882</td>
<td>01.1880-12.2005</td>
<td>15</td>
<td>80</td>
<td>F. sylvatica, (Quercus spp.)</td>
</tr>
<tr>
<td>Basel</td>
<td>47.5</td>
<td>7.6</td>
<td>317</td>
<td>9.2</td>
<td>784</td>
<td>01.1864-12.2003</td>
<td>15</td>
<td>80</td>
<td>F. sylvatica, (Quercus spp.)</td>
</tr>
<tr>
<td>Schwerin</td>
<td>53.6</td>
<td>11.4</td>
<td>45</td>
<td>8.2</td>
<td>625</td>
<td>01.1890-12.2005</td>
<td>24</td>
<td>60</td>
<td>F. sylvatica, Quercus spp.</td>
</tr>
<tr>
<td>Cottbus</td>
<td>51.8</td>
<td>14.3</td>
<td>76</td>
<td>8.8</td>
<td>573</td>
<td>01.1951-12.2003</td>
<td>24</td>
<td>60</td>
<td>Quercus spp., Tilia spp., C. betulus</td>
</tr>
<tr>
<td>Sion</td>
<td>46.2</td>
<td>8.6</td>
<td>542</td>
<td>9.7</td>
<td>597</td>
<td>01.1864-12.2003</td>
<td>15</td>
<td>60</td>
<td>P. sylvestris, Quercus spp.</td>
</tr>
</tbody>
</table>
From the climate database of the Swiss Meteorological Agency, we derived long-term means, standard deviations and cross-correlation coefficients of monthly mean temperatures and log-transformed (cf. Risch et al. 2005) precipitation sums for all sites. Since current climate data were not available for the site Cleuson (46.1°N, 7.4°E, 2100 m a.s.l.) that had been used by Bugmann and Solomon (2000), we replaced this site with the nearby, climatically very similar site Grande Dixence (46.1°N, 7.4°E, 2166 m a.s.l., Table 2).

All simulations were run from bare ground for 1500 years and 200 patches using these climatic data and with values of soil water holding capacity (i.e., bucket size) and available nitrogen as described in Table 2, again with all other parameters unchanged. Thirty species for central Europe were used in the simulations (Bugmann 1994) except for *Castanea sativa* L., which was not included in the simulations at Cottbus and Schwerin, as this species is probably absent in the drier parts of eastern Germany due to the vegetation history of the area (Bugmann and Cramer 1998).

Since the purpose of these simulations was to evaluate whether the model modifications to improve its local accuracy affected the model’s generality, we compared the performance of the new FORCLIM v2.9.5 with that of FORCLIM v2.9.1 (Bugmann and Solomon 2000) at the 11 sites using the following criteria and methods:

- Information on the expected dominant species in the PNV (cf. Table 2) was used to evaluate the simulated species composition at equilibrium by the two models based on the respective species’ shares of total biomass.

- Observed growing stock in the Swiss National Forest Inventory (NFI; EAFV and BFL, 1988, Table 29) was converted to aboveground biomass using scaling factors for wood density (0.55 for deciduous and 0.4 for coniferous species) and biomass expansion factors (1.49-1.70 for deciduous and 1.43-1.61 for coniferous species) developed for Swiss forests (Thürig and Schmid 2008) to calculate aboveground biomass. This we compared against the simulated biomass by the two models for the nine Swiss sites (i.e., not for Cottbus and Schwerin).

- Findings from studies with previous model versions showing that tree establishment was underestimated compared to observation (Risch et al. 2005; Didion et al. 2009) were used as rationale to assess the performance of the two model versions regarding the number of trees <12cm dbh.

By doing so, we used a pattern-oriented approach: in the absence of a single test data set that could be used to evaluate the model, we propose that the matching of several, partly quantitative and partly qualitative patterns still provides a strong test of an ecological model (cf. Grimm et al. 2005).
3. Results

3.1. Evaluating local model accuracy using long-term forest research plots

3.1.1. St. Moritz

From the start of the observations in 1932, this subalpine *Picea abies*–*Pinus cembra*–*Larix decidua* stand (~600 trees/ha; ~38 m²/ha basal area, Fig. 2a) experienced a slight decrease in basal area over the next three observations (~36 m²/ha after 24 years, Fig. 2a) due to a decline of mainly *P. cembra*. Until the last observation 23 years later, an increase in *P. abies* brought basal area to 41 m²/ha (Fig. 2a). This same trend was also evident from measured total tree numbers (Fig. 2d).

![Figure 2](image-url)
The new FORCLIM v2.9.5 simulated a stand that was closer to these observations than FORCLIM v2.9.1. (Fig. 2a, d, g and Table 3). Predicted basal area and total tree numbers during the observation period (Fig. 2a, d, g) and simulated long-term trends (Fig. 3 and Tables 4 and 5) were more accurate in the new model version. Percentage similarity (PS) between observed and simulated dbh distribution amounted to ca. 80% after 47 simulation years for version 2.9.5 compared to merely ca. 30% for version 2.9.1 (Fig. 2g). In the final observation year (1979), total tree numbers <36 cm dbh (class 5) simulated with FORCLIM v2.9.5 were lower than in the observed stand, which was mainly due to the underestimation of *P. abies* (Fig. 3); tree numbers of *P. cembra* and *L. decidua* were similar between simulation and observation, as were the tree numbers of all species >36 cm dbh (dbh classes >5). In FORCLIM v2.9.1, *P. cembra* disappeared, no trees occurred <36 cm dbh (dbh classes ≤ 5) and the distribution of trees >36 cm was strongly skewed towards very large trees (Fig. 3).

### Table 3. Percentage deviance calculated as \([(\text{simulated } - \text{observed basal area})/\text{observed basal area}]\) for FORCLIM v2.9.5 and FORCLIM v2.9.1 for three measured stands. Observation # refers to the chronological order of observations at a particular site, starting with the second observation, as the initial inventory was used to initialize the models, and hence percentage deviance was 0 (cf. Fig. 2 for the respective calendar years).

<table>
<thead>
<tr>
<th>Site</th>
<th>Observation #</th>
<th>St. Moritz v2.9.1</th>
<th>St. Moritz v2.9.5</th>
<th>Rougemont v2.9.1</th>
<th>Rougemont v2.9.5</th>
<th>Niederhünigen v2.9.1</th>
<th>Niederhünigen v2.9.5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>-16</td>
<td>1</td>
<td>-12</td>
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<td>3</td>
<td>-11</td>
<td>6</td>
<td>-8</td>
<td>-5</td>
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<td>0</td>
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<td>-2</td>
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<td>-13</td>
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<td>-3</td>
<td>-3</td>
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<td>10</td>
<td>-16</td>
<td>-4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### 3.1.2. Rougemont

In Rougemont, the initial stand in 1928 was dominated by *Abies alba* and *P. abies* with very few *Acer pseudoplatanus*, *Fagus sylvatica*, and *Sorbus aucuparia* individuals (~460 trees/ha; ~30 m²/ha basal area, Fig. 2b). Measured basal area increased initially by ca. 10% and then remained nearly constant before rising again slightly during the last two observations in 1963 and 1969 (Fig. 2b). This measured increase was supported by *A. alba* and *P. abies*, while for the other species no change was found.

Throughout the observation period, both model versions simulated a similar basal area increase (~30 to ~32 m²/ha, Fig. 2b) that was close to the observed data (Table 3), but total tree numbers differed (~460 to 363 trees/ha in v2.9.5 vs. 156 trees/ha in v2.9.1, Fig. 2e). This was reflected in the PS between observed and simulated dbh distribution.
(after 41 simulation years: ~75% in v2.9.5 vs. ~45% in v2.9.1, Fig. 2h). In the long-term projections, basal area remained similar in both model versions (Table 4). In FORCLIM v2.9.1, total tree numbers decreased in the long-term but recovered in FORCLIM v2.9.5 (Table 5). The final diameter distribution of the observed stand showed a steeper decline in the first half of the distribution (i.e., up to a dbh of 40 cm) and a longer tail than the one simulated with version 2.9.5 (Fig. 2). In version 2.9.1, total tree numbers increased with dbh and were clearly lower than observed numbers. In FORCLIM v2.9.5, the diameter distribution after 250 years showed a good regeneration with a decrease in tree numbers toward larger dbh classes (Fig. 3).

![Figure 3](image.png)

Figure 3. Observed (upper panels), and simulated (FORCLIM v2.9.1 central panels; FORCLIM v2.9.5 lower panels) species-specific tree numbers in 11 dbh classes in the final observation years for the long-term research sites St. Moritz (1979), Rougemont (1969), and Niederhünigen (1977). In the central and lower panels the lines indicate simulated total tree numbers per dbh class after 250 years. The 11 dbh classes as in Fig. 2.

### 3.1.3. Niederhünigen

In the first inventory in 1923, *A. alba* and, to a lesser extent, *P. abies* with few *F. sylvatica* dominated the stand at this montane site (~500 trees/ha; ~33 m²/ha basal area, Fig. 2c). The observed basal area fluctuated between 32 and 35 m²/ha for the most part.
of the observed period before rising by ca. 20% from 1969 to 1977 (Fig. 2c), mainly supported by *A. alba*.

The basal area and total tree numbers predicted by FORCLIM v2.9.5 closely followed the observed data over the 54-year observation period (Fig. 2c, f and Table 3). FORCLIM v2.9.1, however, increasingly underestimated basal area (Fig. 2c and Table 3) and particularly tree numbers (Fig. 2f). This trend continued in the long-term projection (Tables 4 and 5). Percentage similarity between observed and simulated dbh distribution was twice as high in version 2.9.5 (~75%) than in version 2.9.1 (~38%) in the final observation year (1977). With the exception of trees with dbh <20 cm (classes 1 to 3), total tree numbers declined similarly with increasing dbh in the observation and in the simulation by FORCLIM v2.9.5 (Fig. 3), whereas the dbh distribution simulated by version 2.9.1 was again skewed towards large trees (Fig. 3). In FORCLIM v2.9.5, after 250 years regeneration had filled the lower diameter classes, and tree numbers decreased with increasing dbh class (Fig. 3).

**Table 4. Long-term basal area (m²/ha) projections by FORCLIM v2.9.1 and FORCLIM v2.9.5 for three measured stands beyond the observation period.**

<table>
<thead>
<tr>
<th>Site</th>
<th>St. Moritz</th>
<th>Rougemont</th>
<th>Niederhünigen</th>
</tr>
</thead>
<tbody>
<tr>
<td>year</td>
<td>v2.9.1</td>
<td>v2.9.5</td>
<td>v2.9.1</td>
</tr>
<tr>
<td>Final</td>
<td>34</td>
<td>40</td>
<td>33</td>
</tr>
<tr>
<td>observation</td>
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<td>75</td>
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<td>28</td>
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<td>32</td>
</tr>
<tr>
<td>250</td>
<td>30</td>
<td>36</td>
<td>32</td>
</tr>
</tbody>
</table>

**Table 5. Long-term tree number >8 cm dbh (trees/ha) projections by FORCLIM v2.9.1 and FORCLIM v2.9.5 for three measured stands beyond the observation period.**

<table>
<thead>
<tr>
<th>Site</th>
<th>St. Moritz</th>
<th>Rougemont</th>
<th>Niederhünigen</th>
</tr>
</thead>
<tbody>
<tr>
<td>year</td>
<td>v2.9.1</td>
<td>v2.9.5</td>
<td>v2.9.1</td>
</tr>
<tr>
<td>Final</td>
<td>174</td>
<td>411</td>
<td>156</td>
</tr>
<tr>
<td>observation</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>75</td>
<td>124</td>
<td>350</td>
<td>102</td>
</tr>
<tr>
<td>100</td>
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<td>150</td>
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<td>294</td>
<td>166</td>
</tr>
<tr>
<td>250</td>
<td>165</td>
<td>357</td>
<td>171</td>
</tr>
</tbody>
</table>

### 3.2. Evaluating model generality using potential natural vegetation along an environmental gradient

Bugmann and Cramer (1998) and Bugmann and Solomon (2000) discussed PNV at the 11 study sites in detail. Thus, we present only the changes between the new model version 2.9.5 and version 2.9.1. Considering the species composition (by biomass) at
equilibrium simulated by the two model versions relative to the expected PNV, the performance of FORCLIM v2.9.5 clearly improved over v2.9.1 (Table 6) at the sites

- Davos, with an almost pure *P. abies* forest with some *L. decidua* Mill. but no *A. alba* and *Populus nigra* L. (Fig. 4 and Table 2);

- Schwerin and Cottbus, where the transition from *F. sylvatica* to *Quercus robur* L. and *Tilia cordata* Mill. was simulated correctly and *A. alba* had disappeared in Cottbus (Fig. 4 and Table 2).

FORCLIM v2.9.5 did not perform as well as v2.9.1 at three sites in the center of the environmental gradient: In Bern, Schaffhausen and Basel, *Castanea sativa* became co-dominant with *F. sylvatica* in the new model version, although the latter species is expected to be dominant, because these areas are in the core of the distribution range of beech.

FORCLIM v2.9.5 performed better than v2.9.1 regarding the simulated total biomass as evaluated by the measured growing stock per region and elevation zone in the Swiss National Forest Inventory (EAFV and BFL 1988; Table 6). Corresponding data and scaling factors for the two German sites Schwerin and Cottbus were not available.

![Figure 4. Simulations along an environmental gradient in Europe (left = cold-moist, right = warm-dry): Simulated equilibrium species biomass for FORCLIM v2.9.1 (Bugmann and Solomon 2000; upper panel) and FORCLIM v2.9.5 (lower panel). Acer comprises Acer campestre and A. platanoides (see Methods). See Table 2 for site abbreviations.](image-url)
At all 11 sites, FORCLIM v2.9.5 simulated a higher number of trees than FORCLIM v2.9.1 with the single exception of trees with dbh 8 - <10 cm at the site Sion (Table 7). This presented an improvement over the poor regeneration simulated by version 2.9.1 (Table 5).

Table 6. Results for the comparison between FORCLIM v2.9.1 and FORCLIM v2.9.5 for simulated species composition, biomass and dbh distribution at equilibrium at 11 sites along an environmental gradient from the cold to the dry treeline where ‘+’ denotes that the representation of a particular criterion improved in v2.9.5 compared to v2.9.1, ‘=’ denotes no change, and ‘–’ denotes a decline in the performance. The detailed data underlying this comparison can be found in Appendix I.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species composition</th>
<th>Biomass</th>
<th>DBH distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bever (cold treeline)</td>
<td>=</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Grande Dixence</td>
<td>=</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Davos</td>
<td>+</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Adelboden</td>
<td>=</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Huttwil</td>
<td>=</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bern</td>
<td>–</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Schaffhausen</td>
<td>–</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Basel</td>
<td>–</td>
<td>=</td>
<td>+</td>
</tr>
<tr>
<td>Schwerin</td>
<td>+</td>
<td>na</td>
<td>+</td>
</tr>
<tr>
<td>Cottbus</td>
<td>+</td>
<td>na</td>
<td>+</td>
</tr>
<tr>
<td>Sion (dry treeline)</td>
<td>=</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 7. Percentage deviance between tree numbers per hectare simulated by FORCLIM v2.9.5 and FORCLIM v2.9.1 for trees <12 cm presented in intervals of 2 cm calculated as (trees/ha simulated with v2.9.5 - trees/ha simulated with v2.9.1)/ trees/ha simulated with v2.9.1.

<table>
<thead>
<tr>
<th>DBH class</th>
<th>2-&lt;4</th>
<th>4-&lt;6</th>
<th>6-&lt;8</th>
<th>8-&lt;10</th>
<th>10-&lt;12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bever</td>
<td>2.94</td>
<td>2.03</td>
<td>3.01</td>
<td>1.31</td>
<td>2.37</td>
</tr>
<tr>
<td>Grande Dixence</td>
<td>4.65</td>
<td>4.75</td>
<td>3.45</td>
<td>3.44</td>
<td>3.71</td>
</tr>
<tr>
<td>Davos</td>
<td>3.71</td>
<td>3.58</td>
<td>2.52</td>
<td>2.43</td>
<td>2.42</td>
</tr>
<tr>
<td>Adelboden</td>
<td>3.08</td>
<td>3.25</td>
<td>3.63</td>
<td>2.46</td>
<td>1.72</td>
</tr>
<tr>
<td>Huttwil</td>
<td>6.93</td>
<td>5.62</td>
<td>5.55</td>
<td>4.40</td>
<td>3.63</td>
</tr>
<tr>
<td>Bern</td>
<td>4.33</td>
<td>5.06</td>
<td>3.53</td>
<td>3.11</td>
<td>3.18</td>
</tr>
<tr>
<td>Schaffhausen</td>
<td>4.45</td>
<td>3.97</td>
<td>3.10</td>
<td>3.48</td>
<td>3.24</td>
</tr>
<tr>
<td>Basel</td>
<td>5.21</td>
<td>3.80</td>
<td>3.49</td>
<td>3.16</td>
<td>2.96</td>
</tr>
<tr>
<td>Schwerin</td>
<td>4.71</td>
<td>3.74</td>
<td>2.65</td>
<td>2.92</td>
<td>1.91</td>
</tr>
<tr>
<td>Cottbus</td>
<td>4.06</td>
<td>2.74</td>
<td>2.14</td>
<td>1.79</td>
<td>1.37</td>
</tr>
<tr>
<td>Sion</td>
<td>1.54</td>
<td>1.30</td>
<td>1.80</td>
<td>0.71</td>
<td>1.02</td>
</tr>
</tbody>
</table>

4. Discussion

4.1. Evaluating local model accuracy using long-term forest research plots

The simulations for the three forest research plots over several decades confirmed that the crown regulation feature in combination with the new growth regulation improved the local accuracy of the model compared to previous model versions. FORCLIM v2.9.5 was able to simulate stand development in a satisfactory manner and certainly much
more accurately than v2.9.1, as corroborated by the percentage deviance between simulated and observed basal area at the three sites (cf. Table 3).

The dynamics simulated by the new model version closely approximated the observed development of basal area and tree numbers in the long-term forest research stands as shown by the >75% percentage similarity (PS; Fig. 2). This was very encouraging since it is a measure for the agreement of tree numbers in 11 dbh classes, and especially considering that the underestimation of trees in the lower dbh classes is due to data limitations: the strong underestimation of simulated tree numbers in the first dbh class (8-12 cm, Fig. 3) can be explained by the lag of ingrowth in the model that is due to the absence of trees <8 cm dbh in the initialization data set. It is known that in all observations at Rougemont and Niederhünigen a well-developed understory existed with good regeneration of trees <8 cm (A. Zingg, pers. obs.). In the absence of quantitative data, this could not be included in our initialization. Thus, there was a delay of several decades before regeneration processes in the model filled this diameter range, which resulted in the underestimation. Once the lag of trees <8 cm is compensated for by new regeneration, PS should increase, as seen over the final observations in Niederhünigen, which features the longest time series (cf. Fig. 2).

