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Above- and belowground patterns and processes following land use change in subalpine conifer forests of the Central European Alps

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Summary

Traditional agriculture and forestry are no longer economically viable in many mountain regions in Western Europe. As a result, ecosystems that were managed for centuries become less intensively used or completely abandoned. This leads to increases in the percentage of forested areas as former agricultural land becomes reforested, and to secondary forest succession in no longer managed stands.

Since these mountain regions were managed for centuries, little is known on how forested ecosystems will develop after ceasing management. Thus, the interest in understanding and predicting secondary successional patterns and processes in these systems increased considerably over the last two decades. The Swiss National Park (SNP) is one of the few mountain areas in Western Europe that was not influenced directly by humans during most of the 20th century, and therefore it offers the opportunity to study the processes outlined above. The objectives of this thesis were to investigate 1) how the Park's forests developed during the last century while focusing on changes in i) tree composition, ii) forest structure and iii) above- and belowground biomass, carbon (C) and nutrient pools, and 2) how long the observed processes will likely take.

Section I of this thesis was dedicated to the development of forest composition and structure. In a first step, long-term empirical data (1957 to 2001/02) of selected forest stands were compared in order to investigate changes in forest composition (Paper I). The relative importance of mountain pine (*Pinus montana* Miller) trees (> 130 cm tall) decreased (75 to 46%), while the one of Swiss stone pine (*Pinus cembra* L.), European larch (*Larix decidua* Miller), Norway spruce (*Picea abies* (L.) Karst and Scots pine (*Pinus sylvestris* L.) increased over the 45 years of observation. A similar development was found for tree saplings (21 – 130 cm tall). The observed changes indicated that considerable successional shifts are taking place in the stands studied. To analyse these changes in greater detail and to determine which forest types likely can be found during succession, time-series analyses, space-for-time substitution and multivariate methods (PCoA, minimum spanning tree analysis) were used in a second step (Paper II). The results showed that forest succession in the SNP is dominated by three major forest types: An early-successional mountain pine stage is replaced by a mid-successional mixed

species stage (mountain pine, stone pine, larch, Norway spruce, Scots pine), which in turn is replaced by a stage dominated by Swiss stone pine / European larch in late-succession.

The delineation of the different stand types was used in a third step to analyse stand structural changes. Paper III assessed this using empirical long-term data (1957 – 2001/02): After a stand initiation phase, stand dynamics are controlled by self-thinning processes, which are replaced by vertical/horizontal stratification. During this development, shade-intolerant mountain pine gradually becomes replaced by shade-tolerant species, leading to an increase in non-standing dead wood biomass (t/ha) and a decrease in standing dead wood density (stems/ha).

Based upon the delineation of dominating forest types during succession, space-for-time substitution was used again in Section II to investigate changes in above- and belowground C and nutrient pools following land use change. As Paper IV shows, nutrient pools decreased during the transition from grassland to forest, and during secondary forest succession. Aboveground C pools were found to increase continuously. Mineral soil C pools remained unchanged during transition from pasture to forest, but decreased during secondary succession, contrasting the currently prevailing opinion that assumes the opposite development. These findings were closely related to changes in understory vegetation composition, in particular to changes in ericaceous shrub cover, which increased during re-forestation, but decreased during secondary forest succession. Litter from ericaceous shrubs decomposes very slowly (high phenol and lignin content, low nitrogen content) and therefore provides high amounts of recalcitrant C to the mineral soil. The observed changes in understory species composition likely are responsible for the observed changes in mineral soil biomass and C pools. Overall, the decrease in mineral soil biomass and C offset the aboveground gains, leading to unchanged ecosystem biomass and C pools during forest succession. Thus, within the SNP, only pasture to forest succession can be considered a C sink, while secondary forest succession is neither a sink nor a source.

Since red wood ants (*Formica rufa* group) retrieve large amounts of forest floor to build their nests, they could have a strong impact on belowground C pools during forest succession (Paper V). Carbon pools stored in ant mounds were highest in the late-successional forests, but they were not able to significantly alter total belowground C budgets.

As a final part of this thesis, the time frame for the changes described above was estimated (Section III). This was done by simulating vegetation development with three models of conceptually different background (Paper VIII): i) a forest gap model (Paper VI), ii) a Markov chain model (Paper VII), and iii) a minimum spanning tree model (Paper II). Starting with a 95 to 125 year old mountain pine forest, all three models predicted a similar time frame of 500 to 550 years to the late-successional stage that is composed of stone pine/larch.

Zusammenfassung

Die traditionelle land- und forstwirtschaftliche Nutzung der Landschaft ist in vielen Gebirgsregionen Westeuropas nicht mehr rentabel und damit langfristig mit grosser Wahrscheinlichkeit nicht mehr überlebensfähig. Viele durch jahrhundertlange traditionelle Nutzung entstandene Ökosysteme werden deshalb in Zukunft weniger intensiv oder überhaupt nicht mehr bewirtschaftet werden. Diese Entwicklung wird einerseits infolge Wiederbewaldung von aufgelassenem Landwirtschaftsland zu steigenden Waldanteilen und andererseits zu sekundärer Sukzession in nicht mehr genutzten Wäldern führen.

Gerade weil die meisten Gebirgsregionen über Jahrhunderte wirtschaftlich genutzt wurden, ist kaum bekannt wie sich beispielsweise Gebirgswald - Ökosyteme nach Nutzungsaufgabe entwickeln werden. In den vergangenen Jahrzehnten stieg infolge der einsetzenden Nutzungsaufgabe das Interesse, die sekundären Sukzessionsprozesse in Gebirgswäldern zu verstehen bzw. zu prognostizieren. Der Schweizerische Nationalpark (SNP) ist eine der wenigen Gebirgsregionen Westeuropas, welche während des ganzen 20. Jahrhunderts nicht direkt durch den Menschen beeinflusst wurde. Der Park eignet sich deshalb besonders gut, um die erwähnten Sukzessionsprozesse zu analysieren. Die Ziele dieser Arbeit waren zu untersuchen 1) wie sich die Wälder im SNP in den vergangenen Jahrzehnten bezüglich i) Bestandszusammensetzung, ii) Bestandesstruktur, und iii) ober- und unterirdischer Biomasse, Kohlenstoff (C)- und Nährstoffpools entwickelt haben und 2) in welchen Zeiträumen die beobachteten Entwickungen ablaufen dürften.

Im ersten Teil dieser Arbeit wurde die Entwicklung der Bestandeszusammensetzung und -struktur mittels empirischen Zeitreihendaten (1957 bis 2001/02) aus ausgewählten Waldtypen untersucht. Die Baumarten-Zusammensetzung veränderte sich in der 45-jährigen Beobachtungsperiode deutlich (Artikel I): Die relative Bedeutung der Bergföhre (*Pinus montana* Miller) sank bei Bäumen > 130 cm Höhe von 75% auf 46%, während diejenige der Arve (*Pinus cembra* L.), der Lärche (*Larix decidua* Miller), der Fichte (*Picea abies* (L.) Karst) und der Waldföhre (*Pinus sylvestris* L.) zunahm. Die selbe Entwicklung wurde auch bei den Jungbäumen (21 - 130 cm Höhe) festgestellt. Diese beobachteten Veränderungen zeigten, dass in den untersuchten Beständen bedeutende

Sukzessionsprozesse ablaufen dürften. Um diese vermuteten Prozesse detailliert studieren und darstellen zu können, wurden Methoden der Zeitreihen-Analyse, "space for time substitution" und der multivariaten Statistik (PcoA, "minimum spanning tree") verwendet (Artikel II). Die Untersuchungen zeigten, dass die Waldsukzession im SNP von drei Waldtypen dominiert wird: In einer frühen Sukzessionsphase sind die Wälder durch eine Berföhrendominanz gekennzeichnet. In einer mittlern Sukzessionsphase werden diese Wälder durch Mischbestände (Bergföhre, Arve, Lärche, Fichte, Waldföhre) abgelöst, welche wiederum in einer späten Sukzessionsphase durch Bestände, in welchen Arve und Lärche dominieren, ersetzt werden.

Im dritten Teil des ersten Teils wurden die Strukturdaten analysiert. In Artikel III wurden die empirischen Zeitreihendaten (1957 –2001/02) auf Strukturveränderungen untersucht: Nach einer initialen Etablierungsphase des Waldbestandes, werden Veränderungen in der Bestandesstruktur grösstenteils von Ausdünnungsprozessen gesteuert. In einer weiteren Phase werden diese Prozesse durch jene der vertikalen und horizontalen Stratifikation ersetzt. Die beschriebene Entwicklung der Bestandesstruktur war sowohl von der allmählichen Ablösung der Lichtbaumart Bergföhre durch schattentolerante Arten als auch von einem Anstieg in der Menge liegenden Totholzes (t/ha) und sinkenden Anteilen an stehendem Totholz (Stämme/ha) begleitet.

Ausgehend von den sich während der Sukzession ablösenden Waldtypen, wurde im zweiten Teil wiederum mittels "space for time substitution" untersucht wie sich ober- und unterirdische C- und Nährstoffpools in Gebirgsregionen nach Landnutzungsänderungen entwickeln könnten. Wie Artikel IV zeigt, sanken die Nährstoffpools in der Phase der Wiederbewaldung von Grünland, um während der sekundären Wald-Sukzession auf praktisch gleichem Niveau zu verharren. Anders verhielt sich der oberirdische C-Pool, welcher über die gesamte Sukzession anstieg. Wiederum anders entwicklete sich der C-Pool des Mineralbodens: er veränderte sich in der Wiederbewaldungsphase nicht, nahm dann aber während der sekundären Waldsukzession ab. Diese Entwicklung widerspricht der vorherrschenden Meinung, die von einer Abnahme des C-Pools im Mineralboden während der Wiederbewaldung und einer Zunahme während der sekundären Waldsukzession ausgeht. In dieser Studie war die Abnahme des C-Pools im Mineralboden in den untersuchten Wäldern stark mit sukzessionsbedingten

Veränderungen in der Krautschicht korreliert, insbesondere mit der Abnahme von Zwergsträuchern (*Ericaceae*). Ericoide Zwergsträucher sind bekannt für ihre langsame Zersetzung, welche durch einen hohen Phenol- und Lignin-Gehalt sowohl tiefen Stickstoffgehalt der Pflanzen bewirkt wird und führen deshalb dem Mineralboden hohe Mengen an organischem C zu (abbauresistenter Kohlenstoff). Für den total C-Pool bedeutet dies, dass sich die beiden Effekte, Abnahme von Kohlenstoff im Mineralboden und Zunahme von oberirdisch gespeichertem C, gegenseitig aufhoben, und somit der totale C-Pool während der Wald-Sukzession unverändert blieb. Im SNP kann deshalb nur die Phase der Wiederbewaldung von Grünland als C-Senke betrachtet werden, nicht jedoch die Phase der sekundären Wald-Sukzession, welche weder C-Quelle noch C-Senke bezeichnet werden kann.

Rote Waldameisen (*Formica rufa* Gruppe) tragen in den Wäldern des SNP viel Streuematerial zum Bau ihrer Nester zusammen. Aus diesem Grund könnten sie eine wichtige Rolle in der Entwicklung des C-Pools während der Waldsukzession spielen (Artikel V). C-Pools von Ameisenhaufen waren denn auch in der späten Sukzessionsphase am höchsten, jedoch zu wenig hoch, um das gesamte C-Budget der Bestände massgeblich beeinflussen zu können.

Der dritte und letzte Teil dieser Arbeit war der Frage gewidmet, in welchen Zeiträumen die beschriebenen Sukzessionsprozesse ablaufen könnten. Dazu wurde die Vegetationsentwicklung mit drei grundsätzlich verschiedenen Modellen simuliert (Artikel VIII): 1) einem "forest gap model" (Artikel VI), 2) einem "Markov-Modell" (Artikel VII) und 3) einem "minimum spanning tree model" (Artikel II). Die simulation wurde in allen drei Modellen mit einem 95- bis 125-Jahre alten Bergföhren-Bestand gestartet. Alle Modelle schätzten einen ähnlichen Zeitrahmen für die sekundäre Wald-Sukzession, welcher 500 bis 550 Jahre umfasste.

General introduction

*"Ecological succession is an important concept to understanding ecological systems.
Successions may be observed at a broad range of scales, from the microscopic to the
continental, from minutes to millennia [...].
The field has generated both excitement and controversy for biologists for over a century
[...] In fact, understanding succession is as important today as ever, both in terms of
amount of research effort and in terms of understanding changes in natural and managed
environments."*

McCook 1994, Vegetatio 110: 115-147.

The understanding of successional pathways has been a major focus of ecological
research since the 19th century, and many different theories explaining successional
processes were developed over time. Extensive reviews can be found e.g. in Shugart
(1984), Glenn-Lewin et al. (1992), McCook (1994) or Walker and de Moral (2003).
Generally, two major schools of thought have formed: Clements (1936) supported a
facilitation-based approach, where the dominant species (or community) sequentially
modifies its environment (e.g. soil properties) in such way that it becomes less favourable
for itself. Consequently, invaders that are better adapted to the changed conditions slowly
out-compete the earlier occupants. This development is strongly unidirectional, leading to
a climax stage that is maintaining itself. When a major disturbance occurs, the
successional process will start again (Clements 1936). In contrast to this view, Gleason
(1926) suggested an individualistic concept, where every plant reacts within its
physiological and ecological constraints, so that the vegetation development underlying
this concept is largely stochastic, and thus less predictable. Therefore, communities
themselves (and not the sequence of communities) emerge from the interactions between
the plants. When this view is applied at the community level, it implies that each
community can change into virtually any other community, thus contrasting the
directional succession promoted by Clements (1936).

In order to evaluate the applicability of these theories, many studies were conducted
during the past 60 years, investigating both primary and secondary succession in different
ecosystems. Studies on primary succession mainly focused on understanding above- and
belowground processes (e.g. understory changes, changes in soil properties) in sand dune

chronosequenses, river terraces, islands, formerly glaciated areas and lava flows (extensive overview in Svennson and Jeglum 2000), secondary succession on understanding these processes in abandoned farm fields (e.g. Bazzaz 1975, Pickett 1982), wetlands (e.g. Klinger 1996, Gunnarsson et al. 2002), grasslands (e.g. Austin 1980, Collins and Adams 1983), and many different forest types (e.g. Frelich and Reich 1995, Finegan 1996, Archambault et al. 1998). As a result, a multitude of new theories and models, both verbal (e.g. Watt 1947, Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1977, Grime 1977, 1979, Pickett 1989) and mathematical [e.g. Horn 1975, Usher 1979, 1981 (Markov chain models), Botkin et al. 1972, Shugart 1984 (forest succession models), Mladenoff et al. 1996, He et al. 1999) (landscape models)] emerged. These models together with intensive field research helped to considerably increase our knowledge of above- and belowground patterns and processes during succession.

One may argue that natural succession processes are not very important in many terrestrial ecosystems today, since the patterns and dynamics in these systems have been influenced strongly by management activities. Yet, economically induced extensification of land use started to take place in many developed countries in the past decades. Thus in many of the ecosystems in these regions secondary successional processes have re-gained in importance. However, little is known about the natural development of these systems, since they often have been managed for centuries.

Among these ecosystems are high-elevation forests, which are important landscape components of many countries (~24% of the earth's terrestrial surface is mountainous; see Kapos et al. 2000), and of great relevance for hydrology and biodiversity (see Riederer 1996; Becker and Bugmann 2001, Brun 2002), carbon storage (Schimel et al. 2002) as well as for protection against natural hazards, e.g. avalanches (Schönenberger 2000, Bebi et al. 2001, Bachofen and Zingg 2001). In order to be able to assess how these functions can be maintained over time, it is important to understand how mountain forests develop and function after ceasing management.

However, as pointed out by Bugmann (1996), it often is difficult to investigate successional processes in forests, since these ecosystems develop very slowly, and long-term data therefore often are lacking. In addition, in order to investigate long-term ecosystem development following land use change, not only long-term data are required, but also data that originate from areas released from management 50 to 100 years ago.

One of the few areas within western Europe that offers these conditions is the Swiss National Park (SNP), which was not managed for most of the 20th century. In the SNP, the successional development started in 1914, and the area may therefore serve as a model for scenarios that are likely to occur in similar areas of the Alps in the coming decades. In addition, the historical land-use (forest management) in the SNP is known (Parolini 1995), and considerable data on forest development are available for a 45-year period (Kurth et al. 1960). The present study aims to exploit this rich data source to improve our understanding of successional processes in high-elevation forests.

Figure 1: Mountain pine (*Pinus montana* Miller) forests (Las Crastatschas) in the SNP (picture: Anita Risch)

Objectives

The three main objectives of this study are:

I)   To investigate how subalpine conifer forests in the SNP developed over the past 45 years (stand dynamics of specific forest types), and to assess whether successional processes can be detected using these long-term data. Papers I, II, and III deal with these topics.

II)   To investigate how above- and belowground biomass, carbon and nutrient pools change during succession following land use change in the SNP (Papers IV and V).

III)   To estimate the time elapsing during secondary forest succession in the SNP based on these data sets and on simulation results from tree mathematical models of different background (Paper II, VI, VII and VIII).

The three objectives are assessed separately in three sections, followed by an overall conclusion. Below, an overview of the different papers contained within each section is given.

Section 1: Stand development after abandonment of subalpine conifer forests (Papers I, II, III)

The forests in the SNP have been clear-cut several times since the 16th century (Parolini 1995), resulting in regenerating forests dominated by mountain pine (*Pinus montana* Miller). In some stands, selective timber extraction occurred until 1914, but these activities were stopped entirely when the Park was founded. Today, mountain pine stands occupy large parts of the SNP, but some slopes are covered with forests comprised of Swiss stone pine (*Pinus cembra* L.) or a mixture of Swiss stone pine and European larch (*Larix decidua* Miller) and mixed stands. Presumably, the Swiss stone pine / larch stands represent late-successional forest conditions of the area (Kurth et al. 1960; Holtmeier 1990; Zoller 1995; Kienast et al. 1999).

It is not known, however, whether the currently dominating mountain pine forests will ever reach a late-successional stage, or whether the current level of disturbances, such as fungal diseases, parasitic insects, ungulate browsing, small-scale windthrows and snow pressure incidents will keep these forests in an early- to mid-successional stage. Therefore, disturbances could potentially have a significant impact on successional processes in the Park. The aim of this section was (1) to study the overall forest development (Paper I), (2) to analyse whether a successional transition from mountain pine to Swiss stone pine/European larch forests occurred over the past decades in the SNP (Paper II), and 3) to evaluate forest dynamics of particular forest types based on empirical data (Paper III).