The tree numbers simulated by FORCLIM v2.9.5 beyond the observation period fluctuated around the value of the final observation at a level of 2-4 times that of FORCLIM v2.9.1 (cf. Table 5), which indicates that tree regeneration in v2.9.5 was improved indeed. The diameter distributions in v2.9.5 after 250 years at the three sites corroborated this, but the lack of long-term data on growth of seedlings and saplings below 8 cm dbh precludes a quantitative comparison.

The dbh distributions at Rougemont and Niederhünigen after 250 simulation years (i.e., additional 209 and 196 years) resembled closely the structure in the final observation (cf. Fig. 3), which indicated that regeneration recovered after the initial lag that was due to data limitations. The poorer long-term predictions of the model at St. Moritz were likely caused by an overestimated mortality due to harsher environmental conditions, which limit tree growth in response to shorter growing seasons.

**4.2. Evaluating model generality using potential natural vegetation along an environmental gradient**

The comparison of model performance at 11 sites along a gradient from the cold to the dry treeline showed that the generality of the new model version FORCLIM v2.9.5 was not affected by the modifications to improve its local accuracy (cf. Table 6). Indeed, the model was better at discerning the effects of competition for light between species. As more light was available due to the improved representation of the light regime, the remaining factors, particularly minimum winter temperatures, degree-day-sums and
soil moisture, became more important, as did the differences in the associated species parameters. Hence, the model was more sensitive to environmental factors and, consequently, FORCLIM v2.9.5 represented better the species transitions that occur along the simulated environmental gradient. For example, at the transition from subalpine to montane conditions in Davos, the fast-growing *P. abies* outcompeted the more shade-tolerant, slow-growing *A. alba* in FORCLIM v2.9.5 as a consequence of higher light availability in the stand.

At low elevations of the northern Swiss Plateau and the Jura (Schaffhausen and Basel), *A. alba* reaches the northern fringe of its natural occurrence (Ellenberg 1996). Indeed, in FORCLIM v2.9.5 *A. alba* recedes, allowing fast-growing deciduous species to outcompete *A. alba*, and also leading to a higher importance of the other environmental constraints on tree population dynamics. With the decline of *A. alba* at lower elevation sites, *F. sylvatica* is expected to become the dominant species in the PNV together with *P. abies* in Huttwil and Bern, and with *Quercus* spp. in Basel and Schaffhausen (Ellenberg 1996; cf. Table 2).

In FORCLIM v2.9.5 the abundance of *F. sylvatica* was increasingly underestimated with warmer conditions. We found that the competitiveness of *F. sylvatica* relative to the species replacing it in model version 2.9.5 (i.e., particularly *C. sativa* but also *A. pseudoplatanus*, Fig. 4) was restricted by the comparatively low potential maximum age of *F. sylvatica* in the model (430 years; *A. pseudoplatanus* 550 years; *C. sativa* 1510 years; Bugmann, 1994), whereas other sources such as Wagenführ (1989) indicate a maximum age of 800 years for *F. sylvatica*. Sensitivity tests showed that at sites on the Swiss Plateau the simulated abundance of these three species is linked closely to their maximum age (Bugmann 1994), which is tied to mortality probability. As a consequence of the asymptotic height-diameter function implemented in FORCLIM v2.9.3 (Risch et al. 2005), which allows trees to grow in dbh much longer as they approach maximum height, long-lived species are likely to achieve much higher basal area values and thus higher dominance than short-lived species. Hence, a re-estimation of some species-specific parameters such as maximum age based on improved data sources would be desirable. It must be noted, though, that the presence of *C. sativa* at sites such as Schaffhausen and Basel is not unrealistic, although *F. sylvatica* is expected to be a stronger dominant (EAFV and BFL, 1988).

Despite the drawbacks of using PNV for model evaluation alone, the use of this concept is still required due to the lack of appropriate large-scale data covering broad environmental gradients (cf. Didion et al. 2009). As used in this study supported by appropriate quantitative data, i.e., observed growing stock to compare simulated biomass (see Appendix I), and augmented by local site data, PNV provides a useful
means to evaluate model performance at a range of environmentally different sites (cf. Didion et al. 2009).

### 4.3. Recommendations regarding the modeling approach

In order to correct the deficiencies of FORCLIM v2.9.4 regarding the representation of the light regime across a patch, our rationale was to maintain the structure of the model simple to minimize parameter requirements for ease and generality of model applications. We strove to identify the most parsimonious but ecologically sound approximation of the missing self-pruning and the feedback on tree growth, which had caused the overestimation of stand LAI and basal area. It may have appeared more obvious and more “realistic” to adopt a more complex approach such as an explicit 2D- or even 3D-representation of tree crowns. Instead, we explored simpler alternatives that were still based on empirical data while at the same time being ecologically plausible. We are confident that our line of reasoning is appropriate and will have long-term benefits by keeping the model still simple: we believe that the way to go also in future model development is to reduce the complexity of the process in question to a level that is consistent with a) the purpose of the model and thus the research question at hand, and b) ecological data as well as theoretical expectations.

### 5. Conclusion

In an attempt to gain model accuracy without sacrificing generality, we chose a pattern-oriented approach (Grimm et al. 2005) to improve the representation of tree morphology (crown geometry) and thus the light regime in FORCLIM v2.9.5. Matching multiple patterns (here, forest growth data and potential natural vegetation) is strong evidence that the model captures reality in a trustworthy manner (cf. Grimm et al. 2005). Moreover, these patterns were not used to structure the components or estimate the parameters of the model. The implementation of the self-pruning process of trees and the feedback to tree growth presented a fundamental modification to the simulation of light competition. This was achieved without introducing a considerably higher model complexity and parameter requirements of approaches that explicitly model a 2-D or even 3-D crown. We thus adhered to the principle of parsimony against the trend of increasing complexity built into simulation models without a concurrent increase in our system understanding (Harte 2002). Model parsimony ensures that simulated effects can be attributed to the responsible factors (Kimmins et al. 2008).

The higher structural realism of the model led to greater accuracy, as was evident from the simulations for three forest research plots. Here, FORCLIM v2.9.5 reproduced
measured basal area and tree numbers closely. The good performance of FORCLIM v2.9.5 in simulations of forest research plots across many decades suggests that the model is a valuable alternative to more data-intensive and less general growth and yield models for projecting stand development.

A first advantage of FORCLIM over growth and yield models is that it does not require any site-specific parameter tuning and can be used with a minimum amount of data on temperature, precipitation and tree species diameters. This is particularly promising for studies where the site-specific data required for growth yield models (see, for example, Pretzsch et al. 2002) cannot easily be acquired. A second advantage of FORCLIM and other forest gap models is that they can be used to simulate multi-species stands including species that are of limited economic concern but contribute to ecosystem services such as biodiversity. In contrast, growth and yield models tend to focus on a few commercially important species (Liu and Ashton 1995), a limitation that is often ignored in studies advocating this type of model (e.g., Yaussy 2000).

Acknowledgements

We are grateful for many fruitful discussions with members of the Forest Ecology Group at the Institute of Terrestrial Ecosystems, ETH Zürich. The programming support by Dr. K. Jasper (now with the Swiss Federal Office for the Environment) is gratefully acknowledged. The comments by two anonymous reviewers and the Associate Editor helped to improve the quality of the paper. This research was funded by the Wildlife and Forest Biodiversity Management Section of the Swiss Federal Office for the Environment under contract no. 2004.L.02.

References


Appendix I

Appendix I presents the data that were used to compare the performance of the new FORCLIM v2.9.5 with that of FORCLIM v2.9.1, which is presented in Table 6. To evaluate the plausibility of the simulated equilibrium species composition, the biomass proportions of the dominant species was used (Table A.1). The simulation of total biomass was considered to have improved if it was within 3 standard deviations of the measured growing stock (Table A.2). The simulation of a south-facing slope, which limits tree growth resulting in a lower biomass, was taken into account in the comparisons in Bever and Sion. The simulation of juvenile trees <12 cm dbh was evaluated based on the findings that previous model versions underestimated the number of these trees by up to an order of magnitude (Wehrli et al. 2005; Wehrli et al. 2007; Didion et al. 2009).

Table A.1. Share of total biomass of expected dominant species simulated with FORCLIM v2.9.5 and v2.9.1 at 11 sites. For the simulations with v2.9.5 the site Cleuson was substituted with Grande Dixence.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Share of simulated biomass (%)</th>
<th>v2.9.5</th>
<th>v2.9.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bever</td>
<td>P. cembra</td>
<td>82</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P. montana</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L. decidua</td>
<td>2</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Grande Dixence</td>
<td>P. cembra</td>
<td>60</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td>(Cleuson)</td>
<td>P. abies</td>
<td>32</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L. decidua</td>
<td>8</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Davos</td>
<td>P. abies</td>
<td>92</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L. decidua</td>
<td>4</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P. abies</td>
<td>59</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>Adelboden</td>
<td>F. sylvatica</td>
<td>18</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A. alba</td>
<td>10</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P. abies</td>
<td>24</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Huttwil</td>
<td>F. sylvatica</td>
<td>27</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>Bern</td>
<td>F. sylvatica</td>
<td>27</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>Schaffhausen</td>
<td>F. sylvatica</td>
<td>30</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>Basel</td>
<td>F. sylvatica</td>
<td>26</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>Schwerin</td>
<td>F. sylvatica</td>
<td>28</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quercus spp.</td>
<td>41</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quercus spp.</td>
<td>47</td>
<td>53</td>
<td></td>
</tr>
<tr>
<td>Cottbus</td>
<td>Tilia spp.</td>
<td>30</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C. betulus</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Sion</td>
<td>P. sylvestris</td>
<td>73</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quercus spp.</td>
<td>4</td>
<td>10</td>
<td></td>
</tr>
</tbody>
</table>
Table A.2. Simulated equilibrium total biomass at 11 sites, corresponding measured growing stock by region and elevation band, and estimated biomass using scaling factors for wood density and biomass expansion factors for a particular region (Thürig and Schmid 2008). For the estimation, the fraction of coniferous and deciduous species was taken into account. For the simulations with v2.9.5 the site Cleuson was substituted with Grande Dixence.

<table>
<thead>
<tr>
<th>Site</th>
<th>Simulated total biomass (t/ha)</th>
<th>Observed growing stock (m³/ha)</th>
<th>Estimated biomass (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>v2.9.5</td>
<td>v2.9.1</td>
<td>221 ±7¹</td>
</tr>
<tr>
<td>Bever</td>
<td>208.83</td>
<td>245.86</td>
<td>221 ±7¹</td>
</tr>
<tr>
<td>Grande Dixence (Cleuson)</td>
<td>220.19</td>
<td>250.33</td>
<td>221 ±7¹</td>
</tr>
<tr>
<td>Davos</td>
<td>307.79</td>
<td>324.95</td>
<td>314 ±9²</td>
</tr>
<tr>
<td>Adelboden</td>
<td>327.06</td>
<td>394.72</td>
<td>413 ±14³</td>
</tr>
<tr>
<td>Huttwil</td>
<td>342.52</td>
<td>446.90</td>
<td>439 ±15⁴</td>
</tr>
<tr>
<td>Bern</td>
<td>354.28</td>
<td>415.26</td>
<td>389 ±7⁵</td>
</tr>
<tr>
<td>Schaffhausen</td>
<td>324.72</td>
<td>409.05</td>
<td>389 ±7⁵</td>
</tr>
<tr>
<td>Basel</td>
<td>312.97</td>
<td>416.00</td>
<td>324 ±8⁶</td>
</tr>
<tr>
<td>Schwerin</td>
<td>245.48</td>
<td>397.20</td>
<td>na</td>
</tr>
<tr>
<td>Cottbus</td>
<td>182.47</td>
<td>388.77</td>
<td>na</td>
</tr>
<tr>
<td>Sion</td>
<td>61.23</td>
<td>178.74</td>
<td>235 ±22⁷</td>
</tr>
</tbody>
</table>

¹The site was simulated assuming a south-facing slope
²High Alps, >1800 m; ³High Alps, 1601-1800 m; ⁴Pre-Alps, 1201-1400 m; ⁵Pre-Alps, 601-800 m; ⁶Swiss Plateau, <600 m; ⁷Jura, <600 m; ⁸High Alps, <600 m.

Table A.3. Simulated equilibrium dbh distribution with FORCLIM v2.9.5 and v2.9.1 at 11 sites. For the simulations with v2.9.5 the site Cleuson was substituted with Grande Dixence.

<table>
<thead>
<tr>
<th>DBH class (cm)</th>
<th>FORCLIM v2.9.5 (stems/ha)</th>
<th>FORCLIM v2.9.1 (stems/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;4</td>
<td>4 - &lt;8</td>
</tr>
<tr>
<td>Bever</td>
<td>240</td>
<td>120</td>
</tr>
<tr>
<td>Grande Dixence (Cleuson)</td>
<td>239</td>
<td>175</td>
</tr>
<tr>
<td>Davos</td>
<td>173</td>
<td>130</td>
</tr>
<tr>
<td>Adelboden</td>
<td>1018</td>
<td>416</td>
</tr>
<tr>
<td>Huttwil</td>
<td>1207</td>
<td>586</td>
</tr>
<tr>
<td>Bern</td>
<td>1013</td>
<td>571</td>
</tr>
<tr>
<td>Schaffhausen</td>
<td>1114</td>
<td>489</td>
</tr>
<tr>
<td>Basel</td>
<td>1126</td>
<td>487</td>
</tr>
<tr>
<td>Schwerin</td>
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</tr>
<tr>
<td>Cottbus</td>
<td>1391</td>
<td>509</td>
</tr>
<tr>
<td>Sion</td>
<td>1040</td>
<td>302</td>
</tr>
</tbody>
</table>
Model sensitivity analysis of browsing impacts

Effects of ungulate browsing on forest composition and structure

– a model sensitivity analysis

published as:
Abstract

The impact of ungulate herbivores on tree regeneration and its possible consequences for long-term forest dynamics has raised concerns worldwide. In many countries, ungulate management aims at constant animal densities, whereas unmanaged ungulate populations tend to fluctuate over time. The ecosystem consequences of constant vs. varying ungulate densities are largely unknown, and the exact density that is acceptable from a forestry point of view is highly uncertain as well.

We used the gap model FORCLIM v2.9.5 to examine the effects of three browsing-related phenomena: a) temporal changes in animal densities and thus oscillations in browsing intensity; b) changes in the importance of browsing as a limiting factor relative to other limitations for ingrowth; and c) growth suppression by browsing and hence different ingrowth rates for slow vs. fast growing trees. Results showed that ungulate herbivory can induce profound compositional and structural changes in forest stands: a) oscillations in the browsing intensity led to compositional shifts that were less severe than under the corresponding constant browsing intensity; b) an increase in the importance of browsing relative to other environmental factors caused a decrease in the incidence of palatable species; and c) growth suppression strongly affected the numbers and composition of small trees of all species.

We conclude that browsing can cause a shift not only in the structure and composition of tree regeneration, but also of the upper canopy in the long term. Management can manipulate forest ecosystems through the control of animal densities, and our results suggest that alternative management strategies for ungulate populations may be worth considering so as to provide “windows of opportunity” for forest regeneration in time and/or space.

Keywords: sensitivity analysis; cyclic animal populations; mountain forests; gap model; patch model; FORCLIM
1. Introduction

Forests are exposed to a variety of disturbances that operate at different spatial and temporal scales. Depending on the disturbance, the effects can be obvious such as the large-scale removal and mortality of trees in a stand through forest fires, insect outbreaks and windthrows; or they may lead to slow changes in stand structure such as the selective herbivory by ungulates on seedlings and saplings (e.g., Motta, 1999; Côté et al., 2004). Many studies have examined the effects of ungulate browsing on tree regeneration and the short-term consequences on forest structure and species composition (e.g., Persson et al., 2005; Pépin et al., 2006; Carter and Fredericksen, 2007; Olesen and Madsen, 2008; Ward et al., 2008), showing, among others, that ungulates selectively browse tree species. This can prolong the exposure of saplings to browsing as their height growth is reduced (Motta, 2003; Vila et al., 2003) and even cause regeneration failure (Augustine and McNaughton, 1998). Particularly in mountain forests, where tree establishment and growth are limited by unfavorable environmental conditions, selective browsing of tree species by ungulates can have severe consequences (Motta, 1999). In the long term, ungulates have the potential to shift tree species composition (Augustine and McNaughton, 1998; Côté et al., 2004) and to alter the horizontal and vertical distribution of trees in a forest (Motta, 1999).

The composition and distribution of the tree layer is crucial for the protection function that many mountain forests provide, such as erosion control, protection against rockfalls and snow avalanches (Ammer, 1996; Dorren et al., 2004). Therefore, the impact of ungulate herbivores on the long-term development of mountain forests, i.e., over decades to centuries, is of key importance for forest management (e.g., Reimoser, 2003; Côté et al., 2004; Vavra et al., 2007). However, our understanding of long-term ungulate-vegetation relationships is limited and associated with high uncertainty (Seagle and Liang, 1997; Augustine and McNaughton, 1998; Weisberg and Bugmann, 2003).

As the density of unmanaged ungulate populations tends to fluctuate over time (Peterken and Tubbs, 1965; Patterson and Power, 2002), the intensity of their impact on seedlings and saplings varies, with consequences for the temporal pattern of forest regeneration (Peterken and Tubbs, 1965; Augustine and McNaughton, 1998). Periods of low animal populations can serve as “windows of opportunity” allowing the establishment of species that are highly sensitive to browsing (Peterken and Tubbs, 1965; Danell et al., 2003; Sage et al., 2003). However, the long-term impact of different browsing intensities on a specific forest is still unclear (Augustine and McNaughton, 1998; Côté et al., 2004).
To explore long-term ungulate-vegetation interactions, simulation models have proven useful (cf. Weisberg and Bugmann, 2003). Typically, these simulation studies (e.g., Jorritsma et al., 1999; Kienast et al., 1999; Seagle and Liang, 2001) have assumed that browsing intensity is constant over time. Here, we use a sensitivity analysis to evaluate the impact of changes in browsing intensities over time (i.e., simulating oscillations in animal populations) and differences in the species-specific susceptibility of trees to ungulate browsing regarding forest composition and structure (e.g., basal area and the frequency distribution of diameter at breast height [dbh]). This provides an opportunity to examine potential feedbacks between various effects of browsing by ungulates. 

We investigated the effects that browsing can have on tree ingrowth as a function of three distinct mechanisms:

a) Temporal variation in browsing intensity as the size of ungulate populations oscillates over time (cf. Mysterud et al., 2002) with a corresponding change in the incidence of browsing (cf. Motta, 2003);

b) Importance of browsing vs. other environmental pressures for regeneration success (cf. Seagle and Liang, 1997; Augustine and McNaughton, 1998; Motta, 2003) where an increase in the importance of browsing correlates to the fraction of years in which browsing is a limiting factor for ingrowth;

c) Suppression effect of ungulate browsing on tree height growth, which extends the time until a sapling grows beyond the reach of ungulates (cf. Augustine and McNaughton, 1998; Motta, 2003), thus leading to different ingrowth rates for slow- vs. fast-growing trees.