Section 2: Changes in carbon and nutrient pools during secondary succession in subalpine conifer forests(Paper IV and V)

Total carbon (C) pools have been shown to increase when management of former agriculture land and forests ceases (e.g. Kauppi et al. 1992, Houghton 2003), while the fate of C in belowground pools is much more controversial. Increases, decreases and insignificant changes have been reported (Alriksson and Olsson 1995, Thuille et al. 2000, Guo and Gifford 2002), but most information has been obtained from low-elevation ecosystems and not much is known on how C pools develop after land abandonment in high-elevation ecosystems. Modelling studies have indicated that high-elevation systems in Switzerland and the Western US could become increasingly important for C storage, given the ongoing land use changes (Perruchoud et al. 1999, Schimel et al. 2002). Therefore, it is important to gain information on changes in total C during succession in high-elevation ecosystems, as well as on soil nutrients that can limit ecosystem productivity and therefore could impact C sequestration.

The aim of this section therefore was twofold: In a first step, the above- and belowground C and nutrient pools are determined for all major ecosystem components along a successional gradient from subalpine grasslands to late-successional forests (Paper IV).

In a second step, we calculated C and nitrogen (N) pools for mounds of red wood ants (*Formica rufa* group). These conspicuous components of many forest ecosystems have not been studied to date when assessing forest C or N pools. Since red wood ants build large above-ground nests (mounds) composed of litter collected from the surrounding forest floor (Wisniewski 1976; Gösswald 1989a,b), they could be important for C and N storage and ecosystem carbon and nutrient cycling. Therefore, the aim of the second part of this section was to determine C and N pools of red wood ant mounds in subalpine forests of different successional age, so as to determine the importance of these structures for the C and N budget of mountain forest ecosystems in the SNP (Paper V).

Figure 2: Red wood ant mound (*Formica rufa*-group) composed of litter collected from the surrounding forest floor (picture: Anita Risch).

Section 3: Modelling the development of subalpine conifer forests in the Central European Alps (Paper VI, VII and VIII)

Up to date, little is know on how long the successional changes described in Section I and II of this study will likely take. Thus, the objective of this section was to estimate the time elapsing during succession from mountain pine to stone pine forests of the SNP. In a first step, a Markov chain model was developed (Paper VII), and a forest gap model (ForClim) calibrated for the SNP (Paper VI). In a second step, the long-term forest development was simulated with three models of different conceptual background, and the time frame for succession was estimated (Paper VIII). The three models used were i) the forest gap model ForClim as modified in section III (Paper IV), ii) the Markov chain model developed in section III (Paper VII), and iii) the minimum spanning tree model developed in section I (Paper II).

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Section I

Stand development after abandonment of subalpine conifer forests

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Paper I

Long-term empirical data as a basis for the analysis of successional pathways in subalpine conifer forests

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Abstract

As a result of free market forces in the agricultural and silvicultural sector, mountain regions in Western Europe are at great risk of experiencing increasing land abandonment, particularly of land with low production potential. In order to mitigate undesirable negative effects on landscape qualities or to initiate incentives for remedial actions, the importance of understanding natural succession in these abandoned systems increased considerably within the last two decades.

The Swiss National Park (SNP) is one of the few areas in Western Europe that was not influenced directly by humans during most of the 20th century. Therefore, the Park provides a unique opportunity to study how mountain forests may develop in the absence of human intervention. Fortunately, long-term data on forest development in the SNP are available for a 44-year period. This study is based on a comparison of historic (1957) and present data (2001) from subalpine forest stands.

Our results showed that the SNP's forests are developing from an early-successional stage dominated by mountain pine (*Pinus montana* Mill.) through a mid-successional mixed-species stage into a late successional stage dominated by Swiss stone pine (*Pinus cembra* L.) and European larch (*Larix decidua* Mill.).

With the present study we were able to empirically elucidate major successional pathways. In addition, we found that current natural disturbances, such as fungal diseases, parasitic insects, ungulate browsing, small-scale wind-throw or snow pressure, do not prevent succession from mountain pine to Swiss stone pine-European larch communities.

Keywords

Mountain pine, long-term data, subalpine conifer forests, succession, Swiss National Park, Swiss stone pine

Introduction

In spite of the importance of mountain regions, traditional agriculture and forestry are no longer viable in many mountainous areas. Traditional agricultural and silvicultural land-uses are unlikely to be continued in many places, due to an economically-caused decrease in management interest, which will lead to drastically reduced management of meadows and forests, or complete land abandonment (Price 1995; Riederer 1996; Bätzing 1996; Broggi 1998). Understanding the vegetation development in absence of human intervention therefore became more and more important in the recent past. Assessing the long-term development of abandoned or less intensively used areas, however, is difficult, especially in areas like Western Europe, which has a long history of intense human land use, and only few areas where no or low management impact exist.

One of the few areas in Western Europe that was not influenced directly by humans during most of the 20th century is the Swiss National Park (SNP). The Park provides a unique opportunity to study how mountain forests may develop in the absence of human intervention. Fortunately, long-term data on forest development in the SNP is available for a 44-year period. Today, mountain pine (*Pinus montana* Mill.; PIMO) stands occupy large parts of the SNP, but some slopes are covered with forests comprised by either a mixture of Swiss stone pine (*Pinus cembra* L.; PICE), European larch (*Larix decidua* L.; LADE), Norway spruce (*Picea abies* (L.) Karst; PIAB) and Scots pine (*Pinus sylvestris*

L.; PISY), or by PICE and LADE. The latter forest type is supposed to represent the late-successional forest conditions of the area (Kurth et al. 1960; Holtmeier 1990; Zoller 1995; Kienast et al. 1999).

It is not known whether the forests that are currently dominated by regenerated PIMO will ever reach a late-successional stage, or if the current level of natural disturbances such as fungal diseases, parasitic insects, ungulate browsing, small-scale windthrows and snow pressure incidents that act on a single tree basis will keep these forests in an early-successional stage. Dobbertin et al. (2001), for example, reported that infection by root rot (*Heterobasidion annosum*, *Armillaria* spp.) led to a significant partial breakdown within PIMO stands in the SNP. Therefore, disturbances could potentially have a significant impact on successional pathways in the Park.

Since an extensive database of SNP forest composition exists for the year 1957 (Kurth et al. 1960), we have the opportunity to investigate the temporal development of these forest stands based on long-term data in an area that was abandoned in 1914. Therefore, the objective of this study was to investigate how selected forest stands within the SNP developed between 1957 and 2001, and to examine how the tree species composition changed over the 44 years of observation.

Study area and methods

The SNP is located in the southeastern part of Switzerland and covers an area of approximately 170 km^2, 50 km^2 of which are covered with forests. The elevation of the area ranges from 1350 to 3170 m a.s.l. (above sea level), the mean annual precipitation and mean annual temperature ± standard deviation are 925 ± 162 mm and 0.2 ± 0.7 °C (mean ± standard deviation, measured at the weather station Buffalora 1980 m a.s.l.).

In 2001, we re-sampled 16 of the 131 stands delineated in 1957 by Kurth et al. (1960). Elevation ranged from 1700 to 2200 m a.s.l. In 1957 the forested area was covered with 73% PIMO forests, 11% PICE forests and 16% other, not well described forest and shrub communities (Kurth et al. 1960). Based on the stratified 1957 data we randomly chose (A) twelve stands dominated by PIMO, which were characterized by 4 different sapling assemblages, (B) one stand dominated by both PIMO and PICE, and (C) three stands dominated by PICE or mixtures of PICE andLADE. In each of the 16 stands, we sampled

16 points using the point-centered quarter method (Greig-Smith 1983) on a systematic grid of 70 x 70 meters or 40 x 40 meters, depending on stand size. Species name, distance to the sample point (m), diameter at breast height (DBH: 1.3 m) (cm) (for trees taller than 1.3m only), age (for trees taller than 1.3 m increment cores of two of the four trees per point were taken at 30 cm stem height), height (m) (using a clinometer), and browsing incidence (presence/absence of leader shoot browsing for trees shorter than 1.3 m) were recorded. Tree rings were counted, the values adjusted for the core height of 30 cm (using regression equations developed for the Park, unpublished data) and then averaged to obtain average stand age.

Results and discussion

By examining long-term data covering a period of 44 years, we found that the 16 forest stands showed different development, but that there was clear evidence that succession from early/mid successional to late successional forests is currently taking place. Overall, we found that within the studied stands the overstory species composition changed markedly: the relative importance of PIMO decreased from 75 to 46% over the past 44 years, while PICE, LADE, PIAB and PISY increased from 9 to 13%, 6 to 23%, 5 to 12% and 5 to 6%, respectively (Table 1). In 2001, we found approximately half the stand density recorded in 1957, while basal area (BA) increased in all but three stands (Table 1). The development of sapling composition showed similar changes. PICE and PIAB increased from 16 to 24%, and 2 to 16%, respectively, while PIMO decreased from 80 to 58%. LADE and PISY saplings remained unchanged comparing the two surveys (Table 1). Comparing the number of saplings found 1957 and 2001, we detected a decrease of more than 66%.

Focusing on the development of the individual stands, we found that the younger stands (106 to 130 years in age) did not yet show changes in overstory species composition, but the sapling layer was subject to changes. Especially PICE began to move in, indicating future changes in stand composition (Table 1). In addition, we detected that these younger stands were much denser in 1957 compared to 2001 indicating that the stands currently are in a maturation phase after completing the self-thinning phase (Oliver and Larson 1996; Table 1). In contrast, most of the stands older than 130 years showed changes in overstory composition. Especially the amount of PIMO decreased greatly (Table 1). In

2001, these stands were either dominated by a mixed conifer forest or by the late successional PICE/LADE community.