We expected the following impacts of these three mechanisms for species diversity and forest structure:

a) For oscillating ungulate populations, we expected an overall increase in tree numbers with elongating time intervals between tree population peaks and lows because of the increasing length of the “window of opportunity” that, in particular, allows the establishment of palatable species and, more generally, extends ingrowth opportunities that can be of advantage, especially to fast-growing, light-demanding pioneer species.

b) For an increase in the importance of browsing, we expected a decline in the incidence (i.e., the frequency of occurrence) of palatable species such as *Abies alba* (Senn and Suter, 2003) because browsing becomes more limiting for tree establishment.

c) For a decrease in the suppression effect on sapling growth, we expected the diversity of light-demanding, typically fast-growing (Reich et al., 1998) species
to increase because higher ingrowth rates increase the chance of these species to prevail under not optimal light conditions.

2. Methods

2.1. Model description

We used the forest gap model FORCLIM v2.9.5, which had been shown to reliably simulate species composition, tree numbers and dbh distribution of mountain forests (Didion et al., 2009). FORCLIM simulates on an annual time step the establishment, growth, and mortality of trees on multiple forest patches to derive regional-scale stand dynamics (Bugmann, 1996). Tree growth is simulated as annual diameter increment based on a potential maximum increment that is reduced in response to the current soil moisture and nitrogen status of the stand, growing degree-days and light availability. Most of these factors depend on the abiotic environment, which is represented by the mean monthly temperature and the precipitation sum, as well as soil water holding capacity and nitrogen availability (Risch et al., 2005). Trees grow as a function of species-specific constraints such as maximum growth rate or maximum tree height. Mortality has a random and a growth-related component, the latter being an integral proxy for stress conditions (tree vigor; Bugmann, 1996).

Tree establishment in gap models is described in a simplified manner mainly due to uncertainties and lack of long-term data on seedling and sapling development (cf. Weisberg et al., 2005; Zimmermann and Bugmann, 2008), and trees are established as saplings with a dbh of 1.27 cm. In FORCLIM, binary “establishment flags” for winter temperature (WTEF), number of growing degree-days (DDEF), light availability (ALEF), browsing pressure (BPEF; all described in Bugmann, 1996), and soil moisture (SMEF; described in Didion et al., 2009) are used to determine whether ingrowth of saplings is possible. These flags evaluate to 1 if current conditions meet species-specific limitations, or to 0 if they exceed limitations:

\[ gPEst = kEstP \cdot WTEF \cdot DDEF \cdot ALEF \cdot BPEF \cdot SMEF \]  

where \( gPEst \) is the probability of establishment and \( kEstP \) is the rate of seedling establishment with a range between 0 and 1. This parameter is used to reduce the probability of establishment \( gPEst \) as a proxy for micro-habitat effects (Liang and Seagle, 2002), i.e., to account for environmental factors that are not considered explicitly such as pathogens. In the long term, \( kEstP \) represents the average fraction of years in which establishment is possible when all five establishment flags have a value of 1. The default value of \( kEstP \) is 0.1 (Kienast, 1987).
The occurrence of sapling establishment is determined by Monte Carlo techniques based on the probability of establishment ($gPEst$; Bugmann, 1994). In case of $gP_{Est} < r$, where $r$ is a random number with a uniform distribution between 0 and 1, the number of saplings ($Trs$) that actually establish in the model is determined by a random number with a uniform distribution between 1 and a species-specific maximum ($kEst_{max}$):

$$kEst_{max} = \text{TRUNC}(0.5 + kEstDens \cdot kPatchSize \cdot kLa)$$  \hspace{1cm} \text{and} \hspace{1cm} [2]

$$Trs = U(1, kEst_{max})$$ \hspace{1cm} [3]

where $kEstDens$ is the site-specific maximum tree density for establishment, $kPatchSize$ is patch size (default 800 m$^2$), $kLa$ is a species’ shade tolerance (Table 1), which serves as a proxy for its rate of seed production (Risch et al., 2005), and TRUNC is the truncation function that returns the nearest integer number.

### 2.2. Implementing the sensitivity study

We removed the browsing pressure establishment flag ($BPEF$) from eq. [1] and made the following modifications to the model to control the ingrowth of trees as a function of the three browsing-related mechanisms described above.

#### a) Temporal variation in browsing intensity

For the simulation of the effect of oscillating animal populations and consequent fluctuations in browsing intensity, we assumed that at high browsing intensities no regeneration is possible (Augustine and McNaughton, 1998) and that tree establishment reaches a species-specific maximum when browsing pressure is nil. To describe these temporal fluctuations, we started from sinusoidal oscillations of different wavelengths ($\omega$ in Table 2):

$$gSine = \frac{1 - \sin\left(t \cdot 2 \cdot \pi \cdot \frac{1}{\omega}\right)}{2}$$ \hspace{1cm} [4]

where $gSine$ ranges between 0 and 1, and $t$ is the current simulation time. The wavelength $\omega$ represents the time between two consecutive lows or peaks, respectively. To determine the fractional reduction of sapling establishment relative to unbrowsed conditions, the species’ sensitivity to browsing ($kBrow$, cf. Table 1) was taken into account in the function $gSinMod$ (eq. [5]).
where a power of two was applied in the last term of the equation to differentiate more clearly between the species’ sensitivities to browsing. This resulted in the final sinusoidal oscillation $gOscMod$ (eq. [6]):

$$gOscMod = \begin{cases} 
    gSine - gSinMod & gSine - gSinMod > 0 \\
    0 & \text{else}
\end{cases}$$  \[6\]

which evaluates to a value between 0 (i.e., full browsing) and 1 (no browsing).

### Table 1. Species names, species-specific shade tolerance $kLa$ (from 1=high to 9=low) and sensitivities to browsing $kBrow$ (1=low; 2=moderate; 3=high) for all 30 parameterized species used in ForClim 2.9.5 (adapted from Bugmann, 1994, Tables A-11 and 3.11).

<table>
<thead>
<tr>
<th>Species Name</th>
<th>$kLa$</th>
<th>$kBrow$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies alba</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Larix decidua</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Picea abies</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Pinus cembra</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Pinus montana</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Taxus baccata</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Acer campestre</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Acer pseudoplatanus</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Alnus glutinososa</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Alnus incana</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Alnus viridis</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Betula pendula</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Castanea sativa</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Corylus avellana</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Populus nigra</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Populus tremula</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Quercus petraea</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Quercus pubescens</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Salix alba</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Sorbus aria</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Sorbus aucuparia</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Tilia cordata</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Tilia platyphyllos</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Ulmus glabra</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>
In the case of a constant browsing intensity (i.e., $\omega = \infty$), we assumed that the browsing effect was on average intermediate between allowing no and maximum regeneration. The actual number of trees ($T_{rs}'$) that were established was then calculated as

$$T_{rs}' = \begin{cases} 
  k_{Est_{\text{max}}} \cdot g_{Osc\text{Mod}} & 2 < \omega < \infty \\
  \frac{k_{Est_{\text{max}}}}{2} & \text{else}
\end{cases}$$

[3']

Figure 1 illustrates the form of eq. [3']; note that the maximum establishment rate is species-specific (cf. eq. [2]).

---

**Table 2. Factors and their settings used for the full-factorial design of the sensitivity analysis (default settings used for the standard model are in bold).**

<table>
<thead>
<tr>
<th>Factor settings</th>
<th>Temporal variation in browsing intensity ($\omega$) [years]</th>
<th>Importance of browsing ($k_{EstP}$) [-]</th>
<th>Suppression Effect ($k_{Multi}$) [-]</th>
</tr>
</thead>
<tbody>
<tr>
<td>#1 (default)</td>
<td>$\infty$ (constant intensity)</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td>#2</td>
<td>20</td>
<td>0.0333</td>
<td>0.333</td>
</tr>
<tr>
<td>#3</td>
<td>50</td>
<td>0.05</td>
<td>0.5</td>
</tr>
<tr>
<td>#4</td>
<td>100</td>
<td>0.2</td>
<td>2</td>
</tr>
<tr>
<td>#5</td>
<td>200</td>
<td>0.3</td>
<td>3</td>
</tr>
</tbody>
</table>

---

Figure 1. Temporal change of ingrowth of saplings dependent on the frequency of the sinusoidal oscillation ($\omega$) and the species’ sensitivity to browsing ($k_{Brow}$). This example is based on tree numbers of light-demanding species (i.e., $k_{La} = 9$) and constant browsing intensity ($\omega = \infty$) and of 100 years for the oscillation ($\omega = 100$).
b) Importance of browsing

Due to the fact that the browsing pressure establishment flag (BPEF) was removed from eq. [1], the rate of seedling establishment (kEstP) represents the degree to which other environmental factors (including micro-habitat effects) limit ingrowth in a given year relative to the four other explicitly considered limiting factors (WTEF, DDEF, ALEF and SMEF, cf. eq. [1]). As browsing pressure now acts via the number of trees that actually establish (Trs’, cf. eq. [3’]), an increase in the rate of seedling establishment (kEstP) is associated with an increase in the importance of browsing. For example, if winter temperature, available light, degree-days and soil moisture are favorable (i.e., evaluate to 1), kEstP > 0 and gP_{Est} < r, tree regeneration occurs (cf. eq. [1]), but the number of trees that actually establish (Trs’) is limited as described by eq. [3’]. For the default value of kEstP (i.e., 0.1, Table 2), on a long-term average browsing can determine how much establishment is possible in only 10% of the years and is thus less important. We varied kEstP between 0.0333 and 0.3 (Table 2).

c) Suppression effect

We used a species-specific multiplier (kMulti) to modify eq. [2] as follows:

\[ k_{Est_{max}} = \text{TRUNC} \left( 0.5 + k_{Est Dens} \cdot k_{PatchSize} \cdot k_{La} \cdot k_{Multi} \right) \]  \[ [7] \]

By varying the value of kMulti (Table 2), we were able to examine the impact of different ingrowth rates as a consequence of prolonged exposure to browsing affecting stand development. A change in the value of the multiplier (kMulti) modified the species-specific number of trees given by their shade-tolerance (kLa; cf. section 2.1) that establish in a given year: a value of kMulti < 1, i.e., an increased suppression effect led to fewer trees being established (cf. eq. [7]).

2.3. Simulation experiments

a) Study sites and control simulations

We simulated the effects of browsing at three sites in the Swiss Alps along an elevation gradient. The site Bever is at the upper subalpine level (1712 m) and is dominated by Pinus cembra, P. montana, and Larix decidua. The site Davos (1590 m) is at the subalpine level, where Picea abies is dominant with some L. decidua. The site Adelboden (1325 m) is at the montane level and dominated by P. abies, Fagus sylvatica, and Abies alba, with several other deciduous species in the understory such as Acer spp.

The potential natural vegetation (PNV) at these sites is well studied (e.g., Ellenberg, 1996; Ott et al., 1997) and has already been used for validating FORCLIM v2.9.5.
(Didion et al., 2009). These earlier simulation results thus provided a suitable data set (cf. Fig. 2 for basal area and the frequency distribution of dbh at equilibrium) that we used as baseline (control) for the present sensitivity analysis.

Figure 2. Species DBH distribution and basal area at equilibrium simulated with ForClim 2.9.5 of the stands at the sites Adelboden, Davos, and Bever, which were used as control. Species with a fraction of less than 5% of total tree numbers were subsumed under “other Coniferous”, and “other Deciduous”, respectively.
2.4. Data analysis

To efficiently compare all scenarios with the control regarding the effects on species composition and forest structure, we calculated (i) percentage deviance (%Dev, eq. [8]) of the difference between scenario and control for species-specific basal area, and (ii) Bray-Curtis similarity (BC, eq. [9]; Bray and Curtis, 1957) between scenario and control for tree numbers in the four dbh classes.

\[
%\text{Dev} = \frac{y_j - c}{c} \cdot 100
\]

where \(y_j\) is the value of the variable of interest in the \(j\)th scenario and \(c\) is the corresponding value in the control.

\[
\text{BC}_{jc} = 1 - \frac{\sum |y_{ij} - y_{ic}|}{\sum (y_{ij} + y_{ic})}
\]

where \(\text{BC}_{jc}\) is the similarity between the \(j\)th scenario and the control \(c\), and \(y_{ij}\) represents the abundance of the \(i\)th species, and tree numbers in the \(i\)th dbh class, respectively, in the \(j\)th scenario and for \(c\), the control data. Bray-Curtis similarity is a commonly used measure for comparing multivariate ecological data (cf. Su et al., 2004), where a value of 1 indicates a perfect fit and a value of 0 entirely different datasets.

In order to compare the effect of changes in wavelength, importance of browsing, and suppression effect on species of a) low (i.e., \(kLa > 5\), Table 2) vs. high shade tolerance (i.e., \(kLa < 5\)) and b) low (i.e., \(kBrow = 1\)) vs. high (i.e., \(kBrow = 3\)) sensitivity to browsing, we calculated the relative incidence (\(RI_{SC} [\%]\), eq. [10]) as the incidence of species that have a particular characteristic (\(I_{SC}\)) relative to the total number of species having that characteristic in the data set (\(N_{SC}\); Table 1):

\[
RI_{SC} = \frac{I_{SC}}{N_{SC}} \cdot 100
\]

3. Results

Across all scenarios, total basal area was least affected whereas total tree numbers differed strongly between years with high and low ingrowth, respectively (Fig. 3). The basal area of the control was higher than the median basal area from all scenarios (Fig. 3a, c), with the exception of Bever (Fig. 3e). The pattern for tree numbers was similar at all three sites: Median tree numbers from all scenarios sampled at times of the
oscillation when ingrowth was low were lower than in the control, and for the times were ingrowth was high median tree numbers were higher than in the control (Fig. 3b, d, f).

Shifts in the basal area of the dominant species were evident in most scenarios at all sites (Fig. 4). Particularly in Adelboden the co-dominant species *Abies alba* and *Fagus sylvatica* disappeared entirely in many scenarios with a constant high browsing intensity (i.e., where the median was -100 for %Dev; Fig. 4a). For scenarios with higher browsing intensities than in the control, the species shift was larger than for scenarios with lower browsing intensities (Fig. 4).

The degree to which the examined three factors, temporal variation in browsing intensity, importance of browsing and suppression effect, contributed to compositional and structural changes differed by factor and response variable, as presented below.

![Figure 3. Boxplots with notches indicating the 95% confidence limits on the medians over all scenarios for samples from 10 oscillation cycles and 200 independent patches of total tree numbers and total basal area from years with lowest ingrowth (low) and highest ingrowth (high) at the sites Adelboden, Davos, and Bever. Dashed lines show the respective value of the control.](image)

**a) Temporal variation in browsing intensity**

Wavelength $\omega$ had a nearly negligible effect on total basal area for the wavelengths considered here (Table 2; results not shown), but there was a strong effect on the basal...
area of the dominant species depending on whether a constant browsing intensity was simulated or browsing intensity was oscillating (Fig. 4).

![Figure 4. Percentage deviance of the simulated basal area of species which are dominant in the PNV from that of the control at each site: The panels under “higher browsing” refer to all scenarios where the settings for $k_{EstP}$ and $k_{Multi}$ were higher than for the default values (cf. panels above the diagonal from top-left to bottom-right in Figs. 5-7) while the panels under “lower browsing” refer to all scenarios where the settings for $k_{EstP}$ and $k_{Multi}$ were smaller than for the default values (cf. panels above the diagonal from top-left to bottom-right in Figs. 5-7). In both cases scenarios with constant browsing (white panels) and oscillating browsing (grey panels) are distinguished. Species abbreviations are as follows: A.alb - Abies alba; F.syl - Fagus sylvatica; P.abi - Picea abies; L.dec - Larix decidua; P.cem - Pinus cembra; P.mon - Pinus montana.]

The differences in tree numbers due to oscillations depended strongly on the DBH class. The number of trees in DBH class 4 (>51 cm) that to a large extent determine stand basal area was most affected in Adelboden (solid black line in each panel for a unique combination of importance of browsing and suppression effect, Fig. 5) but experienced very little change under different wavelengths in Davos and Bever (Figs. 6, 7). In Adelboden, Bray-Curtis similarity for trees in DBH class 4 typically peaked in scenarios with fluctuating browsing intensity over time ($\omega \neq \infty$, Fig. 5). The difference between sampling times (years of low and high ingrowth, respectively) was minimal for trees in DBH class 4 at all sites (results not shown).
The effect of wavelength on tree numbers increased from DBH class 4 to class 1 (<12 cm). In class 1, a difference between the two sampling times was also evident (dashed and dotted vs. solid lines, Figs. 5-7). A consistent pattern at all three sites was that for tree numbers in DBH class 1 the difference between the two sampling times increased with increasing wavelength (dashed vs. dotted lines, Figs. 5-7). Thus, the difference in total tree numbers between the two sampling times (Fig. 3) was driven to a large extent by the size class <12 cm dbh (dashed vs. dotted lines, Figs. 5-7).

At the site Adelboden, both higher and lower browsing resulted in changes to the basal area of the dominant tree species, as (i) %Dev reached values of -100% (Fig. 4a) and (ii) the Bray-Curtis similarity for trees >51 cm decreased to ca. 50% (Fig. 5). This was much less pronounced at the sites Davos and Bever (Figs. 6, 7).

The incidence of light-demanding species relative to the 14 species with shade tolerance ($k_{La}$) > 5 in the model (cf. Table 2) increased concurrent with an increase in...
wavelength at the sites Adelboden and Davos for both sampling times (i.e., $RI_{SC}$ increased, Fig. 8a and d). In contrast, a slight decrease with increasing wavelength was apparent at the site Bever (Fig. 8g).

The response of palatable species to changes in wavelength was determined by the incidence of these species relative to the 8 species with browsing sensitivity ($kBrow$) = 3 (cf. Table 2). Changes in wavelength did not produce a clear pattern with regard to the relative incidence of these species at any of the three sites (Fig. 8a, d, g).

![Figure 6. Bray-Curtis similarity for species-specific tree numbers from 125 scenarios at the site Davos, details see Fig. 5.](image)

b) Importance of browsing and c) Suppression effect

The impacts of the importance of browsing ($kEstP$) and the suppression effect ($kMulti$) were similar for trees >51 cm dbh at all 3 sites, being strongest at Adelboden (Fig. 5), the site with the highest species diversity (cf. Fig. 2) compared to the less diverse sites Bever and Davos (Figs. 6, 7).

The impacts of the importance of browsing (represented by the rate of seedling establishment $kEstP$) and the suppression effect ($kMulti$) were similar for trees >51 cm
dbh at all 3 sites, being strongest at Adelboden (compare the difference between panels that represent a unique combination of $k_{EstP}$ and $k_{Multi}$, Fig. 5), the site with the highest species diversity (cf. Fig. 2) compared to the less diverse sites Bever and Davos (Figs. 6, 7).

Generally, the effects of the two factors were not linear, i.e., a stepwise change in one factor (moving vertically or horizontally through the panels in Figs. 5-7) did not affect the Bray-Curtis similarity of the examined variables in a similar fashion. The response of the examined variables also depended strongly on the wavelength (x-axis in each panel in Figs. 5-7).

**Figure 7. Bray-Curtis similarity for species-specific tree numbers from 125 scenarios at the site Bever, details see Fig. 5.**

An increase in the importance of browsing (i.e., an increase in $k_{EstP}$) and the corresponding decrease in the fraction of years in which browsing was a limiting factor for tree establishment was expected to result in an increase in the relative incidence of species of low sensitivity to browsing ($k_{Brow} = 1$). This was true in Adelboden and for trees sampled during low ingrowth in Davos, but not in Bever (Fig.
8b, e, h). At all three sites the magnitude of the effect differed for trees from the two sampling times, indicating feedbacks to changes in wavelength.

Light-demanding species ($k_{La} > 5$) did not, as hypothesized, profit from a decrease in the growth suppression ($k_{Multi}$; Fig. 8c, f, i) in response to the increased establishment rates (cf. eq. [7]). In contrast, the relative incidence of shade-tolerant species ($k_{La} < 5$) increased with an increase of $k_{Multi}$ in Adelboden (Fig. 8c). In Bever, truly shade-tolerant species were generally not present (Fig. 8i). With the exception of Bever, the effect of the suppression effect ($k_{Multi}$) was similar for the two sampling times, i.e., at low and high ingrowth (Fig. 8c, f, i).

![Figure 8](https://via.placeholder.com/150)

**Figure 8.** Mean relative incidence ($RI_{sc}$) of the species that have a particular characteristic relative to the total number of species having that characteristic in the data set (Tab. 1) at sampling times with low (solid lines) and high (dashed lines) ingrowth, respectively:

- **a, d, g:** mean $RI_{sc}$ over all scenarios for species with high browsing sensitivity (i.e., $kBrow = 3$) and low shade tolerance (i.e., $kLa > 5$).
- **b, e, h:** mean $RI_{sc}$ over all scenarios with $k_{Multi} = 1$ for species with low browsing sensitivity ($kBrow = 1$) and high sensitivity ($kBrow = 3$), where $kEstP = 0.0333$ denotes low importance and $kEstP = 0.3$ denotes high importance of browsing.
- **c, f, i:** mean $RI_{sc}$ over all scenarios with $kEstP = 0.1$ for species with high shade tolerance ($kLa < 5$) and low shade tolerance ($kLa > 5$), where $k_{Multi} = 0.333$ denotes high growth suppression and $k_{Multi} = 3$ denotes low growth suppression.
4. Discussion

Our results complement findings from field studies (as summarized by Côté et al., 2004) that high ungulate abundance may cause compositional shifts in forests. In many of the scenarios with an increased browsing intensity, the decrease in the basal area of one browsing-sensitive dominant species was compensated by another, co-dominant species. Typically, the species whose basal area decreased were more sensitive to browsing. For example, at the site Adelboden, the basal area of *Abies alba* and *Fagus sylvatica* decreased strongly in the majority of scenarios, and so did *Pinus cembra* at the site Bever albeit to a smaller extent (Fig. 4); they all are species with a high browsing sensitivity (Kienast, 1987; see also Risch et al., 2003; Senn and Suter, 2003; Rozas, 2004).

These shifts in species composition simulated with the model FORCLIM correspond with field studies (e.g., Engelmark et al., 1998; Rooney et al., 2000; Potvin et al., 2003). Furthermore, smaller size classes were more affected than larger ones both in the model simulations (cf. Fig. 5-7) as well as in field studies (Whitney, 1984). An observed increase in the effect of browsing with an increasing site productivity (Husheer et al., 2003) was also apparent in our simulations along the gradient from the least productive site Bever to the most productive site Adelboden. Thus, the good agreement between model results and patterns from empirical studies suggests a high degree of realism of the model, although the predictive ability of the model cannot be directly quantified due to a lack of corresponding long-term data.

The simulated trend towards a stronger dominance by *P. abies* at the site Adelboden (cf. Fig. 4) presents a concern, because on steep slopes, the protective function of mountain forests against processes such as avalanches, rockfall and mudflows depends to a large degree on species properties (e.g., rooting depth and resistance to pathogens). Therefore, species with a low vulnerability regarding large-scale disturbances, such as *F. sylvatica* and particularly *A. alba*, are highly desirable to enhance the resistance and resilience of mountain forests (cf. Brang et al., 2001; 2006; Frehner et al., 2005) and the loss of these species compromises the ability of a stand to provide certain functions (Frehner et al., 2005).

The compositional changes of stand basal area that resulted from browsing were associated with alterations in vertical and horizontal stand structure: particularly in the lower diameter classes, tree numbers decreased strongly under high browsing. While this is unlikely to constitute a problem for the continued existence of forest cover, the protective effect regarding natural hazards (particularly rockfall events comprising smaller rock volumes; Stoffel et al., 2006) is certainly affected. The simulated changes of stand composition and structure thus are important in a management context; we addressed them further by examining (a) the temporal variation in browsing intensity,
(b) the relative importance of browsing, and (c) the growth suppression effect, as discussed below.

4.1. Temporal variation of browsing intensity

With increasing wavelength, i.e., increasing time between peaks of ingrowth, we expected tree numbers of light-demanding species to increase and total basal area to decrease. Although there was a trend for the incidence of light-demanding species to increase with longer oscillations (Fig. 8a, d, g), total basal area changed little over the scenarios (Fig. 3). Thus, according to the FORCLIM model a key effect of ungulate browsing in the context of long-term forest dynamics is the reduction of stem numbers in the juvenile tree stage, which subsequently leads to lower competition among the regeneration and thus a higher survival rate (cf. Senn and Suter, 2003), but with low impacts on overall basal area. Yet, the effect of increasing wavelength was inconclusive with regard to the species’ susceptibility to browsing (Fig. 8a, d, g), indicating that species can compensate for deficiencies in one trait by another, for example, chemical defenses, growth rates, and nutrient uptake (Augustine and McNaughton, 1998). Feedback effects between different intraspecific and interspecific (e.g., susceptibility to browsing, light requirements, and growth rates) species traits all play an important role in the model as well as in reality (Augustine and McNaughton, 1998; Côté et al., 2004; Ward et al., 2008). Hence, it is not necessarily true that species with a high browsing susceptibility will suffer most strongly in terms of their abundance and survival probability in the long-term (cf. Augustine and McNaughton, 1998).

It is noteworthy that at the site Adelboden under constant browsing the co-dominant species *A. alba* and *F. sylvatica* disappeared in 50% of the scenarios where browsing was higher than under default conditions, while with oscillating ingrowth rates, their basal area decreased only minimally (Fig. 4a). This is a strong indication that “windows of opportunity”, which become available under fluctuating browsing intensities over time, indeed provide the opportunity for species of high browsing susceptibility to persist (Peterken and Tubbs, 1965; Danell et al., 2003; Sage et al., 2003). Such windows of opportunity may arise, for example, because of intrinsic population processes (Sage et al., 2003) or because of large-scale climatic variability (Post and Forchhammer, 2002).

Still, our long-term simulations suggest that at some sites (such as Adelboden), even under very long animal population cycles (i.e., 100 and 200 years) the forest may not recover from periods of heavy browsing despite the existence of strong “windows of opportunity” in the model (Côté et al., 2004). In addition, the guaranteed ingrowth as simulated here may not occur in reality, where regeneration success is highly uncertain.
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(cf. review in Augustine and McNaughton, 1998) for example due to limited seed availability or competition by ground vegetation, processes that were not simulated here. Ungulate effects on tree numbers and species composition thus are likely to be more severe in reality than in the model, i.e., the model provides a conservative estimate of these effects.

Our results also suggest that when the impact of browsing is high, maintaining constant animal densities and thus relatively constant browsing intensities over time is less suitable when the aim is to minimize compositional and structural changes in forest stands (Frehner et al., 2005), as compared to a strategy that favors oscillations in animal densities and thus browsing pressure (Sage et al., 2003). However, when browsing impacts are low, managing for a constant browsing pressure may be efficient (cf. Augustine and McNaughton, 1998). It should be kept in mind that for those scenarios that featured a constant browsing intensity, we had chosen a fairly low level of browsing pressure (i.e., ~30% browsing-induced total mortality of seedlings of the most sensitive species until reaching a dbh of 1.27 cm).

Lastly, we need to emphasize that a constant high presence of ungulates implies that other effects of browsing, such as feedbacks between the seasonal timing of browsing and nutrient turnover (cf. Augustine and McNaughton, 1998; Côté et al., 2004), continuously affect tree and ecosystem development. Such impacts were not considered here, and thus their consequences cannot be assessed based on our results.

4.2. Importance of browsing and suppression effect

At the two sites at the subalpine level, Davos and Bever, the impact of browsing on species composition by basal area (Fig. 4) and on tree numbers >51 cm dbh (Figs. 5-7) was typically lower than in Adelboden. However, in the scenarios with a combination of a high suppression effect (low $k_{Multi}$) and a low importance of browsing (low $k_{EstP}$), the Bray-Curtis similarity for trees >51 cm dbh decreased even at these sites to ca. 70-80% compared to control conditions (cf. upper left panels in Figs. 6, 7). This is consistent with observations showing that other factors such as long periods of snow and ice cover, high radiation and wind (Ott et al., 1997; Körner, 1998; Senn, 1999) gain in importance for regeneration success at the subalpine level, so that the time required for a tree to grow beyond ungulate reach height is prolonged (cf. Motta, 1999, 2003).

Under an increase in the importance of browsing (i.e., a reduction of $k_{EstP}$), we expected a reduced dominance of palatable species such as *Abies alba*. The species *A. alba* and *Fagus sylvatica* were absent entirely in 50% of the scenarios at the site Adelboden when browsing was higher than under default conditions, i.e., these conditions prevented their establishment by causing mortality at the seedling and
sapling stage. In contrast, *Pinus cembra*, which became rare at the site Bever, was able to establish but its growth was strongly suppressed compared to *Larix decidua* and *Pinus montana* (cf. Fig. 4), which are less sensitive to browsing. Even in scenarios with higher browsing intensities compared to the control, *Pinus cembra* in Bever was much less affected than *Abies alba* and *Fagus sylvatica* in Adelboden (Fig. 4). An assessment of the vulnerability of a forest to browsing must therefore be site-specific, and browsing effects should be distinguished with regard to mortality vs. a mere suppression of growth (cf. Long et al., 2007).

We had expected that the incidence of fast-growing, light-demanding pioneer species would increase when the suppression effect on sapling growth decreases (i.e., under an increase in $k_{Multi}$). Yet, this was not the case at any of the three sites (cf. Fig. 8c, f, i), which is counter-intuitive and hard to explain. On the one hand, it can be attributed to interactions among the site-specific light and environmental limitations; on the other hand, it may also be due to artifacts resulting from the fact that in the FORCLIM (and most other forest succession) models, ingrowth is treated rather simplistically, and ungulate effects cannot be modeled mechanistically in this framework, but they must be parameterized via proxies. Specifically, at the site Adelboden the density of the simulated stand did not allow sufficient light to penetrate to the lower canopy layers, which caused a high mortality of light-demanding saplings that may be erroneous. At the sites Davos and Bever, environmental limitations, particularly cold temperatures, strongly controlled the species mix, thus limiting the incidence of light-demanding species as well (Ott et al., 1997). The approximation of the suppression effect by altering ingrowth rates additionally increased competition for light in the lower canopy, which may be too simplistic to accurately represent the range of browsing-related effects on sapling growth (e.g., Oesterheld and McNaughton, 1991). These model limitations have to be taken into account when interpreting the results from the present sensitivity study.

### 4.3. Implications and conclusions

The sites used in this study represent typical mountain forests in the Swiss Alps (Frehner et al., 2005). A major concern in such forests is their protective role against disturbances such as avalanches and rockfall (cf. Stoffel et al., 2006), but also their resistance and resilience with regard to windthrow events and insect attacks. The species composition and stand structure are key properties in this regard (see above and cf. Brang et al., 2001; 2006; Frehner et al., 2005). Both were affected by ungulate browsing in our simulations but also in empirical studies (e.g., Ammer, 1996; Motta, 1999, 2003). Therefore, our results confirm that ungulate browsing is a very important...
factor that needs to be taken into account, as it can have profound effects on the long-
term regeneration success and forest properties in general.

Since the intensity of browsing depends primarily on animal density (Tilghman, 1989;
Welch et al., 1991; Augustine and McNaughton, 1998), which tends to vary strongly
in space and time, it is critical to understand the long-term role of herbivores on
forests. Although the browsing intensities used in this study cannot be directly
translated into animal densities due to a lack of a quantitative basis (cf. Weisberg et al.,
2005), simulations of observed stands with FORCLIM using default settings for
browsing suggested a good correlation between default browsing in the model and
average browsing intensity in Swiss forests (cf. Didion et al., 2009).

Our results demonstrated that the effect of heavy browsing on the basal area of the
dominant species can differ strongly between a constant and a fluctuating browsing
intensity. Management can manipulate forest ecosystems through the control of animal
densities, and thus a re-evaluation of management strategies of constant vs. fluctuating
animal densities is warranted.

Models are deliberate simplifications of reality, and complex processes such as
browsing may not be represented explicitly but through proxies. We used such an
approach to simulate browsing effects, and we are aware of the limitations relating
particularly to the assumption of sinusoidal animal population fluctuations and an
according change in browsing intensity. The large uncertainties surrounding forest-
wildlife interactions (cf. Augustine and McNaughton, 1998; Weisberg and Bugmann,
2003) and the limitations of field research to examine large temporal and spatial scales
(cf. Seagle and Liang, 1997) justify the use of models to evaluate potential future
development patterns and to identify knowledge and research gaps relating, for
example, to:

- the length and amplitude of oscillations in animal densities and associated
changes in browsing intensity that allow for the persistence of highly browsing-
sensitive species (Peterken and Tubbs, 1965; Danell et al., 2003; Sage et al.,
2003).

- the effects of interactions between browsing and other environmental factors
such as soil nutrient status (cf. Augustine and McNaughton, 1998; Côté et al.,
2004).

- the effects of browsing on mortality and growth suppression of saplings,
particularly in mountain forests (Motta, 1999).

The knowledge gained from field research should be used to improve modeling efforts
examining forest-wildlife interactions, for example towards a more robust estimation
of species parameters regarding browsing sensitivity. Also, the simulated low
sensitivity of the large dbh classes to browsing effects warrants a close examination of the simulated light profile across the canopy, as the model may simply “suffocate” browsing-induced effects on regeneration by overly large mortality rates in the low diameter classes. Generally speaking, research towards improving models of long-term forest dynamics is a high priority. In particular because climate change will bring about new challenges for forest management as species will have to adapt to new climatic regimes, and browsing effects are likely to play an important role by delaying or even preventing the establishment of a species.

Given the widespread concerns about the effects of ungulate herbivory in forests worldwide (e.g., Ayres and Lombardero, 2000; Senn and Suter, 2003; Vila et al., 2003; Ward et al., 2008), studies such as ours should help to improve the scientific understanding of mid- and long-term tree-ungulate interactions. By investigating the effects of several browsing-related disturbance processes and feedbacks between them, we were able to demonstrate the risks regarding changes in the diversity and structure of forests that are associated with a high abundance of ungulates, particularly when they are managed with the aim of constant densities (cf. Senn and Suter, 2003).

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**References**


Part 4


Interactions between ungulate browsing and climate change

Ungulate herbivory modifies the effects of climate change on mountain forests

submitted as:
Didion, M., Kupferschmid, A.D., A. Wolf and Bugmann, H. Ungulate herbivory modifies the effects of climate change on mountain forests. Climatic Change
Abstract

The general warming trend causes the range of tree species to shift to higher latitudes or altitudes. Since disturbances such as herbivory can change species composition, it is important to understand the combined effect of such factors and climate change. To investigate the response of forests to climate change and herbivory by wild ungulates, we used the forest gap model FORCLIM v2.9.6 to simulate forest development in three climatically different valleys in the Swiss Alps. We used altitudinal transects on contrasting slopes covering a wide range of forest types from the cold to the dry treeline. This allowed us to investigate (i) altitudinal range shifts in response to climate change, (ii) the consequences for tree species composition, and (iii) the combined effect of climate change and ungulate herbivory.

We found that ungulate herbivory changed species composition and reduced both basal area and tree numbers. Tree species responded differently to the change in climate and did not migrate concurrently, which caused a succession to new stand types. While climate change partially compensated for reductions in basal area caused by ungulate herbivory, the combined effect of these two agents on the mix of the dominant species and forest type was non-compensatory as browsing selectively excludes species from establishing or reaching dominance and alters competition patterns, particularly for light. We conclude that there is an urgent need for adaptive forest management strategies that address the joint effects of climate change and ungulate herbivory.

Keywords: Succession model; FORCLIM; IPCC; species composition; valley transect; treeline; Swiss Alps
1. Introduction

The general anthropogenic warming trend (IPCC 2007) causes tree species to shift to higher latitudes or altitudes (Davis and Shaw, 2001; Theurillat and Guisan, 2001; Walther et al., 2002). It is expected that some previously unforested regions at high latitudes and altitudes become suitable for tree growth, whereas other areas may not sustain forest cover any more due to increase in droughts (Cairns et al., 2007; Gehrig-Fasel et al., 2007). However, the range shifts of tree species depend, in addition to climate, on various other natural and anthropogenic factors such as seed availability, resource availability and land use (Walther et al., 2002; Thuiller et al., 2005). Feeding on aboveground plant tissue by wild ungulates such as deer and reindeer has been identified as an important driver for the local position of treelines in mountain and high-latitude ecosystems (e.g., Kullman, 2001; Grace et al., 2002; Moen et al., 2004). In these systems and beyond, ungulate herbivores can prevent tree establishment entirely or modify the tree species mix and thus influence long-term forest development (Augustine and McNaughton, 1998; Côté et al., 2004).

Forest development in response to changes in climate has been explored in a wide range of modeling studies (e.g., Lexer et al., 2002; Bugmann, 2003; Wallentin et al., 2008). However, the role of ungulate herbivores as a driver of forest succession in response to a changing climate has, to our knowledge, not been addressed in modeling studies. We aim to fill this gap by using the forest gap model FORCLIM (Didion et al., 2009c) to simulate forest development under climate change and different ungulate browsing pressure.

The objective of this study was to examine the combined effects of climate change and ungulate browsing along elevation transects. We selected three climatically different valleys in the Swiss Alps to investigate (i) altitudinal range shifts in response to climate change, (ii) the consequences for tree species composition, and (iii) the combined effect of climate change and ungulate browsing.

2. Materials and methods

2.1. Study area

We selected transects across three valleys in climatically different regions of the Swiss Alps: (i) dry and warm continental climate; (ii) moist and cold continental climate; and (iii) moist and warm continental climate. All transects ran from a predominantly south-facing to a predominantly north-facing slope via the valley bottom.
2.1.1. Dry and warm continental climate

The Anniviers valley (Val d’Anniviers) is a side valley of the Rhone River valley in the Valais, Western Central Alps. The catchment is ca. 255 km\(^2\) in size and ranges from 500 m to 4400 m a.s.l. The transect crosses the valley in a north-east to south-west direction from a small peak near Mt. Illhorn (ca. 2300 m; 46°15´N, 7°36´E) to Mt. La Brinta (ca. 2600 m; 46°13´N, 7°32´E) via the village of Fang in the valley bottom (ca. 850 m). This valley is characterized by a warm climate with dry conditions in the summer (Table 1) especially on south-facing slopes. Due to the dry climate, current forests in the valley bottom are composed mainly of drought-resistant species, such as *Quercus* spp. and *Pinus sylvestris* (Lock et al., 2003). With increasing elevation, the dominant species change to *Picea abies* (high-montane to subalpine, ca. 1000-1800 m) and further up to *Larix decidua – Pinus cembra* (upper subalpine ca. 1800 m to treeline ca. 2500 m; Ott et al., 1997; Gödeckeimer, 1998). The transition between *Pinus* and *Picea* forest is found around 200-400 m lower on the colder north-facing slope than on the warmer south-facing slope (Ott et al., 1997).