These changes in stand structure and composition indicate that the current level of small-scale disturbances, which act at a single-tree basis, do not appear to halt successional development in the stands studied. Such disturbances for example are the infection of PIMO by root rot (*Heterobasidion annosum*, *Armillaria* spp.), which were found to significantly affect the development of forest stands in the Park (Dobbertin et al. 2001), snow blight fungus (*Phacidium infestans*), small windthrows or snow pressure. Another disturbance frequently found in the Park is ungulate browsing. However, although 15% of the PIMO saplings, 31.4% of the PICE saplings, 92% of the LADE saplings and 58.5% of the PIAB saplings were found to be browsed in 2001, browsing does not appear to prevent the succession toward the late successional stage either, thus confirming earlier findings (Kienast et al. 1999, Senn 2000, Krüsi and Moser 2000). The only large-scale disturbances currently influencing the Park's forests are avalanches, which act at the stand scale rather than at the single tree scale. However, avalanches usually follow the same runs, and thus would influence forest succession in these areas, but not in the investigated stands.

In conclusion, our study depicted the successional trends that might take place in many high elevation areas of the Alps once agricultural or silvicultural management of meadows and forests ceases. This assessment is based on the assumption that the frequency of natural disturbances remains similar to the historical level, which clearly is not high enough to keep the succession of these forests at an early stage (i.e. PIMO stage).

Table 1: Stand age, tree species composition of trees > 130 cm (in % of total basal area) and saplings (20 to 130 cm, in % of total saplings), trees/ha, saplings/ha and total basal area for both years of investigation. Averages of all stands given in bold. Stratification of stands in 1957: (A) stand dominated by PIMO, (B) stands dominated by PIMO, (C) stands dominated by stone pine, (C) stands dominated by PIMO and PICE. - = 0%

Stand age 2001 (years)	Type 1957	PIMO (%)				PICE (%)				LADE (%)				PIAB (%)				PISY (%)				Stems/ha (n trees)				Basal area (m²/ha)	
		>130 cm		20-130 cm		>130 cm		20-130 cm		>130 cm		20-130 cm		>130 cm		20-130 cm		>130 cm		20-130 cm		>130 cm		20-130 cm			
		'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01	'57	'01
106	A	100	100	94.7	82.0	-	-	5.3	18	-	-	-	-	-	-	-	-	-	-	-	-	2781	1985	6467	1082	14.5	30.9
109	A	97.1	31.7	94.1	66.7	-	-	4.9	25	2.9	64.8	-	-	-	-	1.0	8.3	-	3.4	-	-	4300	1435	5787	889	16.7	30.9
114	A	99.3	100	99.4	88.7	-	-	0.6	9.7	-	-	-	-	-	-	-	1.6	0.7	-	-	-	1939	1100	3747	826	21.4	16.7
125	A	100	100	100	96.8	-	-	-	3.2	-	-	-	-	-	-	-	-	-	-	-	-	2707	1856	4583	3588	23.2	18.2
127	A	100	100	97.3	100	-	-	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-	1866	1400	4570	1326	14.0	13.5
129	A	62.1	39.4	99.1	80.0	-	-	0.9	1.7	18.1	58.4	-	1.7	0.9	2.2	-	16.7	18.9	-	-	-	1468	1115	2156	914	18.0	37.7
131	A	71.7	15.0	97.2	25.0	-	0.1	-	6.7	0.7	40.5	-	-	10.2	27.0	2.8	68.3	17.4	17.4	-	-	1800	772	2238	568	20.0	47.1
138	A	96.3	81.1	99.4	75.8	-	12.6	0.6	24.2	1.6	-	-	-	2.1	-	-	-	-	6.3	-	-	3043	1058	3448	774	24.6	32.1
145	C	60.3	15.8	63.1	48.3	17.9	4.1	34.4	35.0	0.7	15.4	1.3	-	21.0	64.7	1.3	16.7	-	-	-	-	2120	898	2344	993	13.0	35.1
148	A	77.2	19.3	88.6	47.4	-	-	3.0	7.0	7.5	20.3	-	-	8.5	40.5	8.4	45.6	6.8	19.9	-	-	1970	812	4111	881	11.1	38.3
149	A	79.2	13.7	97.0	50.9	-	-	-	1.8	0.7	30.5	-	1.8	0.2	21.1	3.0	41.8	20.0	34.6	-	3.6	1715	878	1901	695	17.4	44.1
151	B	45.0	2.9	28.7	21.8	29.2	39.5	57.0	78.2	19	57.6	11.5	-	5.1	-	2.9	-	1.7	-	-	-	1462	866	1799	386	19.1	60.6
151	A	99.6	94.9	100	100	-	-	-	-	0.4	5.1	-	-	-	-	-	-	-	-	-	-	2290	2543	1076	826	20.7	36.5
160	A	66.6	21.7	85.1	34.4	-	0.9	1.3	19.7	8.2	52.1	2.7	-	6.4	16.3	10.8	42.6	18.8	9.0	-	3.3	1164	562	2099	451	16.6	46.6
169	B	8.2	2.6	2.0	5.0	64.2	84.9	92.7	80.0	24.2	12.5	4.9	15	3.5	-	0.5	-	-	-	-	-	562	336	1730	517	26.8	35.0
229	B	30.7	2.6	36.4	13.1	33.9	65.5	60.6	67.2	15.6	6.2	1.6	1.6	19.7	22.5	1.4	18.0	-	3.2	-	-	947	529	1724	860	38.7	67.2
Mean		**75**	**46**	**80**	**58**	**9**	**13**	**16**	**24**	**6**	**23**	**1**	**1**	**5**	**12**	**2**	**16**	**5**	**6**	**0**	**0**	**2008**	**1134**	**3111**	**973**	**19.7**	**36.9**

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Paper II

Detecting successional changes in long-term empirical data from subalpine conifer forests

Anita C. Risch[1], Martin Schütz[1], Bertil O. Krüsi[1], Felix Kienast[1], Otto Wildi[1], and Harald Bugmann[2]. Detecting successional changes in long-term empirical data from subalpine conifer forests. *Plant Ecology*. In press.

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Abstract

In many mountain regions, traditional agriculture and forestry are no longer economically viable and less intense land-use is becoming more and more widespread. Thus, the importance of understanding secondary succession in these abandoned systems increases. This study is based on a comparison of historic (1957) and present tree data (2001) from subalpine forest stands located in the Swiss National Park (SNP), where all management was stopped in 1914. The two data sets contain information on tree and sapling density as well as diameter distribution for all tree species present. Using time-series analyses, space for time substitution and multivariate methods (PCoA, minimum spanning tree analysis), we investigated if successional changes can be detected within the forest stands in the SNP.

Our results showed that the stands studied are developing from a stage dominated by mountain pine (*Pinus montana* Miller) to a late-successional stage dominated by Swiss stone pine (*Pinus cembra* L.) and European larch (*Larix decidua* Miller). This shift in

species composition, which was observed in both the tree and sapling layer, was accompanied by a significant decrease in tree density (stems/ha). We also found that stand disturbances, such as fungal diseases, parasitic insects, ungulate browsing, windthrow or snow pressure, have not prevented succession from mountain pine to Swiss stone pine-larch communities. The minimum spanning tree analysis revealed that the sixteen observed 44-year-time-series cover at least 110 years of succession. This time frame is the shortest possible duration for a successional development starting from a 95 to 125-year-old mountain pine stand. The successional changes depicted in our study, indicate how similar areas in the Central European Alps might develop in the near future when management ceases.

Keywords

Central European Alps, forest stand, mountain pine, successional development, Swiss National Park, Swiss stone pine

Introduction

In many mountain regions of Europe, traditional agriculture and forestry have been practiced for hundreds of years. However, with recent changes in the economy, these practices are no longer viable in many of these areas, and traditional agricultural and silvicultural land-uses are unlikely to be continued in many places (Price 1995; Riederer 1996; Bäntzing 1996; Broggi 1998). Therefore, the interest in understanding vegetation development in absence of human intervention has increased considerably over the past decades. It is difficult, however, to assess the long-term development of abandoned or less intensively used ecosystems, especially in Western Europe, where only few areas exist that were not managed over longer time periods.

The Swiss National Park (SNP) is one of the few areas in Western Europe that was not influenced directly by humans during most of the 20th century. Therefore, the Park provides a unique opportunity to study how no longer managed mountain forests may develop in the absence of human intervention. This development, which may take place over large parts of the Alps in the near future, started in the SNP in 1914. Fortunately, long-term data on grassland and forest development of this area is available for an 85-year and 45-year period, respectively. While secondary succession of grasslands has been the focus of numerous studies (Krüsi et al. 1996; Bärlocher et al. 2000; Märki et al. 2000;

Achermann et al. 2000; Schütz et al. 2000a,b,c; Risch et al. 2001), only few have focused on successional processes within the forested areas of the Park (Kienast et al. 1999; Krüsi and Moser 2000). It is known that large parts of the forests were clear-cut several times between the 16th and 19th century (Parolini 1995). Most of these clear-cuts regenerated to mountain pine (*Pinus montana* Miller) dominated forests. Selective timber extraction was maintained within the Park's forests until 1914, but was stopped entirely after the foundation of the Park. Today, mountain pine forests occupy large parts of the SNP, but some slopes are covered with stands dominated by Swiss stone pine (*Pinus cembra* L.) or a mixture of Swiss stone pine and European larch (*Larix decidua* Miller). The latter two forest types represent the late stages of subalpine forest succession in this region (Kurth et al. 1960; Holtmeier 1990; Zoller 1995; Kienast et al. 1999).

It is not known, however, whether the forests that are currently dominated by mountain pine will ever reach a late-successional stage, or if disturbances such as fungal diseases, parasitic insects, ungulate browsing, windthrows and snow pressure incidents will keep these forests in an early- to mid-successional stage. Dobbertin et al. (2001), for example, reported that infection by root rot fungi (*Heterobasidion annosum* (Fr.) Bref., *Armillaria* spp.) led to a partial breakdown within mountain pine stands, which could significantly impact secondary succession within the Park. In contrast, Krüsi and Moser (2000) observed that snow pressure and ungulate browsing in the SNP only marginally affected the successional development within a mountain pine stand.

Based on succession theory (Clements 1936, Watt 1947, Gleason 1926) and existing knowledge on local biotic and abiotic forces (Kurth et al. 1960, Krüsi and Moser 2000, Dobbertin et al. 2001), we developed a forest succession scheme for the forests in the Park (Figure 1). Since an extensive database on the tree and sapling composition of the stands in the SNP exists for the year 1957 (Kurth et al. 1960), we have the opportunity to investigate how the forests developed over time, and to check our theoretical succession scheme based on long-term data. Therefore, the overall objective of this study is to investigate successional patterns based on long-term empirical forest stand data (trees and saplings) in conifer forests of the SNP. Specifically, we address the following questions: i) Are we able to detect succession from mountain pine forests to Swiss stone pine or to Swiss stone pine/larch forests? ii) Which of the theoretically possible successional

changes postulated in Figure 1 can we support with empirical evidence? iii) If forest succession is taking place, how much time is needed to reach the late-successional stage?
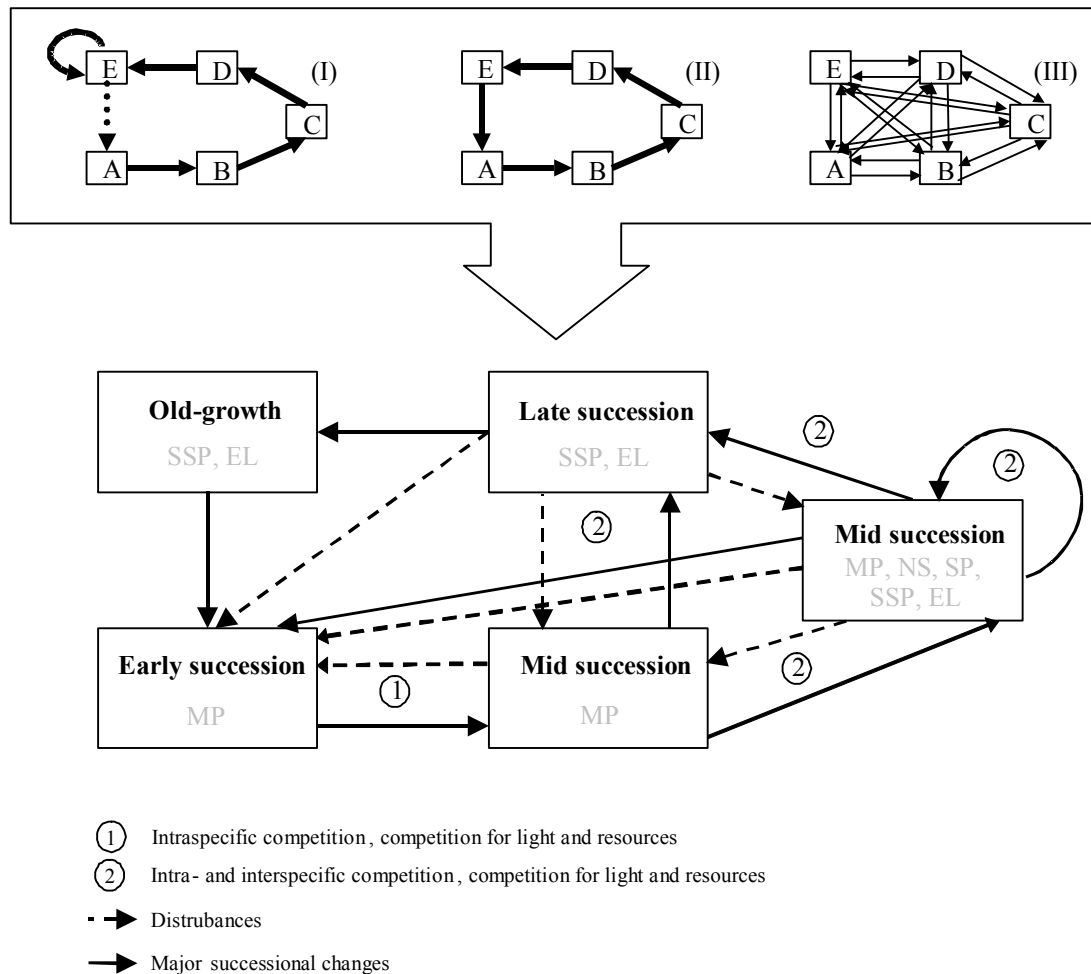

Figure 1: Theoretical models of succession. Upper part: Different schemes of succession theory: (I) convergent model by Clements (1936), (II) cyclic model by Watt (1947), (III) largely stochastic, less predictable model by Gleason (1926). Lower part: Theoretical successional forest stages within the SNP. Driving factors are disturbances, intra- and interspecific competition as well as competition for light and other resources. The dominating tree species of each successional stage are shown: MP = mountain pine, SSP = Swiss stone pine, NS = Norway spruce, EL = European larch, SP = Scots pine.

Study Area

The SNP is located in the southeastern part of Switzerland, covering an area of approximately 170 km^2 (Figure 2); 50 km^2 are comprised with forests, 33 km^2 with alpine grasslands, and 3 km^2 with subalpine grasslands, while ice, snow and rocks occupy the other half of the Park. The elevation of the area ranges from 1350 to 3170 meters above sea level (m a.s.l.). A meteorological station located outside the Park (Buffalora, 1977 m a.s.l.) recorded a mean annual precipitation of 925 ± 162 mm (average ± standard

deviation) and a mean annual temperature of $0.2 \pm 0.7°C$ between 1917 and 1998. The Park's forests are composed of five conifer species. Most abundant are mountain pine, Swiss stone pine and European larch, while Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) occur less frequently (Zoller 1995). Scots pine is not competitive in the cold, high elevation forests found in the SNP (Keller et al. 1998), while Norway spruce is not well adapted to the central alpine climate with relatively low rainfall and mean annual temperatures below 1.5°C (Ellenberg 1996).
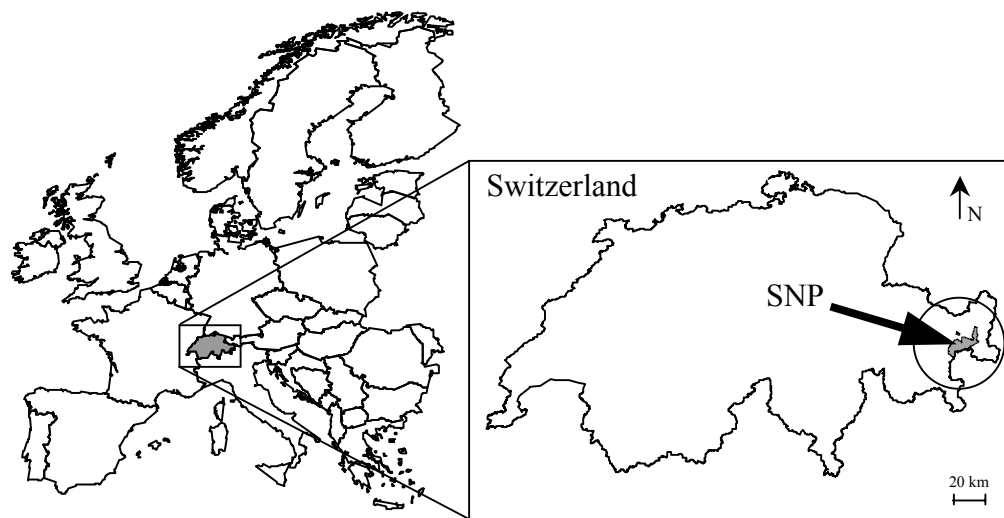

Figure 2: Location of the study area. The Swiss National Park (shaded) is located in the southeastern part of Switzerland.

Methods

Historical data and design for sampling present data

In 1957, Kurth et al. (1960) established a sampling design for the entire forested area of the SNP, excluding avalanche runs. They collected data on stand structure and stand composition on circular plots around the intersections of a systematic 143 m x 143 m grid, resulting in an extensive database. In this database all information on saplings (21 to 130 cm) and trees (> 1.3 m) was aggregated to the stand level. For trees taller than 1.3 m, diameter at breast height (DBH) was recorded (Kurth et al. 1960). Only the stand-level data are available today, but not the plot-level (grid-point level) data. This database forms the historical basis for our study.

In 2001, we re-sampled 16 of the 131 stands delineated by Kurth et al. (1960) in 1957. They were located within an area of approximately 80 km^2 in the center of the Park.