<table>
<thead>
<tr>
<th>Table 1. Long-term mean seasonal temperature (°C) and precipitation sum (cm) of the current climate (1961-2000) and mean anomalies (°C and % precipitation, respectively) for future climate (2075-2099). Data were presented for the lowest and highest point of each transect.</th>
<th>Temperature</th>
<th>Precipitation</th>
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<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Summer</td>
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<tr>
<td>Anniviers valley</td>
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<td>16.7</td>
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<tr>
<td>2650 m</td>
<td>-3.6</td>
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<tr>
<td>Anomalies</td>
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<td>+5.9</td>
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<tr>
<td>Tuors valley</td>
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<tr>
<td>1650 m</td>
<td>1.7</td>
<td>10.8</td>
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<td>2700 m</td>
<td>-4.7</td>
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<td>Anomalies</td>
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<tr>
<td>Maggia valley</td>
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<tr>
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<td>11.0</td>
<td>19.7</td>
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<tr>
<td>Anomalies</td>
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<td>+5.3</td>
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</tbody>
</table>

2.1.2. Moist and cold continental climate

The Tuors valley (Val Tuors) is an inner alpine valley in Graubünden situated in the Eastern Central Alps. The catchment is ca. 57 km\(^2\) in size and ranges from 1350 m to 3350 m a.s.l. in altitude. The transect runs in a straight north-south direction from Piz Valmela (ca. 2700 m; 46°39´N, 9°47´E) via the village of Tuors Davant in the valley of the Tuors (ca. 1700 m) to Piz Darlux (ca. 2600 m; 46°37´N, 9°47´E). Cold winters with high amounts of snow (Table 1) restrict the species diversity and successional pathways in the montane and subalpine forests (Ott et al., 1997). The dominant species change with elevation from *P. abies* at the high-montane and lower subalpine region
(i.e., up to ca. 2000 m) of the valley (Ott et al., 1997; Didion et al., 2009b) to *L. decidua* and *P. cembra* in the upper subalpine level up to treeline (ca. 2500 m; Ott et al., 1997).

### 2.1.3. Moist and warm insubrian climate

The Maggia valley (*Valle Maggia*) is located in the northern part of the Ticino in the Southern Swiss Alps. The catchment covers ca. 574 km² and ranges from 200 to 3200 m a.s.l. The transect runs in a north-south direction from Piz Spluga (ca. 2200 m; 46°19´N, 8°39´E) via the Maggia River (ca. 400 m) to Piz Güi (ca. 2200 m; 46°15´N, 8°37´E). The insubrian climate in this part of the Southern Alps is characterized by warm summers and mild winters with high annual precipitation (Table 1), but still extended periods of drought in spring and summer, which allows for a diverse mix of deciduous tree species at low to moderate elevations (Gobet et al., 2000). In the colline belt below ca. 700 m, *Castanea sativa*, *Fagus sylvatica* and *Quercus* spp. are expected to dominate (Ott et al., 1997). The montane belt (ca. 700-1600 m) is dominated by *Fagus sylvatica* at the lower and *P. abies* together with *Abies alba* at the upper level (Ott et al., 1997; Didion et al., 2009b). The subalpine region between ca. 1600 and 2100 m is dominated mainly by *P. abies* and *L. decidua* (Ott et al., 1997).

### 2.2. Gap model FORCLIM

The gap model FORCLIM simulates the establishment, growth, and mortality of trees on multiple small forest patches to derive stand-scale dynamics (Bugmann, 1996). Tree growth is specified as a species-specific maximum that is reduced to a realized growth rate by taking into account key limiting factors (temperature, drought, light availability, and nitrogen availability). Trees are established as saplings with a diameter at breast height (dbh) of 1.27 cm, whereby the number of new trees is a function of species-specific responses to winter temperature, light availability, growing degree-days, and a simplified formulation of browsing pressure (Bugmann, 1994). FORCLIM performed well in several studies comparing local, site specific forest data (Risch et al., 2005; e.g., Didion et al., 2009b; Didion et al., 2009c), but also potential natural vegetation along large temperature and precipitation gradients within and between various mountain regions (e.g., Bugmann and Solomon, 2000; Shao et al., 2001; Didion et al., 2009c). As input the model requires monthly means and standard deviations of temperature and precipitation as well as their cross-correlation (Bugmann, 1994).

The model allows to account for the effect of slope and aspect on the amount of incident radiation, which affects evapotranspiration (cf. section 3.3.3 in Bugmann, 1994 and references therein). The parameter *kSLAsp* [-2...+2] is used to modify
potential evapotranspiration (PET; Bugmann, 1994, eq.[3.74]) by decreasing PET by a maximum of 12.5% on steep north-facing slopes ($k_{SLAsp} = -2$) and by increasing PET by a maximum of 25% on steep south-facing slopes ($k_{SLAsp} = +2$).

In this study we used the most recent model version 2.9.6 (Didion, 2009) that was supplemented by a refined relationship between browsing pressure ($k_{BrPr}$) and browsing-induced mortality of seedlings up to 1.27 cm dbh ($k_{BrP}$). In addition, the species-specific sensitivities to browsing ($k_{Brow}$) were revised based on an extended literature search and expert opinion (cf. Appendix III in Didion, 2009). It is important to note that the mortality rate due to browsing as included in FORCLIM (i.e., $k_{BrP}$, Fig. 1) encompasses all browsing-related mortality during the lifespan of a tree as seedling before reaching a dbh of 1.27 cm.

The model includes 30 European tree species (Fig. 1) and assumes unlimited seed availability of all species. As Castanea sativa is mostly absent in the northern part of the Swiss Alps (EAFV and BFL, 1988; Brassel and Brändli, 1999), we assumed that this species will remain absent due to its heavy seeds. Thus, we excluded C. sativa from the species pool at the two transects in the Western (i.e., Anniviers valley) and Eastern (i.e., Tuors valley) Central Alps. In the Southern Alps (i.e., Maggia valley),
however, *C. sativa* is a common tree species and was therefore included in the species pool for the simulations. Since the three *Quercus* species that are included in the model, i.e., *Q. petraea*, *Q. pubescens* and *Q. robur*, have similar traits and are known to hybridize (Aas and Friedrich, 1991), we subsumed them under *Quercus* spp. in the presentation of the results. Similarly, we combined *Acer campestre* and *A. platanoides* as *Acer* spp.

### 2.3. Climate data

#### 2.3.1. Current climate

We obtained monthly data for mean temperature and precipitation sum from the database of the Land Use Dynamics Research Group at the Swiss Federal Institute for Forest, Snow and Landscape Research. The database contains climate data for the period from 1960 to 2006 interpolated to a 1-hectare grid across Switzerland based on the DAYMET model (Thornton et al., 1997). In order to derive temperature and precipitation data representing the current climate along each valley transect, we used the following procedure: First we selected from the respective catchment area those 1-ha grid cells that were within the altitudinal range of the transect and aggregated them into 50-m elevation bands. This resulted in a dataset of daily mean temperature and precipitation sum representative for each 50-m elevation band. We then calculated for each of those elevation bands the long-term monthly means (1961-2006), standard deviations and cross-correlations of mean temperature and precipitation sum (Fig. 2 and Table 1). This approach eliminated potential inaccuracies occurring when single grid cells (i.e., only those intersected by a transect) are chosen from interpolated climate data.

To represent the change in aspect and slope along the transects, we used the model parameter $k_{SLAsp}$ (cf. section 2.2). Using the number of 50-m elevation bands on the north- and south-facing slopes, we linearly interpolated the range of $k_{SLAsp}$ on each slope from north facing top ($k_{SLAsp} = -2$) passing the valley bottom ($k_{SLAsp} = 0$) to the south-facing top ($k_{SLAsp} = +2$).

Due to differences in topography, the transects in the three valleys comprised different numbers of 50-m elevation bands: 68 data points for the transect in the Anniviers valley, 42 in the Tuors valley and 75 in the Maggia valley.
Figure 2. Long-term annual mean temperature and precipitation sum by 50-m elevation bands in the three examined catchments based on interpolated climate data from 1960 to 2006 obtained from the Land Use Dynamics Research Group at the Swiss Federal Institute for Forest, Snow and Landscape Research.

2.3.2. Future climate

To represent the anticipated change in climate in each of the three study regions, we used the most recent regionalized climate change data derived from the ENSEMBLES dataset (Hewitt and Griggs, 2004) of the Institute for Atmospheric and Climate Science, ETH Zürich. For this dataset, projected global climate change for the A1B scenario of the IPCC AR4 (IPCC 2007) was regionalized to a 10 by 10 km grid, and transient climate change was simulated until the year 2099.

We derived climate change scenarios for each transect based on the data from the nine 10 by 10 km cells of the ENSEMBLES dataset that covered and surrounded each study area. We used the periods from 1961 to 1990 as baseline and the years 2075 to 2099 as representative years for the future climate and calculated based on the average monthly temperature and precipitation sum of these two periods:

- temperature anomalies for the seasonal mean (Table 1) and the standard deviation of the seasonal mean using the absolute difference between baseline and future temperatures;
- seasonal precipitation anomalies as the relative difference (percent) between the baseline and the future precipitation both for the mean and the standard deviation;
- the anomalies of the monthly cross-correlations using the absolute difference between the corresponding values for the two periods (baseline and future climate).

The anomalies of the means, standard deviations, and cross-correlations were added (in case of absolute differences) and multiplied (in case of relative differences) to the
current climate (section 2.3.1), and the weather generator of FORCLIM (cf. Bugmann, 1996) was used to derive realizations of a future climate along the three transects. We assumed that the climate changed linearly between the baseline (1961-1990) and the future (2075-2099) and did not change after 2099.

2.4. Simulation experiments

Forest succession for a total of 6100 years was simulated for each plot along the three transects, as follows:

2.4.1. Spin-up for 3000 years under current climate

Starting from bare ground, forest succession was simulated for 3000 years under current climate to ensure that the model was in equilibrium with climate prior to imposing scenarios of changes in browsing and climate. The browsing pressure $kBrPr$ was assumed to be 20% (Fig. 1), which represents a moderate intensity considering that the time for seedlings to grow to 1.27 cm dbh can be several decades in montane and subalpine conditions (Ott et al., 1997; Motta, 1999). This spin-up simulation was used for all of the following scenarios in order to have identical starting conditions for the browsing and climate change scenarios.

2.4.2. Browsing and climate change scenarios

Following the spin-up, browsing pressure was varied in a one-step fashion using three settings:

- 20% for a “moderate” browsing intensity;
- 80% for an “elevated” browsing intensity; and
- 95% for a “high” browsing intensity.

In order to separate the effects of browsing and climate change, one set of simulations was done only varying browsing pressure but using current climate conditions. A second set of simulations was performed by varying browsing pressure in combination with a change in climate.

We assumed the changes in climate to occur in a linear fashion, whereby the transient climate change was simulated over a period of 100 years, i.e., starting after the spin-up (year 3000) and reaching the new steady climate (future climate, section 2.3.2) in the simulation year 3100. The simulations were then continued with this new climate state for another 3000 years to obtain forests that are in equilibrium with this specific realization of future climate.
3. Results

3.1. Dry and warm continental climate

3.1.1. Current climate

Based on the control run with no change in browsing and climate, the forests in the bottom of the Anniviers valley consisted mainly of drought-resistant *Pinus sylvestris* and *Quercus* spp. (Fig. 3a). On the south-facing slope, these species disappeared with increasing elevation and were replaced by *P. cembra*, which dominated at high elevations together with *Larix decidua* as co-dominant species; upper treeline was not reached on the south-facing slope (Fig. 3a). On the north-facing slope, *Quercus* spp. and *P. sylvestris* were replaced with increasing elevation by deciduous species such as *Fagus sylvatica* intermixed with *Abies alba*, and further up by *Picea abies*, which dominated the high-montane and subalpine plots between ca. 1700 and 2200 m. *P. cembra* and *L. decidua* dominated a small elevation band just below treeline, which was reached at ca. 2400 m on the north-facing slope (Fig. 3a).

Total basal area varied along the transect from <1 m$^2$/ha at upper treeline (ca. 2400 m a.s.l., north-facing slope) to approximately 35 m$^2$/ha in the *P. abies* dominated montane belt on the north-facing slope of the transect (Fig. 3a). On the south-facing slope, basal area amounted to approximately 30 m$^2$/ha in the montane belt, and approximately 20 m$^2$/ha at the highest elevation (2300 m, Fig. 3a). Basal area in the lower and drier parts of the valley transect was relatively low, varying between 20 and 25 m$^2$/ha (Fig. 3a).

3.1.2. Effect of changes in browsing

On many plots along the transect, changes in browsing pressure led to shifts in the relative and absolute abundance of the dominant and sub-dominant species (Fig. 3b, c), whereby *A. alba*, *F. sylvatica* and *P. cembra* were affected most. The resulting loss in basal area was not fully compensated by other species. Therefore, the magnitude of the decrease in basal area was not uniform along the transect, ranging from <1 m$^2$/ha (treeline on the north-facing slope) to 15 m$^2$/ha (south-facing slope; Fig. 3a-c). Interestingly, although *Quercus* spp. are sensitive to browsing (*kBrow* = 4, Fig. 1), they remained part of the forest community even under high browsing pressure. As light-demanding species, they profited from the increased light availability in the intensively browsed forests (Fig. 3c).
3.1.3. Effect of changes in climate

Keeping browsing pressure constant at a moderate intensity but changing the climate resulted in a collapse of the forest in the valley bottom, where only *P. sylvestris* was able to survive in some plots (Fig. 3d). On the south-facing slope, the *Quercus* spp.-*P. sylvestris* forests were found at much higher elevations (Fig. 3d) compared to the scenario of no climate change (Fig. 3a). The species that currently form the upper
treeline (*P. cembra* and *L. decidua*) disappeared almost entirely on the south-facing slope (Fig. 3d).

The changes in species composition due to climate change were even more pronounced on the north-facing slope, where new forest types had formed in the lower montane belt that were dominated by *Tilia cordata* and *Quercus* spp. (Fig. 3d). With increasing altitude, *F. sylvatica* replaced *T. cordata*. *Picea abies* dominated at elevations above ca. 2200 m (Fig. 3d), including plots that were above treeline under current climate (control run, Fig. 3a).

Due to climate change, basal area dropped sharply from more than 20 m²/ha to 5 m²/ha or less in the valley bottom (Fig. 3d). The *Quercus* spp.-*P. sylvestris* forest (Fig. 3d) that developed on the south-facing slope had a somewhat lower basal area than the *L. decidua*-*P. cembra* forest under current climate (Fig. 3a). However, climate change resulted in higher basal area at high elevations on the north-facing slope (Fig. 3d).

### 3.1.4. Effect of changes in browsing and climate

An increase in browsing pressure in addition to climate change led again to a strong reduction in *A. alba* and *F. sylvatica* but not of *Quercus* spp. (Fig. 3e, f). Furthermore, browsing exacerbated the collapse of the forests in the valley bottom (Fig. 3e, f and 4c, d).

Elevated browsing pressure delayed forest development above current treeline on the north-facing slope (Fig. 4e, f), so that at the end of the climate transition (100 years after spin-up), basal area was about twice as high under moderate browsing (Fig. 4e) compared to elevated browsing (Fig. 4f). Additionally, elevated browsing pressure reduced total basal area by approximately 10% (Fig. 4f) compared to moderate browsing (Fig. 4e). After 3000 years under the new climate and moderate browsing, the forest at the elevation of current north-facing treeline was mainly composed of *P. abies* with some *A. alba*, which are typical for the current montane level (Fig. 3d). Under elevated and high browsing pressures, however, *A. alba* was not able to persist (Fig. 4f).

On the south-facing slope, the climate change-induced transition from the current subalpine *L. decidua*-*P. cembra* forest to a *Quercus* spp.-*P. sylvestris* forest took place over several centuries as *P. cembra* was gradually replaced by new species irrespective of the browsing scenario (Fig. 4a, b). Increased browsing pressure (Fig. 4b) resulted in more *P. montana* but less *P. cembra* compared to the moderate browsing pressure (Fig. 4a).

The effect of browsing on basal area along the transect after 6100 years was more pronounced in the scenarios with climate change (Fig. 3d-f) than without climate
change (Fig. 3a-c). The decrease in basal area was on average ca. 4 m²/ha or ca. 20% for an increase from moderate to elevated browsing regardless of the climate, but was more variable under climate change (6-78% relative decrease) along the transect than in scenarios without climate change (5-37% relative decrease).

Figure 4. Forest succession over time in the Anniviers valley for moderate ($kBrPr = 20\%$) and elevated browsing pressure ($kBrPr = 80\%$) on the two highest plots on the south-facing (a, b) and the north-facing slope (e, f), and for the lowest plot in the valley bottom (c, d). Dotted lines indicate the end of the spin-up period under current climate coinciding with the start of the climate transition (i.e., first line at simulation year 3000) and end of the climate transition period in simulation year 3100 (second line). Species legend as in Fig. 2.

Total tree numbers differed by a factor of more than two between moderate and elevated browsing pressure at the south-facing slope and in the valley, both directly
after the end of the transition to the new climate (i.e., simulation year 3100) and after 3000 years of further forest growth (i.e., simulation year 6100, cf. Table 2). Model behavior near the north-facing peak was different, as it was above treeline under current climate; although basal area was developing at a lower rate under high browsing pressure (Fig. 4e, f), the number of trees was not affected by browsing after 100 years of climate transition (Table 2). The 115 trees ha\(^{-1}\) that were estimated by the model for the north-facing peak (Table 2) are an artifact of the model simulations due to the representation of the establishment process; small trees were established if climate permits, even if they are not able to persist: their total basal area amounted to merely 0.03 m\(^2\)/ha.

Table 2. Total tree numbers per hectare on the two highest plots on the south-facing and north-facing slopes and on the plot in the valley bottom for all three transects under moderate (i.e., 20%) and elevated (i.e., 80%) browsing pressure. Data are presented for current climate (i.e., year 3000), after the transition to the new climate (i.e., year 3100) and after additional 3000 years under the future climate (i.e., year 6100). * indicates plots above treeline where trees can establish but not persist, which resulted in the reported numbers of very small stem.