Elevations ranged from 1700 to 2200 m a.s.l. In 1957 the forested area was covered with 73% mountain pine forests (*Erico-Pinetum montanae* and *Rhododendro hirsute-Pinetum montanae*), 11% Swiss stone pine/larch forests (*Larici-Pinetum cembrae*), and 16% different, not clearly defined forest and shrub communities (Kurth et al. 1960; Keller et al. 1998). Using the stratified forest stands in the 1957 survey, 16 stands were randomly selected based on the dominant tree species. Twelve stands were dominated by mountain pine, three stands by stone pine or Swiss stone pine/larch, and one stand by both mountain pine and Swiss stone pine. Since the sapling layer of a forest is important for predicting future species composition, the twelve mountain pine stands were split in three groups of four stands each, based on the number of late-successional Swiss stone pine saplings observed per hectare in 1957 (0, 1-99, and 100-999).

In each of the 16 stands we sampled 16 points using the point-centered quarter method (Greig-Smith 1983) on a systematic grid of 70 m x 70 m or 40 m x 40 m, depending on stand size. At each of the 16 points, four trees taller and four trees shorter than 1.3 m were sampled separately. Species name, distance to the sample point (m), DBH (cm) (for trees taller than 1.3 m only), age (for trees taller than 1.3 m, increment core of two of the four trees per point) and height (m) (using a clinometer) were recorded. Species names follow Lauber and Wagner (1996).

Numerical analyses

We calculated the number of stems per hectare for different DBH classes for trees taller than 1.3 m (0 = 1 – 4 cm; 1 = 5 – 9 cm; 2 = 10 – 19 cm; 3 = 20 – 29 cm; 4 = 30 – 49 cm; 5 = > 50 cm) per species and stand as well as the number of saplings (20 – 130 cm) per hectare for both years of observation. Since the 1957 and 2001 data were collected within the same 16 stands, the paired data sets (1957 and 2001) represent 16 time series. In order to increase the temporal resolution of these time series, we calculated three intermediate relevés per stand by linear interpolation. In a first step, we carried out a principal co-ordinate analysis (PCoA) using untransformed data and van der Maarel's resemblance measure (Wildi and Orlóci 1996). The different DBH classes of each species were treated as separate descriptors. In a next step, we substituted space for time to obtain the general successional development of the forest stands in the SNP (Pickett 1989). The time series were merged based on relevé similarity with the method described in detail by Wildi and Schütz (2000). The minimum spanning tree method applied, yielded the order of the

merging stages, and the number of relevés corresponding to the same point in time (Gower and Ross 1969; Wildi and Schütz 2000). All relevés belonging to the same point in time were averaged. For each average relevé we then calculated a stand density index (SDI) per species and DBH class, using the formula (1):

$$SDI \ = \ \sum_{i} \{[(DBH_i/25.4)^{1.6}] * stem_i\} \tag{1}$$

where DBH_i is the midpoint of each DBH class, and $stem_i$ the number of trees/ha in a particular DBH class. For the DBH class bigger than 50 cm, the average of all trees bigger than 50 cm sampled in 2001 was used for calculations. Since late-successional stages are represented by fewer but larger trees than early-successional stages, the SDI allows us to compare the different successional stages more easily (Long and Daniel 1990).

Results

The principal co-ordinate analysis (PCoA) of the tree and sapling data showed a clear successional trend (Figure 3A). We found that the points in the lower right corner of Figure 3A represent stands dominated by mountain pine only, while the points in the lower left corner represent stands dominated by Swiss stone pine or Swiss stone pine/larch (Figure 3A). The speed of successional development varied considerably among the 16 stands, as indicated by the different lengths of the arrows in Figure 3B.
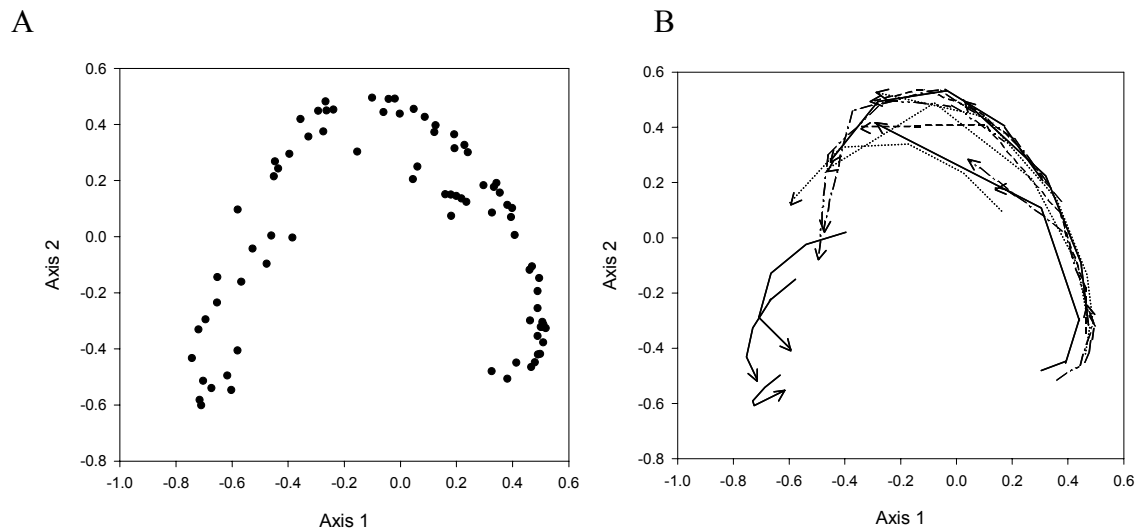
A

B

Figure 3: PCoA results derived from 16 time series. Each series consists of two original and three interpolated relevés. The first two axes explain 34.16% and 21.9% of the variance, respectively. A: The black dots represent the 80 relevés of the 16 time series. The ones in the lower right corner belong to mountain pine dominated stands, the ones in the lower left to Swiss stone pine/larch dominated stands. B: The 16 arrows represent the temporal development of the 16 different time series. The starting point of each arrow represents a reléve in 1957, while its end point represents the respective reléve in 2001. The longer the arrow, the faster the successional development.

The minimum spanning tree analysis generated a merged time series of eleven successive time stages (t_1 to t_{11}). The number of relevés (n) averaged at each time stage were $t_1 = 1$, $t_2 = 1$, $t_3 = 4$, $t_4 = 6$, $t_5 = 6$, $t_6 = 12$, $t_7 = 16$, $t_8 = 13$, $t_9 = 9$, $t_{10} = 9$, and $t_{11} = 3$, respectively. Since the eleven time stages were separated by eleven years (or ten time steps) each, the shortest possible time period needed for the succession from mountain pine to Swiss stone pine or Swiss stone pine/larch forest was 110 years. The tree layer composition at time t_1 (time stage one) contained 100% mountain pine. Larch trees were found first at t_3, but contributed less than 1% of the total stems/ha, while Norway spruce and Scots pine appeared first at t_4, and Swiss stone pine at t_5. At time stage t_{11} (after ten time steps or 110 years), we found a tree composition (total stems/ha) of 24.8% mountain pine, 38.5% Swiss stone pine, 29.6% larch, and 3.6% Scots pine and Norway spruce, respectively (Figure 4). Between t_1 and t_{11} the total number of stems per hectare dropped significantly from 2707 to 492 stems/ha ($p < 0.0001$, Figure 4).
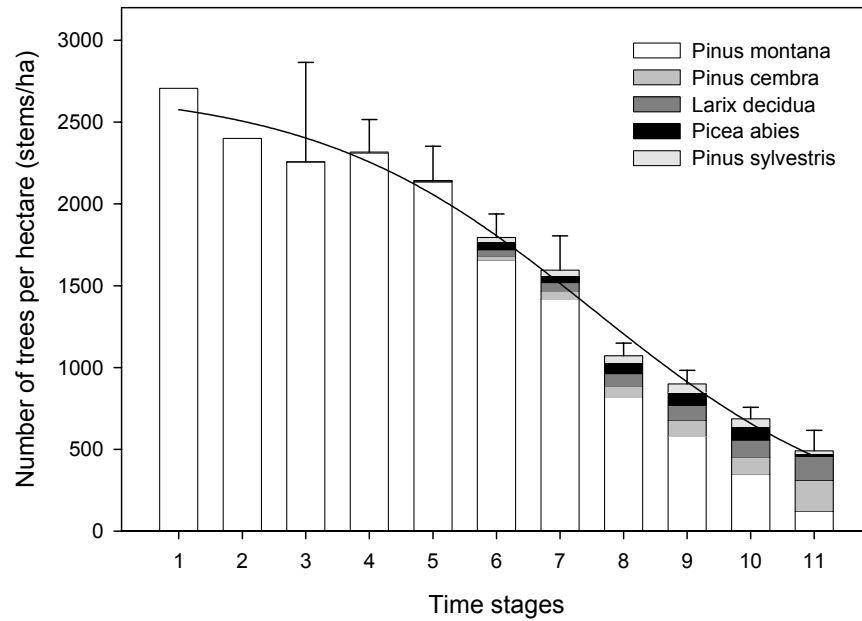
Figure 4: Temporal changes in total number of trees per hectare (total stems/ha) for all species over 11 time stages (t_1 to t_{11}). The number of stems/ha are added for each time stage and all species. Standard errors (SE) of the total number of stems/ha are shown as error bars (n: $t_1 = 1$, $t_2 = 1$, $t_3 = 4$, $t_4 = 6$, $t_5 = 6$, $t_6 = 12$, $t_7 = 16$, $t_8 = 13$, $t_9 = 9$, $t_{10} = 9$, $t_{11} = 3$), and the sigmoidal regression line is shown in black (n = 11, $r^2 = 0.985$).

The development of SDI between t_1 and t_{11} of each of the five species and each different DBH class is shown in Figure 5 (A-E). The SDI of mountain pine in DBH classes 0, 4 and 5 only changed little over time, while the SDI for classes 1, 2 and 3 decreased considerably between t_1 and t_{11} (Figure 5A). The strongest decrease was found for trees in DBH class 2 (10 to 19 cm), where the SDI dropped from 384 at t_1 to 12 at t_{11}. In contrast, the development of the two late-successional species, Swiss stone pine/larch, showed a strong increase in SDI for the DBH classes 4 and 5 after t_5, while the SDI for the DBH classes 0, 1, 2 and 3 only changed little over the period studied (Figures 5B and 5C). Temporary increases in SDI were detected for both Scots pine and Norway spruce at mid-succession. However, the values for these two species were considerably lower compared to the three tree species, indicating that they do not play a major role during succession in the study area (Figures 5D and 5E).
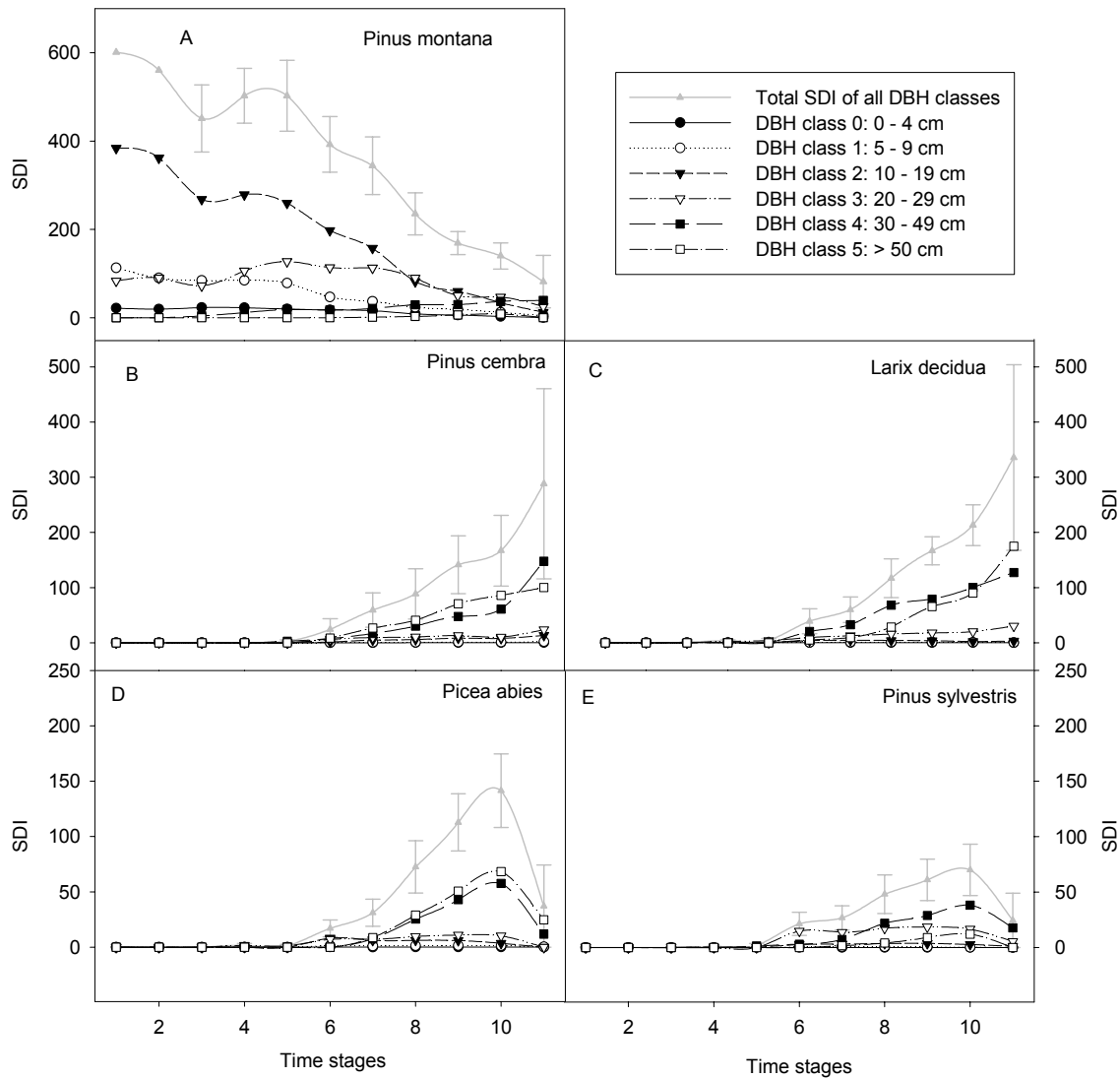
Figure 5: Development of stand density over time. Changes are shown for the total SDI (in grey) of each of the five species and for the SDI of each DBH class and species over 11 time stages (t_1 to t_{11}). Standard errors (SE) of total SDI per species are shown as error bars (n: $t_1 = 1$, $t_2 = 1$, $t_3 = 4$, $t_4 = 6$, $t_5 = 6$, $t_6 = 12$, $t_7 = 16$, $t_8 = 13$, $t_9 = 9$, $t_{10} = 9$, $t_{11} = 3$). A: mountain pine; B: Swiss stone pine; C: European larch; D: Norway spruce; E: Scots pine.

The development of the relative abundance of saplings (trees between 21 and 130 cm in height) of all five tree species between t_1 and t_{11} is shown in Figure 6. The relative abundance of mountain pine saplings decreased strongly over time (p < 0.0001), while the relative number of Swiss stone pine increased significantly (p < 0.0001, Figure 6). Mountain pine saplings decreased from 100% at t_1 to only 19.9% at time stage eleven (t_{11}). The relative abundance of Swiss stone pine saplings increased from 0% at t_1 to 60% at t_{11}, while the one of larch and Norway spruce increased from 0% at t_1 to 5.3% and 13.5% at t_{11}, respectively. The relative abundance of Scots pine changed only little over time (0% to 1%).
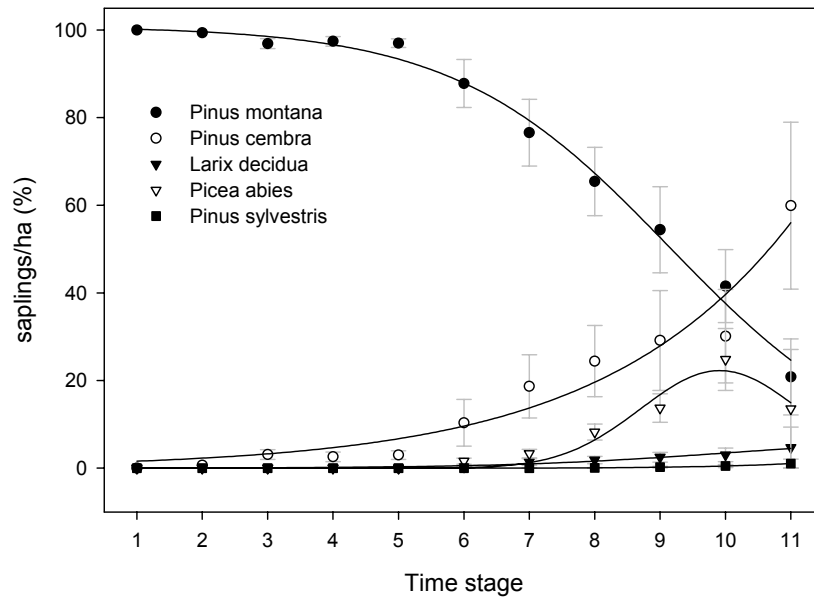
Figure 6: Development of the relative abundance of saplings (%) between t_1 and t_{11} for all five species. Standard errors (SE) of the relative abundance of each species are shown as error bars (n: $t_1 = 1$, $t_2 = 1$, $t_3 = 4$, $t_4 = 6$, $t_5 = 6$, $t_6 = 12$, $t_7 = 16$, $t_8 = 13$, $t_9 = 9$, $t_{10} = 9$, $t_{11} = 3$). Regression lines (sigmoidal and gaussian) are shown: n = 11 time steps for all five species. $r^2_{Pinus\ montana} = 0.99$, $r^2_{Pinus\ cembra} = 0.95$, $r^2_{Larix\ decidua} = 0.95$, $r^2_{Picea\ abies} = 0.95$, $r^2_{Pinus\ sylvestris} = 0.99$. $p < 0.0001$ for all species.

In order to calculate the approximate age of the forest stands at the beginning of the time series (t_1), we examined how old the trees in mountain pine dominated forest were in 1957. Counting tree rings from cores taken in 2001, we found that mountain pines in DBH class 5 were between 140 to 170 years old. Therefore, the average mountain pine tree in DBH class 5 was calculated to be 95 to 125 years old in 1957.

Discussion

The overall goal of this study was to investigate whether successional changes occurred in the mountain pine dominated forests of the SNP during the past 45 years. By examining long-term forest stand data (tree and sapling layer) covering a period of 44 years (1957 to 2001), we found that i) the forest stands studied were in different successional stages and that ii) there is clear evidence that succession from mountain pine to Swiss stone pine or Swiss stone pine/larch dominated forests took place. Although disturbances such as infection of mountain pines by root rot fungi (*Heterobasidion annosum*, *Armillaria* spp.) were found to significantly affect the development of forest stands in the Park (Dobbertin et al. 2001), they do not appear to effectively prevent the successional development. Likewise, ungulate browsing, another frequent disturbance,

does not appear to halt succession toward Swiss stone pine/larch forests. These results agree with other studies conducted in the area (Kienast et al. 1999; Senn 2000; Krüsi and Moser 2000). The same relationship probably holds true for disturbances by snow blight fungus (*Phacidium infestans* Karst.), windthrows and snow pressure. Consequently, we found that the current level of forest disturbance does not permanently favor the regeneration of only mountain pine. Thus, we were able to empirically support some of the successional changes illustrated in Figure 7. The main ecological forces responsible for the successional development depicted are inter- and intraspecific competition, resulting in i) a reduction in the total number of stems/ha and ii) changes in species composition.