<table>
<thead>
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<th>Year</th>
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<th>moderate</th>
<th>moderate</th>
<th>elevated</th>
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<td>435</td>
<td>1671</td>
<td>802</td>
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<td></td>
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<td>525</td>
<td>215</td>
<td>246</td>
<td>73</td>
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<td></td>
<td>North-facing (2564 m)</td>
<td>115*</td>
<td>1213</td>
<td>1160</td>
<td>838</td>
<td>603</td>
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<tr>
<td>Tuors valley</td>
<td>South-facing (2715 m)</td>
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<td>1776</td>
<td>1076</td>
<td>810</td>
<td>561</td>
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<td></td>
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<td>1713</td>
<td>1002</td>
<td>2006</td>
<td>1318</td>
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<tr>
<td></td>
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<td>20*</td>
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<td>1174</td>
<td>707</td>
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<td>682</td>
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<td></td>
<td>North-facing (2061 m)</td>
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<td>964</td>
<td>645</td>
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3.2. Moist and cold continental climate

3.2.1. Current climate

In the Tuors valley, forests did not grow along the whole transect, as the cold treeline was reached on both the south-facing and the north-facing slopes at ca. 2400 m (Fig. 5a). Treeline forests were formed by *L. decidua* and *P. cembra*, while *P. abies* dominated the forests towards the valley bottom (Fig. 5a). Basal area reached a maximum of approximately 38 m\(^2\)/ha in the valley bottom and gradually decreased until treeline was reached (Fig. 5a). Similarly to the Anniviers valley, trees were able to establish above treeline (Table 2), but unable to grow.
3.2.2. Effect of changes in browsing

In the scenarios assuming no change in climate but variation in browsing pressure, particularly the plots above 2000 m elevation were affected, where the basal area of *L. decidua* more than doubled from moderate to high browsing pressure (Fig. 5b, c). Nevertheless, an increase in browsing pressure from moderate to elevated browsing led to a decrease of total basal area on plots below treeline, averaging ca. 3 m²/ha or ca. 15% (Fig. 5a, b). Particularly, high browsing pressure led to a decrease in the basal area of the dominant *P. abies* (Fig. 5c), thus leading to a co-dominance of *P. cembra* also at lower elevations (Fig. 5c).

3.2.3. Effect of changes in climate

Climate change caused a shift of tree species by approximately 1000 m upslope. That is, in the scenario without a change in browsing but with climate change, a forest developed at current treeline that is typical for the current forest at the transition from high-montane to subalpine conditions, i.e., dominance of *P. abies* with some *P. cembra* (Fig. 5a, d). Forests covered the entire transect as the cold treeline moved beyond the highest elevations of the transect. In the valley bottom, new forest types developed that were dominated by *F. sylvatica* and *P. abies* (Fig. 5d).

The temporal development of forests above current treeline under the assumed change in climate proceeded in a similar way as on the north-facing peak in the Anniviers valley (Fig. 4e), moving through an early-successional *L. decidua* forest to dominance by *P. abies* interspersed with *P. cembra* trees (results not shown). Below ca. 2500 m, deciduous species including *F. sylvatica*, *A. pseudoplatanus*, *Quercus* spp., and *T. cordata* together with *A. alba* started to replace *P. abies* with the onset of climate change. This resulted in a reduction of the basal area of *P. abies* (Fig. 5a, d) by about 50% after ca. 400-500 years.

3.2.4. Effect of changes in browsing and climate

Browsing pressure had a strong influence on the change in tree species composition following climate change. The increase in browsing pressure led to a decrease of *F. sylvatica* (Fig. 5e, f). Additionally, the abundance of browsing-sensitive but relatively shade-tolerant tree species such as *A. alba* and *A. pseudoplatanus* was reduced strongly, whereas the browsing-sensitive but more light-demanding *Quercus* spp. and *P. cembra* gained in importance with increasing browsing pressure (Fig. 5e, f).

The increase in browsing from a moderate to an elevated level resulted in a decrease of total basal area along the transect by an average of ca. 3 m²/ha, which corresponded to a relative difference of ca. 10%. The reduction in basal area was strongest on the lower
south-facing slope and in the valley bottom, where particularly *F. sylvatica* decreased (Fig. 5d, e).

Tree numbers were higher in the climate change scenario compared to current climate, independent of browsing pressure (Table 2). An increase in browsing pressure from a moderate to a high level led to a reduction in tree numbers by ca. 30% (Table 2).

![Graph showing basal area distribution](image)

**Figure 5.** Transect in the Tuors valley (moist and cold continental climate); for details cf. Fig. 3. The graph displays the results of 42 independent simulations for the elevation plots along the transect (cf. section 2.3).
3.3. Moist and warm insubrian climate

3.3.1. Current climate

Under current climate the simulated subalpine *P. abies* forest in the Maggia valley extended down to ca. 1700 m on both slopes (Fig. 6a). With decreasing elevation, the forest changed gradually to an *A. alba*-*F. sylvatica*-*P. abies* forest, and eventually to a deciduous forest dominated by *F. sylvatica*, *Castanea sativa*, *A. pseudoplatanus*, *Tilia platyphyllos* and *Ulmus glabra* at elevations below ca. 1000 m (Fig. 6a). In the model, favorable climatic conditions allowed the establishment of a forest with a total basal area ranging between approximately 30 m²/ha at the highest elevations to approximately 50 m²/ha in the valley bottom (Fig. 6a).

3.3.2. Effect of changes in browsing

Leaving climate constant while increasing browsing pressure converted the mixed deciduous forests in the valley bottom to stands dominated by *C. sativa* below ca. 1000 m. At higher elevations, *P. abies* increased in dominance (Fig. 6b, c). *Abies alba*, *F. sylvatica*, *A. pseudoplatanus* and *U. glabra* declined with an increase in browsing pressure.

The effect of a change in browsing pressure was not linear as an increase from moderate to elevated browsing resulted in an absolute decrease of, on average, 3 m²/ha (relative decrease 7%) while an increase from elevated to high browsing induced a basal area decrease of, on average, 5.5 m²/ha (relative decrease 14%). The decrease in basal area in response to a change from moderate to elevated browsing pressure was relatively uniform along the transect, ranging from 1 m²/ha (~2% relative decrease) to 5 m²/ha (~11% relative decrease). The effect of an increase from elevated to high browsing was more varied from 2.5 m²/ha (~5% relative decrease) to 9 m²/ha (~23% relative decrease).

3.3.3. Effect of changes in climate

Similar to the results for the Tuors valley, climate change led to an upslope shift of tree species by approximately 1000 m. This species shift resulted in a replacement of the former *P. abies* forest by an *A. alba*-*F. sylvatica*-*P. abies* forest at the highest plots and below by a deciduous forest dominated mainly by *F. sylvatica* and *C. sativa*, intermixed with *Acer* spp., *A. pseudoplatanus*, *Carpinus betulus*, *Fraxinus excelsior*, *T. platyphyllos*, and *U. glabra* (Fig. 6d). The shift from a conifer dominated forest to a mixed deciduous forest was accompanied by an increase in basal area at the high-elevation plots (Fig. 6d).
In the valley bottom, *Castanea sativa* became dominant at the cost of *F. sylvatica*, but also *T. cordata* and *Quercus* spp. increased (Fig. 6d).

![Graphs showing the effects of moderate, elevated, and high browsing pressures on basal area distribution across different slopes and elevations.](image)

**Figure 6.** Transect in the Maggia valley (moist and warm insubrian); for details cf. Fig. 3. The graph displays the results of 75 independent simulations for the elevation plots along the transect (cf. section 2.3).

### 3.3.4. Effect of changes in browsing and climate

Similar to the simulations with an elevated browsing pressure alone (Fig. 6c), an increase in browsing pressure together with climate change resulted in a more pronounced dominance of *C. sativa* leading to almost pure *C. sativa* stands (Fig. 6e, f). In contrast to the control runs without climate change, however, *C. sativa* reached...
higher elevations (Fig. 6c, f). Plots at elevations higher than ca. 2000 m were an interesting exception regardless of the level of browsing pressure. At these elevations *C. sativa* growth was strongly limited due to low winter temperature and low degree-day sums. On these plots, the decrease of *F. sylvatica* due to the increase in browsing was not compensated by other species, which resulted in a reduction of total basal area (Fig. 6e, f).

The effect of an increase in browsing on total basal area along the transect was similar to the scenarios of no climate change. Total tree numbers were reduced by more than a third under elevated browsing pressure compared to numbers under moderate browsing pressure in both the valley and the high elevation plots (Table 2).

3.4. Common pattern

With increasing browsing pressure, basal area decreased (Figs. 3, 5, 6), and so did total tree numbers (Table 2). In all three valleys, browsing pressure led to a reduction of the abundance of *A. alba* and *F. sylvatica*, while interestingly some browsing-sensitive but more light-demanding species such as *P. cembra* and *Quercus* spp. did not suffer correspondingly.

Climate change led to an upslope shift of species and of the cold treeline. In the valley bottom the current forest types were substituted by deciduous trees in the two valleys with moist climate and non-forest vegetation in the dry Anniviers valley. Furthermore, climate change resulted in the formation of new forest types along all transects (Figs. 3, 5, 6).

Browsing partially counteracted the effects of climate change, for example by retarding forest development at the cold treeline (Fig. 4e, f), but it did amplify the effects of climate change in other plots, for example by exacerbating the collapse of forests near dry treeline (Fig. 4c, d).

Due to the slow nature of forest dynamics, the differences between forests simulated under current climate and those after 100 years of transient climate change were still small (Fig. 4a). Plots near current treelines were exceptions, as large changes in tree number and basal area were simulated due to climate change-induced shifts at the cold (Fig. 4e) and the dry treeline (Fig. 4c).

4. Discussion

4.1. Current climate

Generally, the model simulated the expected forest types for the current climate accurately (cf. sections 2.1, 3.1.1, 3.2.1 and 3.3.1). The dominant species of the
different elevation bands from the colline, the montane to the subalpine level were reproduced accurately with two exceptions. First, at mid-elevations on the south-facing slope in the Anniviers valley, *P. abies* forests would have been expected (Ott et al., 1997; Gödickemeier, 1998). The missing *P. abies* belt on this south-facing slope was either due to an overestimation of drought, which in the model strongly limits the establishment and growth of this species, or to an underestimation of its drought tolerance (cf. Table A-10 in Bugmann, 1994; Ellenberg, 1996). Second, at low elevations in the Maggia valley, the proportion of *Quercus* spp. should have been higher, reflecting the extended dry periods in summer that limit the competitiveness of other deciduous species, particularly *F. sylvatica*. This anomaly was probably due to the fact that the monthly climate data used in the model do not fully capture the very high variability of soil moisture in this part of the Alps, where short thunderstorms often bring heavy precipitation followed by extended periods of drought.

4.2. Effect of changes in browsing

First and foremost, increased browsing caused a reduction in total basal area in all three valleys (Figs. 3, 5, 6), whereby an increase in browsing pressure from “elevated” to “high” levels typically caused a greater (i.e., average ca. 14 - 40% depending on the study region) decrease in basal area than a shift from moderate to elevated browsing pressure (i.e., average ca. 7 - 25% depending on the study region). This finding is not surprising, as it is based on a non-linear function in the model (Fig. 1), but it still corroborates results from other studies that changes in browsing can result in non-linear effects in forest attributes (e.g., Kienast et al., 1999; Didion et al., 2009a).

Second, the impact of changes in browsing pressure on the basal area of individual species and thus on the species composition differed strongly between regions. Particularly in the Anniviers and the Maggia valleys, changes in browsing intensity caused strong shifts in the composition of the dominant species: for example, forests in the valley bottom in the Anniviers valley changed from a co-dominance of *P. sylvestris*, *Quercus* spp. and *T. cordata* to pure *P. sylvestris* stands (Fig. 3a-c); forests in the Maggia valley changed from *F. sylvatica* dominated stands to *C. sativa* dominated stands (Fig. 6a-c, d-f). In contrast, the effect of changes in browsing intensity was less pronounced in the Tuours valley although the simulated browsing intensities were identical in all three valleys. Thus we conclude that the impact of changes in browsing intensity on species composition cannot be extrapolated from one region to others but must rather be evaluated on a regional basis.

Third, we sometimes found a positive effect of an increase in browsing pressure on the basal area of shade-intolerant species such as *L. decidua* (Figs. 3a-c; 5a-c; 6a-c) and *P. montana* (Fig. 3a-c). These species profited more from the improved light conditions
that were induced by the decrease in total basal area than they suffered from the direct effects of browsing. For similar reasons, the reduction in the basal area of the light-demanding *Quercus* spp. differed between the north-facing and the south-facing slopes in the Anniviers valley (Fig. 3a-c). On the north-facing slope, establishment and growth of *Quercus* spp. was limited under moderate browsing by low light availability due to the highly shade-casting canopy of *P. abies, A. alba* and *F. sylvatica* (Ellenberg, 1996). Under higher browsing pressure, the growth of *Quercus* spp. profited from the higher light availability due to the decrease in the basal area of those shade-casting species. In contrast, on the south-facing slope *Quercus* spp. were not light-limited under moderate browsing because the co-occurring *P. sylvestris* had lower basal area and canopy density (Ellenberg, 1996). Thus, on the south-facing slope *Quercus* spp. grew under similar light conditions in all three browsing scenarios, but establishment and hence basal area was increasingly limited when browsing increased. Thus, we conclude that species interactions can strongly modify the net response of tree species to changes in the browsing regime.

Lastly, our results indicate that browsing could cause a decrease in total tree numbers by a factor greater than two (Table 2). A reduction of tree numbers in response to browsing is typically accompanied by a change in the diameter structure of the forest both in the model (cf. Didion et al., 2009a) and in reality (cf. Ammer, 1996; Rossel et al. 2005). Such structural changes influence the light regime and hence subsequent regeneration and growth dynamics (cf. Ammer, 1996; Rossel et al. 2005; Didion et al., 2009a). Improved light conditions can favor light demanding tree species, as seen for *L. decidua, Pinus montana* and *Quercus* spp. Thus, browsing affects species diversity not only directly through the processes of selective feeding, but also indirectly by the alteration of the light regime (cf. Figs. 3-6; Ammer, 1996; Rooney and Waller, 2003; Vavra et al., 2007). These considerations are highly important because in mountain terrain, changes in species composition, forest structure and basal area affect key forest functions such as the protection against avalanches or rockfall (Brang et al., 2001; Dorren et al., 2004; Frehner et al., 2005).

### 4.3. Effect of changes in climate

For the three climatically different valleys, the simulations showed that climate change caused shifts in tree species ranges towards higher elevations (Figs. 3, 5, 6), which is congruent with observed changes in a variety of taxonomic groups and different geographic locations (Kullman, 2001; Walther et al., 2002). Our approach of simulating forest development along a number of valley transects demonstrated the absence of gradual movements of forest types (communities) along the transects (e.g., Fig. 3a vs. 3d with a new *Tilia*-dominated forest). Also, the legacies of the forests that
had developed under current climate sometimes strongly affected successional dynamics during and after climate change (Figs. 3, 5, 6). For example, on the south-facing peak in the Anniviers valley, *Pinus cembra* first increased in basal area under climatic change before decreasing to sub-dominant status (Fig. 4). This initial increase, which is contrary to the fact that the species is less competitive under the new climatic conditions, is a legacy effect, which can delay the establishment of new species at given locations (cf. Davis, 2001).

For a warming of 3.6 to 5.9°C (Table 1), an elevational shift of 600 to 1000 m could be expected for a lapse rate of 0.6 °C per 100 m elevation (cf. Theurillat and Guisan, 2001). The simulated species shifts were generally within this range (Figs. 3, 5, 6). Since the model assumes unlimited seed supply, i.e., it does not address barriers to migration and seed dispersal (cf. Theurillat and Guisan, 2001), establishment rates and thus the speed of the upslope shifts are certainly overestimated. Due to the model assumption that soils are always suitable for tree growth, colonization rates for areas well above the current climatic treeline may also be too high. However, land use has been a major driver for the position of the treeline in the Swiss Alps (cf. Gehrig-Fasel et al., 2007), and the existence of alpine meadows and pastures can be expected to be conducive to the establishment of forests after cessation of grazing (Ott et al., 1997).

The replacement of the current high-montane and subalpine forests that are poor in tree species by more diverse mixed forests under a warmer climate (Figs. 3, 5, 6) may be considered positive in terms of biodiversity. However, there will be strong reductions in the area available for alpine species, thus resulting in a higher risk of local extinctions of these species (e.g., *P. cembra*, Fig. 2d) due to the phenomenon of “summit traps” (cf. Theurillat and Guisan, 2001; Pertoldi and Bach, 2007). At the other end of the gradient, increasing drought risks can lead to the collapse of forests in some areas and steppe formation (Fig. 4c), resulting in a loss of forest species and habitats in these areas (cf. Davis and Shaw, 2001; Theurillat and Guisan, 2001) or an influx of invasive species (cf. McCarty, 2001; Hampe and Petit, 2005). The consequences of the outlined processes need to be considered with regard to the change of forest cover and stand types and the consequences for ecosystem services such as timber production and habitat (Millennium Ecosystem Assessment, 2005), but also protection from avalanches and rockfalls (Brang et al., 2001; Dorren et al., 2004; Frehner et al., 2005).

### 4.4. Effect of changes in browsing and climate

Typically, the combined effects of climate change and browsing on total basal area along the transects was compensatory, as the reduction in basal area induced by an increase in browsing pressure was lower in the case of climate change than under
current climate. The combined effects of climate change and browsing on species composition, however, suggested a dominance of non-compensatory effects. For example, an increase in browsing enhanced the dominance by *C. sativa* that followed climatic change in the Maggia valley or led to a species shift (to *Quercus* spp. rather than to *F. sylvatica*) at low elevations in the Tuors valley. Thus, an evaluation of the joint effects of climate change and browsing needs to consider species-specific direct (e.g., selective browsing, climatic range) and indirect (e.g., light regime, competition) effects.

Browsing as a “bottom-up” driver of forest dynamics influences tree establishment and thus tree numbers (cf. Table 2; Cairns and Moen, 2004) as well as species composition (Figs. 3-6). Climate change as a “top-down” process, however, primarily controls the suite of species that is able to establish and affects tree growth and productivity of a forest, as demonstrated by the changes in basal area (cf. Figs. 3-6; Motta et al., 2006). These different drivers controlling tree numbers, species composition and basal area led to the strong combined effect of browsing and climate change as shown in our modeling study, but also in field studies, e.g., in northern Sweden (Cairns and Moen, 2004) and Canada (Tremblay et al., 2007). For the migration of species in response to climate change, browsing thus presents a significant factor. Close to treelines, where forests are highly sensitive to disturbance (Davis and Shaw, 2001; Hampe and Petit, 2005), the effect of browsing can be expected to be most pronounced. For example, we found that browsing exacerbated the climate-induced collapse of forests at the dry treeline, (Fig. 4c, d), whereas it delayed the upward shift of the cold treeline by several decades (Fig. 4e, f).

### 4.5. Methodological considerations

We used only one regionalized data set for one climate change scenario (A1B, cf. IPCC 2007), because our focus was on the joint effects of climate change and browsing intensity rather than a comprehensive analysis of the range of responses under various climate scenarios. While it is likely that other climate scenarios would have shown somewhat different responses of forest ecosystems in the examined valleys, we expect that the demonstrated interactions of climate change and browsing pressure would not vary strongly between climate change scenarios. We therefore conclude that the results from our study characterize the importance of browsing when dealing with the response of forest ecosystems to climate change. Clearly, our results should not be mistaken as predictions of the future state of these systems, but rather as an evaluation of the importance of the processes shaping the long-term population dynamics of forests trees.
5. Conclusion

Our study showed that climate change can result in large changes in tree species composition, forest basal area and stem numbers, confirming results from previous modeling studies (e.g., Lexer et al., 2002; Bugmann, 2003; Wallentin et al., 2008). We could substantiate the expected upward shift of tree species (Davis and Shaw, 2001; Theurillat and Guisan, 2001; Walther et al., 2002) by examining forest development along a continuous elevation transect in three climatically different zones of the Swiss Alps. We did not usually find a concurrent movement of today’s stand types, but rather remarkable changes in the species composition and the development of new stand types.

The simulated shift in tree species ranges due to changes in climate and browsing pressure resulted in changes in habitat types that present major challenges for the management of mountain forest ecosystems. Management practices designed for current forests based on the historical variability in the ecosystem may no longer be appropriate (Millar et al., 2007), and alterations in the species composition and the succession to new stand types need to be addressed.

Furthermore, by investigating different browsing regimes, we conclude that while climate change may partially compensate for browsing-induced reductions in basal area, the combined effect of climate change and browsing on the mix of tree species and forest types will probably differ between locations, as browsing selectively excludes species from establishing or reaching dominance (Rooney and Waller, 2003; Côté et al., 2004). The responses we found ranged from compensation to enhancement, but they also involved unanticipated feedback loops (e.g., via light availability). Ungulate browsing is only one form of herbivory affecting tree regeneration; other forms of herbivory, for example by insects (Price et al., 2001; Payette and Delwaide, 2003; Moen et al., 2004), are expected to add further to the impact of browsing. Since management decisions today have long-term implications with regard to forest succession under climate change (cf. Millar et al., 2007), there is an urgent need for adaptive management strategies that address the combined effects of climate change and both large and small-scale disturbances such as herbivory.

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Synthesis

In this dissertation, I used a modeling approach to examine the role of ungulate browsing on the species composition and diameter frequency distribution in mountain forests. In this part, I discuss the findings of this dissertation in the context of my four initial objectives, which were to examine

1) the degree of accuracy of the models FORCLIM and PICUS in simulating browsing-related impacts on forest development;
2) the sensitivity of forest species composition and diameter frequency distribution to changes in tree regeneration;
3) the probable impacts of ungulate browsing on tree species composition and structure in forests over decades and centuries;
4) the joint effects of ungulate browsing and climate change on long-term forest succession.

Finally, I discuss research needs that arose from my dissertation work with regard to the further development of the FORCLIM model in addition to general challenges in modeling the role of browsing for forest succession.

1. Accuracy of the models FORCLIM and PICUS in simulating browsing-related impacts

The two versions of FORCLIM as well as PICUS v1.4 satisfactorily reproduced the measured species composition in the basal area of trees >12 cm diameter at breast height (dbh) for 15 different forest types in the Swiss Alps (cf. part 2). Nevertheless, FORCLIM v2.9.1 and 2.9.3 tended to overestimate species diversity, while PICUS tended to simulate species-poor forests with partly unrealistic successional patterns at the early stage of succession.

The fact that all three models simulated accurately the dominant species at the scale of the Swiss National Forest Inventory confirmed my initial decisions regarding a) the use of gap models based on their ability to simulate many species for different site conditions, and b) the selection of three frequently used models with particular strengths to simulate forest dynamics in Central Europe.

However, all three models had a rather poor performance in the simulation of trees between 1.27 and 12 cm dbh (subsequently called “juvenile trees”). This was highly discouraging with regard to my main aim to improve the understanding of the long-
term effect of changes in regeneration patterns on forest development. Since juvenile trees comprise the development stage immediately after the sapling stage that is directly affected by browsing, an accurate simulation of juvenile trees is a key to confidently evaluate browsing impacts on the long-term development of whole stands.

As presented in part 3, I was able to considerably improve the FORCLIM model (leading up to version 2.9.5) with regard to its accuracy of representing crown properties and thus the light environment in a forest patch, which led to a more accurate representation of measured tree numbers and encouraging results in simulations of Swiss forest research plots over several decades as well as European potential natural vegetation. Because the long-term forest research data (Zingg et al., 1999) had not been collected with the aim of model development or validation, they are prone to several limitations in my context. These limitations include a) only trees >8 cm dbh were measured; b) the stands usually consist of only 2-5 species; and c) regular thinning had taken place (Plenterwald). Thus, an analysis of model performance with regard to trees <8 cm dbh was not possible. Furthermore, due to the regular management and the low tree species diversity, these research plots were not representative of natural forests that had been the target of almost all earlier FORCLIM applications. The model evaluation was thus limited in this regard. It would have been valuable to employ data from unmanaged stands such as the ETH forest reserve network (Brang et al., 2008). However, these data have become available during the course of my dissertation only (Heiri, 2009; Heiri et al., 2009; Heiri et al., in prep.), and they will certainly prove highly valuable for further work with the model.

2. Sensitivity of tree species composition and diameter frequency distribution to changes in regeneration

Following the good performance of FORCLIM v2.9.5 with regard to its local accuracy and its generality, albeit based on limited data (cf. above), I decided to subject the model to a sensitivity analysis to investigate a) the sensitivity of the model to changes in the formulation of tree establishment and b) the potential impacts of ungulate browsing on forest species composition and structure over decades and centuries.

FORCLIM v2.9.5 was more sensitive with regard to the establishment of small trees compared to FORCLIM v2.9.3 (cf. part 3). However, the sensitivity of simulated tree numbers to changes in browsing-related formulations and model parameters decreased with increasing dbh, and tree numbers >51 cm dbh had a very low sensitivity to the simulated changes in ingrowth patterns (cf. part 4). Qualitatively, this pattern conforms to theoretical expectations, as small-scale effects are usually dampened at the level of the forest stand (e.g., Körner, 2006) by negative feedback loops. Quantitatively, however, this response appeared exaggerated, thus prompting questions on its cause.
The highly similar species composition and numbers of trees > 51 cm that were simulated by the model for a range of different ingrowth scenarios under otherwise identical conditions (i.e., climate, soil nutrient and moisture status) suggested that an overly strong mortality of sub-dominant trees are causing this anomalous behavior. Due to the fact that the number and composition of juvenile trees was highly sensitive compared to larger trees (cf. part 4), the processes following tree establishment, i.e., growth and/or mortality, must be overly limiting, thus essentially annihilating the large variations in the ingrowth of small trees.

Unfortunately, I was not able to investigate in more detail the causes for the diverging pattern in model sensitivity between juvenile and large trees due to time constraints. I hypothesize that this behavior is at least partly due to either an overestimation of the maximum species-specific longevity or an underestimation of the fraction of trees that reach this species-specific maximum longevity; particularly the species-specific values in relation to other species needs to be considered (e.g., *F. sylvatica* vs. *C. sativa*). Both would result in an overestimation of the number and probably also the size of dominant trees. This in turn reduces light availability for sub-dominant trees in a pathological manner, which limits their growth rate and causes enhanced stress-related mortality of sub-dominant trees. My dissertation provides evidence that the lower sensitivity to regeneration processes of FORCLIM compared to other gap models, i.e., FORECE (Kienast et al., 1999) and FORSKA (Prentice et al., 1993), is most likely unrealistic and warrants further attention.

3. Probable impacts of ungulate browsing on tree species composition and forest structure over decades and centuries

I used a novel approach to examine the effect of browsing intensity on forest dynamics by imposing temporal fluctuations rather than assuming a constant intensity as in previous modeling studies, and I believe that this contributed most to the value of the sensitivity analysis presented in part 4. I found that the resulting “windows of opportunity” for the establishment of tree species that are highly sensitive to browsing can strongly dampen browsing-related reductions in the abundance of such species (cf. part 4). These findings support the view that management practices that aim at constant animal densities may not be generally appropriate. I am confident that this result is robust, independent of the limitations of an overestimated mortality in the model (see above), and that there is indeed a need to re-evaluate management practices. Furthermore, my analyses confirm that over decades to centuries, herbivory can cause shifts in species composition and change tree diameter structure of forest stands (cf. parts 4 and 5). This substantiates the concern of forest managers and ecologists regarding the possible impacts of high levels of herbivory on long-term
forest development. Thus, I conclude that changes in regeneration dynamics as they may result from selective browsing on tree seedlings and saplings by ungulates present a challenge to forest management regarding the maintenance of forest functions, goods and services as far as they depend on specific compositional and structural ecosystem elements.

4. Joint effects of ungulate browsing and climate change on long-term forest succession

Being faced with the decision to spend further efforts on improving the structure of the new model or to use it in an applied context, I pragmatically decided for the latter because the new model, FORCLIM v2.9.5, clearly represented a distinct improvement over earlier versions, such that its application to study the joint effects of browsing and climate change effects appeared appropriate (cf. part 5). This study provided novel insights on the patterns of community re-arrangement based on the individualistic response of tree species to climate change and browsing along elevational transects in several Swiss valleys.

It is expected that anthropogenic climate change will result in an increasing perturbation of ecosystems. Joint effects of and feedbacks between different disturbance types such as large-scale, stand-replacing fires and windthrow may further increase the role of disturbance, rendering forest regeneration and thus factors such as herbivory that modify regeneration dynamics even more crucial than they are today. The findings presented in part 5 demonstrated that a) the upslope movement of tree species in response to global warming is highly sensitive to the establishment and growth of tree saplings, and b) an increase in browsing would have strong impacts on the climate-induced change in forest types and cover.

It is important to note that in model applications like the present one, the scenario data on climate change are based on a model as well. Thus, the accuracy of the simulation results is uncertain not only because of uncertainties in the ecological model, but also because of scenario uncertainties (cf. Bugmann, 2003). Nevertheless, I am confident that the general patterns regarding the joint effects of climate change and browsing presented above and discussed in part 5 are robust. Still, confidence in the results of this study could be increased by, for example, performing additional simulations using further climate scenarios such as A1 and B2 from the IPCC’s 4th Assessment Report (Intergovernmental Panel on Climate Change, 2007), which were not available as regionalized scenarios at the time the present study was conducted.

From the parameter estimation for the revised relationship between browsing pressure and seedling/sapling mortality (cf. Appendix III), which led to FORCLIM version 2.9.6,
a surprising behavior emerged with regard to interactions between tree establishment controlled by browsing and the light regime in the stand (part 5): while an increase in browsing pressure led to the expected reduction of tree numbers and basal area of the highly browsing-sensitive *Abies alba*, it did not do so for *Quercus* spp. although these latter species are also highly sensitive to browsing. In addition, an increased browsing pressure resulted in an increase in the total number and basal area of *Taxus bacata* (*kBrow* = 5, cf. Appendix III).

This counter-intuitive behavior was due to the higher light availability caused by the overall decrease in tree numbers and basal area with increasing browsing pressure. Growth of *Quercus* spp. and *T. baccata* profited from more available light. Moreover, the positive effect of higher light availability for establishment was only partly compensated by the reduction in establishment success due to the increase in browsing. *Quercus* spp. are light-demanding species, and their growth is strongly limited by low light availability, which results in stress-related mortality. If light conditions improve, the model simulates better growth and consequently lower stress-related mortality. Although *T. baccata* is comparatively shade-tolerant in the model, the growth of this species profited from higher light availability because of its very low initial height and low height growth relative to diameter growth (i.e., skinniness parameter *kS*; Risch et al., 2005). Hence from the model logic, this response is consistent and it reflects, albeit exaggerated, the widely postulated mechanism that stressed trees react differently to browsing than trees growing in good conditions (cf. Hilbert et al., 1981; Maschinski and Whitham, 1989; Osterheld and McNaughton, 1991; Wise and Abrahamson, 2007).

### 5. Research needs

#### 5.1. Development of the FORCLIM model

I was able to make a contribution to increase the local accuracy of the FORCLIM model by implementing a more realistic representation of canopy structure (cf. part 3). Based on findings particularly from parts 4 and 5, I perceive the need for several investigations into the performance of the current version of the model, FORCLIM v2.9.6. These follow from the discussion above and are summarized here.

To address the concern of the low sensitivity of the number of large trees and stand basal area in the model, I recommend:

- a) a revision of the assumption of a constant intrinsic mortality and of the species-specific parameter maximum age.
b) an evaluation of the stress-related mortality with regard to differences in mortality probability based on tree age, i.e., assuming that younger trees are able to tolerate more stress than older trees (cf. Keane et al., 2001).

c) an evaluation of the effect of changes in the threshold growth rates for the stress-related mortality, i.e., relative and absolute diameter increment.

d) the implementation of an improved mortality function, e.g., based on the findings by Wunder et al. (2008).

Due to the fact that there are multiple feedbacks between tree growth, mortality and establishment in succession models (as well as in reality), which are mediated primarily through light competition, I propose to firstly evaluate the role of tree mortality before proceeding to growth and establishment. This is because a modification of tree mortality should be geared towards an increased mortality of large, dominating trees. This is likely to lead to increased growth of suppressed trees in the lower and mid-canopy and thus lower mortality of such trees. As a consequence, the sensitivity of the model regarding trees >12 cm dbh could be expected to increase.

In research projects that focus on questions relating to changes in forest composition and development based on biomass or basal area, which are both dominated by the larger trees, I do not perceive an urgent need to consider a modification to the establishment process in the FORCLIM model. This is because the species composition of basal area is only little (cf. results for the site Adelboden, part 4) or not sensitive to browsing at all (cf. results for the sites Davos and Bever, part 4). However, if the focus is on diameter distributions as, for example, in projects that address the protection from natural hazards such as rockfall by forest stands, then the current model version should not be applied before the issues mentioned above have been resolved satisfactorily.

For research that requires accuracy also for juvenile trees, more detail in the regeneration process could be introduced to make a process-based simulation of ungulate effects possible. More detail in the regeneration process can be expected to improve the overall accuracy of the model because of a) a more explicit representation of the competition for resources and the effect of disturbances such as browsing; and b) it would make assumptions such as that of an unlimited seed supply obsolete. However, there may be trade-offs between the available data for implementing more detail, the need for making new assumptions, and the accuracy of the new process formulations in the model. Lastly, the lack of data on growth of seedlings and saplings complicates the introduction of more detail with respect to both a) a change in the formulation of tree establishment in current gap models, i.e., simulation of seedling development into saplings, and b) coupling a gap model with a detailed regeneration model such as HUNGER (Weisberg et al., 2005).
If the introduction of more detail in the regeneration process is not a high priority, the current implementation of the model should still be revised to address the issues discussed above (see also Appendix III). Specifically, I recommend investigating:

a) the combination and relative importance of controlling factors, including browsing, available light, minimum winter temperature, soil moisture and nutrients.

b) the skinniness parameter $k_S$ that determines the initial height of a tree, as it affects the amount of light that is available for a sapling to grow and thus stress-related mortality. The revision of the relationship between tree seedling and sapling mortality and browsing pressure suggested that the parameter value for species that have a very low value could be too low (e.g., *Taxus baccata*, see Appendix III).

c) the values of species parameters that are used to evaluate whether establishment or growth is limited. For example, the establishment of *Pinus sylvestris* and *P. montana* is assumed not to be limited by minimum winter temperature, whereas the cold-tolerant *P. cembra* (Ellenberg, 1996) is limited. Similarly, the parameter values for drought-tolerance of *Quercus petraea* and *Q. robur* are questionable; in the current parameterization, *Q. robur* is more drought-tolerant than *Q. petraea*, which is not consistent with literature data (e.g., Lévy et al., 1992; Gieger and Thomas, 2002). These issues should be addressed because inconsistencies in species parameters can introduce a bias in the performance of species and thus the simulated successional trajectories.

d) the assumption of unlimited seed supply.

e) the effect of fluctuating vs. constant browsing intensities, as addressed in the sensitivity analysis in part 4.

It should be noted that models are deliberate simplifications of reality, and they typically present a compromise with regard to their realism (simulating system behavior based on a qualitatively realistic model structure), accuracy (simulating system behavior in a quantitatively accurate manner), and generality (representing a broad range of system behaviors with the same model). Depending on the research question at hand and thus the purpose of a model, different aspects become important. Thus models are always limited to some degree. This fact should be considered when addressing the research recommendations stated above, especially if the goal is to make the model equally suitable and accurate for simulating dynamics in natural forests on the one hand, and harvesting in managed forests on the other. For applications spanning a large range of forest types from near-natural to intensely managed stands, I perceive that trade-offs on model accuracy will be required.
5.2. Challenges in modeling tree regeneration

A challenge to forest succession modeling is the availability of robust, high-quality data to formulate processes such as tree establishment or mortality and to verify and validate a model. Representative data for tree seedlings and saplings are scarce beyond a few highly specific research sites; this is due to the use of a callipering threshold that typically is in the range of 8 to 12 cm dbh in virtually all forest research and inventory data (cf. part 2). This presents several challenges with respect to the investigation of the significance of changes in regeneration dynamics for forest succession:

a) It presents a limitation to improve our understanding of seedling and sapling survival and growth to mature trees, and thus also to our ability to improve the accuracy of regeneration models.

b) The data are generally not representative enough to allow for an extrapolation to national and landscape scales.

A thorough understanding of the growth and mortality of seedlings and saplings as well as representative data are required for the monitoring of changes in regeneration patterns such as a loss of species due to browsing or other sources that can lead to fundamental alterations in stand structure and composition (cf. part 4).

However, more insight into regeneration processes will probably not reduce the complexity of these process and thus, their implementation in succession models will remain extremely difficult. In particular, the trade-offs between realism, accuracy, and generality (cf. part 3) will continue to present challenges to model development.

The ability to evaluate the risk of changes in successional pathways in response to altered regeneration dynamics is mandatory for informed decision-making in forest management considering the provision of forest functions, goods and services. This applies even more in the light of a change in climate that will result in shifts in species ranges (cf. part 5).

6. Conclusion

Overall, this dissertation contributed to the development and improvement of forest succession models as crucial tools for fundamental and applied research, and it provided new insights regarding the effect of ungulate herbivory on long-term (decades to centuries) forest development.

The model development work towards FORCLIM v2.9.5 addressed an important fundamental question in modeling, i.e., whether general applicability, local accuracy and realism can be reconciled to a certain extent within a single model. These efforts led to a significant improvement in the local accuracy of the FORCLIM model. I was
able to show that model accuracy does not depend on model complexity, which is important since an increase in complexity is typically associated with less tractability, which makes the interpretation of simulation results more difficult.

The results of the sensitivity analysis challenged the management paradigm that aims to maintain constant ungulate densities. For the long-term sustainability of forests, fluctuating animal densities, which would also be expected for natural populations, may be more appropriate. With regard to the combined effect of constant ungulate pressure and climate change, I could show the important role of herbivory on tree species composition, as it exacerbates climate-induced effects typically in a non-linear manner.

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I. History of FORCLIM versions employed in this thesis

FORCLIM versions 2.9.1 (Bugmann and Solomon, 2000) and 2.9.3 (Risch et al., 2005) were described in the respective articles. The major differences between the two versions are (cf. Heiri, 2004; Risch et al., 2005):

- FORCLIM v2.9.3 uses a log-normal distribution for sampling time series of monthly precipitation data from long-term statistical parameters as opposed to the normal distribution used in earlier versions.
- FORCLIM v2.9.3 takes into account that shade-intolerant tree species often produce more seeds under favorable conditions than shade-tolerant ones.
- FORCLIM v2.9.3 features an asymptotic rather than a parabolic height–diameter relationship.

Parallel to the development of FORCLIM v2.9.3, FORCLIM et al. (2007) made modifications to the tree crown representation, resulting in FORCLIM v2.9.4. These two versions were never merged, and only FORCLIM v2.9.3 was translated from the original code in Modula to C#.

FORCLIM v2.9.5 was developed based on the C# implementation of v2.9.3. I have built upon and modified the changes introduced by Wehrli et al. (2007) leading to further improvements to the representation of tree crowns. In addition I have introduced a) a feedback between tree crown and growth and b) a drought establishment filter (cf. part 4 and text below).

In FORCLIM v2.9.6, the relationship between browsing pressure and sapling mortality was modified (cf. Appendix III and text below).

FORCLIM v2.9.5

Representation of tree crowns and feedback to tree growth

In the original static relationship between foliage fresh weight ($g_{FolW}$ [kg]) and diameter at breast height ($dbh$ [cm])

$$ g_{FolW} = kA_1 \cdot kA_2 \cdot dbh^{kA_2} $$

[A-1]

$kA_1$, $kA_2$, and $kC_1$ were allometric parameters (Bugmann, 1994, eq. [3.21]). Wehrli et al. (2007) modified the $dbh$-leaf area relationship of an individual tree by
turning the parameter $kA_1$ of eq. [A-1] into an auxiliary variable, called $gA_1$ that can be interpreted as an indirect linear measure for crown length:

$$gA_1 = kA_{1,max} - (kA_{1,max} - kA_{1,min}) \cdot gLAI_{\text{mod}}$$  \hspace{1cm} [A-2]$$

Here $kA_{1,max}$ and $kA_{1,min}$ are the maximum and minimum envelope of the relationship between foliage fresh weight and dbh, respectively (cf. Wehrli et al., 2007, Fig. 2). The leaf area index (LAI) factor $gLAI_{\text{mod}}$ ranges from 0 (no canopy shading) to 1 (full canopy shading), and is calculated as (cf. part 3, eq. [4])

$$gLAI_{\text{mod}} = \text{MIN} \left( \frac{gLAI_h}{kLAI_{\text{max}}}^2, 1 \right)$$  \hspace{1cm} [A-3]$$

where $gLAI_h$ is the LAI experienced at the top of a tree and $kLAI_{\text{max}}$ is the maximum value of double-sided LAI in a patch resulting from the light compensation point (cf. Bugmann, 1994, eq. [3.22] and [3.23]) of the most shade-tolerant species (i.e., $kLAI_{\text{max}} = 11.98$, based on data for Abies alba Mill. and Fagus sylvatica L.). To account for the reduced growth potential following from a reduction in crown length, a feedback between current crown length and current growth rate was implemented. The resulting “crown length growth factor” ($gCLGF$; cf. part 3, eq. [6]) ranges from 0 to 1:

$$gCLGF = \text{MIN} \left( a \cdot \frac{gA_1}{kA_{1,max}} \cdot \frac{kLCP_S}{kLCP_{\text{mean}}} , 1 \right)$$  \hspace{1cm} [A-4]$$

In this equation $a$ is set to $\frac{4}{3}$, and $kA_{1,max}$ is the maximum envelope of the relationship between foliage fresh weight and dbh, $gA_1$ is the current value of the auxiliary variable to calculate this relationship (cf. eq. [A-2]), $kLCP_S$ is the species-specific light compensation point, $kLCP_{\text{mean}}$ is the mean light compensation point of all 30 species parameterized for European conditions.

The crown length growth factor was used as a multiplier to extend the otherwise unmodified calculation of diameter growth in previous model versions as described in Risch et al. (2005, eq. [4]):

$$\frac{dD}{dt} = gD \cdot \left( \frac{1 - H/H_{\text{max}}}{2H_{\text{max}} - be^{cd}(cD + 2)} \right) \cdot f(e) \cdot gCLGF$$  \hspace{1cm} [A-5]$$
where \( g \) is maximum growth rate (cm/year), \( D \) is tree diameter at breast height (i.e., at 137 cm), \( H \) is tree height (cm), \( H_{\text{max}} \) is maximum tree height (cm), \( b \) is \( H_{\text{max}} - 137 \) cm, \( c \) is \(-s/b\) where \( s \) is a parameter denoting the initial height growth relative to diameter growth (cf. Risch et al., 2005, eq. [4]), and \( f(e) \) is a function to reduce maximum diameter growth based on environmental conditions (cf. Bugmann, 1994, eq. [3.15]).

**Formulation to evaluate whether sapling establishment is possible**

In part 4, a multiplicative, binary drought establishment filter (SMEF) was introduced to the original formulation to evaluate whether sapling establishment is possible (cf. Bugmann, 1994, eq. [3.7]):

\[
GP_{\text{EST}} = k_{\text{EstP}} \cdot \text{WTEF} \cdot \text{DDEF} \cdot \text{ALEF} \cdot \text{BPEF} \cdot \text{SMEF}
\]  

where \( GP_{\text{Est}} \) is the probability of establishment, \( k_{\text{EstP}} \) is a site-specific constant with a range between 0 and 1, and \( WTEF \) (winter temperature), \( DDEF \) (number of growing degree-days), \( ALEF \) (light availability), \( BPEF \) (browsing pressure) are binary “establishment flags” (cf. Bugmann, 1996, Table 1).

**FORCLIM v2.9.6**

In order to provide a more realistic representation (cf. Appendix III) of the impact of browsing on seedlings and saplings before reaching a diameter at breast height (dbh) of 1.27 cm, the original calculation of the browsing establishment flag (BPEF; cf. Bugmann, 1994, eq. [3.4]) was modified, resulting in:

\[
BPEF = \begin{cases} 
0 & \text{U}(0,1) < \left(\frac{k_{\text{BrPr}}}{100}\right)^{k_{\text{Brow}}} \\
1 & \text{else}
\end{cases}
\]

where \( \text{U}(0, 1) \) is a random number with uniform distribution in the range [0..1], \( k_{\text{BrPr}} \) is the browsing pressure ranging from 0% (no browsing) to 100% (heavy browsing where no sapling establishment is possible) and \( k_{\text{Brow}} \) is the species-specific sensitivity to browsing, which encompasses all browsing-related mortality during the lifespan of a tree as seedling before reaching a dbh of 1.27 cm, including growth suppression and ability to compensate. This \( k_{\text{Brow}} \) parameter was revised based on current knowledge (cf. Appendix III):

\[
k_{\text{BrP}} = \left(\frac{k_{\text{BrPr}}}{100}\right)^{k_{\text{Brow}}} \]
where $kBrPr$ represents the degree of browsing pressure that is used to derive the probability $kBrP$ of a species to survive to a dbh of 1.27 cm, and $a_{kBrow}$ is the value of the exponent for the five levels of tree species browsing sensitivity (i.e., $kBrow$, Table A-2, Fig. A-5).

References


II. Results for the evaluation of FORCLIM v2.9.1 with national forest inventory data (NFI 1)

In the preparation of the study presented in part 2.A, the sites for all 15 regional forest types were also simulated with FORCLIM v2.9.1, besides FORCLIM v2.9.3 and PICUS v1.4. Here, the most important results relating to the performance of version 2.9.1 are shown.

Generally, the two FORCLIM versions (see Appendix I for details on the differences between the two versions) produced similar temporal patterns in the percentage similarity coefficient (PS; part 2.A eq. [2]) between observed and simulated fraction of the total basal area (\(s_tBA\)) except for the subalpine fir forests of the Western Central Alps, the montane spruce forests of the Southern Alps, and the subalpine spruce forests of the Southern Alps (Fig. A-1). In the latter, these differences were most evident (Fig A-2). The simulated patterns for the first 200 years were similar, but PS increased further to the end of the simulation for model version 2.9.3 (Fig. A-2d), whereas it reached a plateau and then declined toward the end of the simulation for model version 2.9.1 (Fig. A-2c).

The differences between the examined models were particularly striking for total tree numbers in dbh class 1, where FORCLIM v2.9.3 simulated the highest numbers, followed by FORCLIM v2.9.1, and PICUS simulating the lowest numbers (cf. Figs. A-3 and A-4). In dbh class 2, the medians of tree numbers simulated by FORCLIM v2.9.3 and PICUS were similar and higher than the median of tree numbers simulated by FORCLIM v2.9.1 (cf. Figs. A-3 and A-4b).

Since FORCLIM v2.9.3 performed considerably better than v2.9.1 (cf. Figs. A-1 and A-3), the newer version 2.9.3 was used in all further studies.
Figure A-1. Percentage similarity between relative species basal area observed in the NFI 1 and simulated with the two FORCLIM versions and PICUS for 15 regional forest types. Abbreviations for regions used as defined in part 2.A, Table 1.
Figure A-2. Subalpine spruce forests of the Southern Alps - %BA from NFI 1 data and from every 50th year of the simulations (columns) and corresponding percentage similarity (solid black line). Species abbreviations were: Aalb – Abies alba, Ldec – Larix decidua, Pabi – Picea abies, Pcem – Pinus cembra, Pspp – Pinus sylvestris and P. montana, Fsil – Fagus sylvatica, Qspp – Quercus spp., oDec – other deciduous.
Figure A-3. Medians of tree numbers in 3 dbh classes (< 4 cm, 4-8 cm, 8-12 cm) for 15 regional forest types, simulation time window 200 to 400 years. Open symbols and dashed lines represent the dominant species, filled symbols and solid lines for all species. The values for the 3 dominant species in the montane fir-beech-spruce forests were averaged. Abbreviations for regions used as defined in part 2.A, Table 1. NB the log y-scale with a constant value of 1 added to the number of trees.
Figure A-4. Ratio of simulated to observed medians of tree numbers in 3 dbh classes (< 4 cm, 4-8 cm, 8-12 cm) calculated as the average of all 15 regional forest types for time window 200 to 400 years from Figure A-3.
III. Improving the relationship between browsing pressure and seedling and sapling mortality for FORCLIM v2.9.6

Revision of the kBrow parameter

In the FORCLIM model, the parameter $kBrow$ is a measure for the survival probability of seedlings and saplings before reaching a diameter at breast height (dbh) of 1.27 cm, which is the size with which trees are established in the model (cf. part 5, section 2.2). The parameter $kBrow$ comprises species-specific responses to browsing-related effects on seedlings, including a) the general susceptibility to browsing as a measure of ungulate preference, b) the rate of height growth of seedlings, c) the ability of a tree species to compensate for tissue losses due to browsing, and d) the survival probability after browsing (Table A-1). For each of the 30 European tree species that are included in FORCLIM these browsing-related effects were evaluated by Dr. A.D. Kupferschmid based on existing literature, and refined based on expert opinion of Dr. Monika Frehner.

The following sources were used by A.D. Kupferschmid to evaluate species sensitivity related to

a) Browsing preference by ungulates ($BPU$): Kupferschmid and Brang (2009, Table 5: mainly based on Klötzli, 1965; Gill, 1992; Brändli, 1996; Prien, 1997).

b) Rate of tree height growth ($RHG$): Professur für Waldbau und Professur für Forstschutz und Dendrologie der ETH Zürich (1995);

c) Compensation ability regarding tissue losses ($CA$): Kupferschmid (submitted, Table 1, mainly based on the location of reserve storage and the growth pattern of trees).

d) Survival probability after browsing ($SP$): Estimated based on expert opinion and Professur für Waldbau und Professur für Forstschutz und Dendrologie der ETH Zürich (1995) for a species’ ability to built water sprouts and suckers.

In order to derive a single value for $kBrow$, the weighted mean $\mu$ (Table A-1) of the four browsing-related effects was calculated as follows: Browsing preference by ungulates ($BPU$) received a doubled weight to capture the importance of feeding preferences of ungulates in the selection of tree species (cf. Augustine and McNaughton, 1998). Thus,

$$\mu = \frac{2 \cdot AGF + RHG + CA + SP}{5} \quad [A-9]$$
with $AGF$, $RHG$, $CA$, $SP$, and $\mu$ all ranging from 1 to 5. To distribute the species over five browsing sensitivity classes, the weighted means were scaled to derive the final value for $kBrow$ for FORCLIM v2.9.6 (cf. Table A-1):

$$kBrow = \begin{cases} 
1 & \mu < 2.0 \\
2 & 2.0 \leq \mu < 3.0 \\
3 & 3.0 \leq \mu < 3.5 \\
4 & 3.5 \leq \mu < 4.5 \\
5 & \text{else}
\end{cases}$$

**Revision of the relationship between tree seedling and sapling mortality and browsing pressure**

Eiberle and Nigg (1987) derived a measure for browsing intensity relating measured data on the mortality of tree saplings to a browsing-induced height growth reduction (Fig. A-5).

![Figure A-5. Relationship between height growth reduction and mortality based on measurements of five species: Picea abies, Abies alba, Fagus sylvatica, Acer pseudoplatanus and other deciduous species. Figure redrawn after Eiberle and Nigg (1987).](image-url)
Table A-1. Species-specific measures for the response to browsing-related effects. “old kBrow”: kBrow from previous FORCLIM versions; “BPU”: browsing preference by ungulates with 1 (unpalatable) and 5 (highly palatable and preferred browsed); “RHG”: rate of height growth with 1 (fast growing) and 5 (slow growing); “CA”: compensation ability regarding tissue losses due to browsing with 1 (high) and 5 (low); “SP”: survival probability after browsing with 1 (high) and 5 (low); μ: weighted mean (eq. [A-8]); “new kBrow”: new value for kBrow used in FORCLIM v2.9.6.

<table>
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<tr>
<th>Species</th>
<th>old kBrow</th>
<th>BPU</th>
<th>RHG</th>
<th>CA</th>
<th>SP</th>
<th>μ</th>
<th>new kBrow</th>
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</table>

To be able to relate the measure of a reduction in height growth as used by Eiberle and Nigg (1987, Fig. 2) to browsing pressure as used in the model, I made the following assumptions:

a) Eiberle and Nigg (1987) derived this relationship (Fig. A-5) between sapling mortality and height growth reduction for trees <1.30 m in height. In FORCLIM
Appendix

trees are established with a diameter at breast height of 1.27 cm, which corresponds to a height of ca. 1.40 m for the smallest trees.

b) Since height growth reduction can be expected to increase if browsing pressure increases, I assumed that there is a similar relationship between browsing pressure \((kBrPr)\) and mortality in FORCLIM.

c) Browsing-related effects are nil if browsing pressure is 0%, and no tree establishment is possible when browsing pressure is 100%.

d) A browsing pressure of 0% in the model therefore coincides with a 27.7% reduction in height growth, below which no mortality was observed (cf. Fig A-5). In reality, a browsing pressure greater than zero leads to such growth reductions; thus, the approach used here follows the precautionary principle by over- rather than under-estimating browsing effects.

e) The relationship between tree seedling and sapling mortality and browsing pressure is linear for species of medium sensitivity (i.e., \(kBrow = 3\)) and non-linear for all other species (eq. [A-8] and eq. [A-10]).

Based on the data from Eiberle and Nigg (1987, Fig. 2) and from a study by Guler (2004), I derived estimates for the parameter \(akBrow\) (Table A-2).

Table A-2. Estimates for the exponent \(akBrow\) (eq. [A-2]) for five levels of tree species sensitivity to browsing \((kBrow; cf. Table A-1)\).

<table>
<thead>
<tr>
<th>kBrow</th>
<th>(akBrow^\prime)</th>
<th>(akBrow^\prime\prime)</th>
<th>(akBrow^\prime\prime\prime)</th>
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<td>1</td>
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<td>4</td>
<td>6</td>
</tr>
<tr>
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<td>2</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>6/8</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>5</td>
<td>0.5</td>
<td>0.25</td>
<td>1/6</td>
</tr>
</tbody>
</table>

In simulations with FORCLIM v2.9.6 at the montane site Adelboden, the sensitivity of the model to changes in the exponent \(akBrow\), and the realism of the new relationship was evaluated. Three settings of the exponent \(akBrow\) were used (Table A-2) for evaluating the simulated species basal area. The results were compared with the basal area produced by FORCLIM v2.9.5 (cf. part 3).

The results from the case study in Adelboden for simulations for the three alternative estimates for the exponent \(akBrow\) and for five different browsing pressures: low (5%), moderate (20%), medium (50%), elevated (80%) and high (95%) showed that:

- The exponent set \(akBrow^\prime\) resulted in artifacts for species that have a high sensitivity to browsing and that have low initial height at establishment (i.e., low
skinniness parameter $k_S$; Risch et al., 2005) such as *Taxus bacata* and *Pinus cembra*. The basal area of these species increased with an increase in browsing pressure, which is clearly unrealistic. The causes for this artifact were joint effects of browsing pressure and light availability. Since the establishment success of all species decreases with an increase in browsing pressure (i.e., the mortality $k_{BrP}$ increases, cf. Fig. A-6), the number of trees in the stand decreases leading to more open stands and more available light for establishment and growth. Species with a high sensitivity to browsing (i.e., $kBrow = 5$) and a low initial height at establishment, including *T. bacata*, profited most of these open stands, as they had relative to other species an increased establishment success and a higher growth rate and were thus able to persist. In contrast, under low browsing pressure and a consequently denser stand, these species have a high stress-related mortality due to slow growth.

- The exponent set $a_{kBrow}''$ for browsing pressure 5% resulted in a similar stand as simulated with FORCLIM v2.9.5 (cf. part 3, Fig. 4), except that the basal area fraction of *Abies alba* was a little lower than in v2.9.5, which was compensated for by *Fagus sylvatica*. Thus the results for this combination of the exponent set and browsing pressure resulted in a realistic stand.

- The exponent set $a_{kBrow}'''$ resulted in a clear overestimation of mortality of species with the highest sensitivity to browsing (i.e., $kBrow = 5$). Even for a very low browsing pressure of 5%, *Abies alba* was not able to establish.

Based on these results, I decided to use the exponent set $a_{kBrow}''$ as the basis for the implementation of the new relationship between mortality of seedlings and saplings and browsing pressure (cf. Fig. A-6 and part 5, section 2.2).
Figure A-6. Relationship between mortality of tree seedlings and saplings (kBrP) and browsing pressure (kBrPr) for five levels of tree species sensitivity to browsing-related effects before reaching a dbh of 1.27 cm (kBrow; cf. Table A-1) with exponent a" (cf. Table A-2). Data are shown for species appearing in both Eiberle (1987, open, symbols) and Guler (2004, solid symbols). Other deciduous species appeared only in Eiberle (1987), and Sorbus aucuparia and Pinus sylvestris only in Guler (2004).

References


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A very special thank you goes to my parents, who supported me throughout all these years.
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