The minimum spanning tree analysis showed that a minimum of 110 years elapses from the early- to the late-successional stage. While the 16 stands studied cover an actual time of observation of 44 years each, together they cover a minimum of 110 years of forest succession. Since the tree survey indicated that the average mountain pine forest studied in 1957 had an age of 95 to 125 years, we conclude that a minimum of 205 to 235 years (95 to 125 plus 110 years) after clear-cut is required to reach the late-successional Swiss stone pine/larch stage. Swiss stone pine and European larch are known to live 400 to 1200 years (Mayer 1992; Richardson and Rundel 1998) and 400 to 800 years, respectively (McComb 1955; Mayer 1992). Therefore, the late-successional species present in the 210 to 240 year old stands today could persist for another 200 to 800 years.

However, the 205 to 235 years reflect the shortest possible pathway for the successional development of subalpine conifer forests of the study area, due to the minimum spanning tree approach applied (Gower and Ross 1969). Wildi and Schütz (2000) emphasized that these time stages should be taken as surrogates for hypothetical rather than actual time units, and should therefore be interpreted with caution. When building a succession model for subalpine grasslands (development from tall-grass/tall-herb meadows to mountain pine forests), they found a time frame of 390 to 580 years, depending on the approach they used. Risch et al. (2001) found a range of 290 to 870 years when applying one of the models by Wildi and Schütz (2000) to a subalpine meadow in the Park. These results show that changes in species composition may proceed at different speed in the same area, making a general assessment of succession rates in the SNP difficult.

① Intraspecific competition, competition for light and resources

② Intra- and interspecific competition, competition for light and other resources

③ Past clearcut and timber management

➡ Empirically elucidated successional forest changes
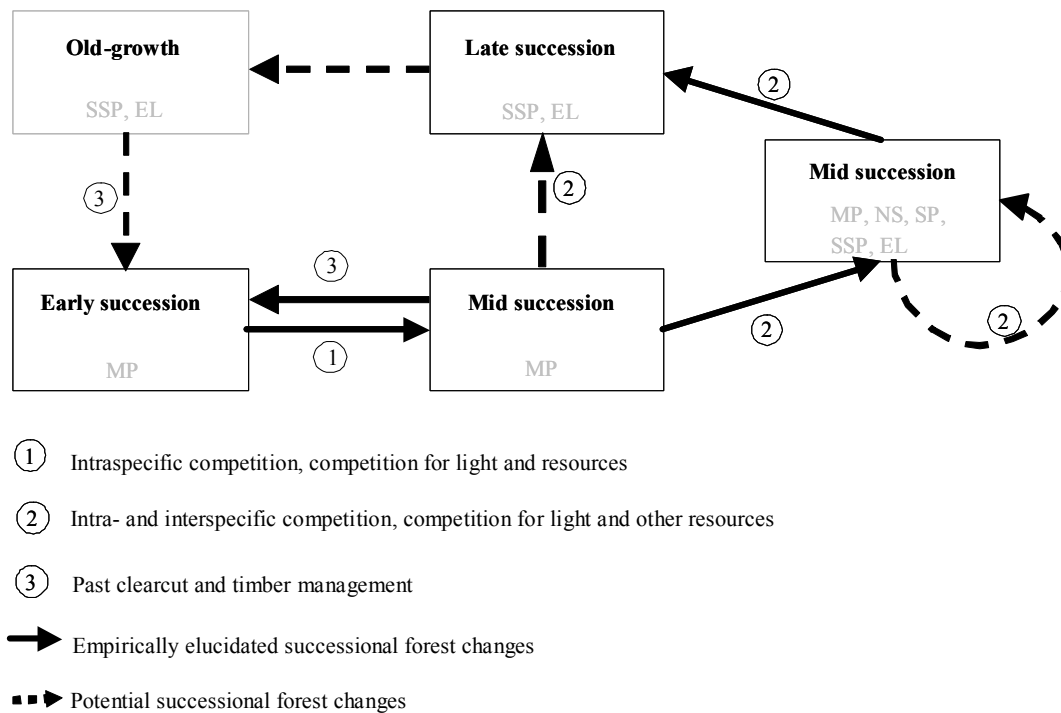
■■▶ Potential successional forest changes

Figure 7: Model of forest succession in the SNP. Empirically delineated changes in tree composition during succession in the SNP are shown with black, solid arrows. Disturbances at the current level of impact were not found to prevent successional changes. The dashed arrows represent other potential changes during succession that were not empirically delineated in this study. Dominating tree species of each successional stage are shown: MP = mountain pine, SSP = Swiss stone pine, NS = Norway spruce, EL = European larch, SP = Scots pine.

Nevertheless, keeping in mind that the successional phase of 205 to 235 years is an estimate of the fastest possible development of mountain pine forests to Swiss stone pine/larch stands, the forest succession reconstructed in this study requires a similar amount of time as successional changes found in a range of other studies. Along the southern edge of the eastern Alps, Italy, Piussi (1994) and De Mas and Piutti (1994) found that forests entering the late-successional stage dominated by Swiss stone pine ranged in age from 200 to 450 years, while Sauermoser (1994) found ranges between 150 and 330 years in the Lechtal Alps, Austria. Smolonogov (1994) suggested that the age of Siberian stone pine (*Pinus sibirica* Du Tour) forests entering the late-successional stage ranged between 180 and 350 years in Eurasia. Keane (2001) modeled succession of subalpine forests in the Western United States, showing that these forests will enter the late-successional stage dominated by whitebark pine (*Pinus albicaulis* Engelm.) within 100 to 200 years. Sala et al. (2001) and Callaway et al. (2000) reported fire intervals averaging 260 years, with a maximum of 458 years in undisturbed whitebark pine forests in the northern Rocky Mountains, USA.

In conclusion, our study depicted the successional trends that are likely to take place in many high elevation areas of the Central European Alps once agricultural or silvicultural management of meadows and forests ceases. This assessment is based on the assumption that the frequency of current disturbances remains similar to the historical level, which clearly is not high enough to keep these forests at an early-successional stage (i.e., mountain pine stage).

Acknowledgements

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Paper III

Structure and long-term development of subalpine *Pinus montana* Miller and *Pinus cembra* L. forests in the Central European Alps

Anita C. Risch[1], Linda M. Nagel[2], Martin Schütz[1], Bertil O. Krüsi[1], Felix Kienast[1], and Harald Bugmann[3]. Structure and long-term development of subalpine *Pinus montana* Miller and *Pinus cembra* L. forests in the Central European Alps. *Forstwissenschaftliches Centralblatt* 122: 219 – 230.

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Abstract

Since traditional agriculture and forestry are no longer economically viable in many regions of the European Alps, subalpine forests will become less managed or completely abandoned in the near future. Therefore, the interest in understanding how forest stands will develop after abandonment has increased considerably over the past two decades. While much is known about stand structure and stand development of Norway Spruce (*Picea abies* L.) forests, almost no knowledge is available about the same processes in forest communities of the Central European Alps. In the Swiss National Park (SNP), the forested area is comprised of mountain pine (*Pinus montana* Miller), Swiss stone pine/larch, (*Pinus cembra* L./*Larix decidua* Miller) and mixed stands. When the Park was founded in 1914 all management activities were stopped. Therefore, this area offers the

opportunity to study stand development and changes in stand structure after abandonment. We compared historic (1957) and present data (2001/02) from 19 stands that were grouped into characteristic stand types: "mountain pine", "mixed", and "stone pine". We detected significant decreases in total tree density (stem/ha) and sapling density (saplings/ha) of 45 to 57%, and 64 to 76%, respectively, over the 45 years of observation for all stand types. These changes were strongly related to decreases in the number of shade intolerant mountain pine trees. Simultaneously the amount of non-standing woody residue increased from less than 4 t/ha to 36 to 67.7 t/ha, and the density of standing dead wood (stems/ha) decreased significantly between 72 and 94%. The biomass of standing dead wood (t/ha), however, only changed slightly between 1957 and 01/02. Our results describe the successional development of continental subalpine forests after abandonment, and outlines changes that might take place in similar areas in the near future.

Introduction

In many regions of the world mountain forests are of great relevance for both the environment and human societies. They are important for the hydrology and biodiversity of entire continents (cf. Riederer 1996; Becker and Bugmann 2001, Brun 2002) as well as for protection against natural hazards, e.g. avalanches (Schönenberger 2000, Bebi et al. 2001, Bachofen and Zingg 2001). Stand structure and development of mountain forests have been studied extensively (e.g. Callaway 1998, Kienast et al. 1999, Binkley et al. 2003, Tomback et al. 2001). Studies in the United States and Canada have generally focused on different high-elevation forest communities (e.g. Binkley et al. 2003, Tomback et al. 2001), while European researchers have mostly studied the dominating forest type in the Alps, the Norway spruce (*Picea abies* (L.) Karst.; PIAB) forests (e.g. Bürki 1981, Strobel 1997, Bachofen and Zingg 2001, Stöckner 2002). Studies in other mountain forest communities, such as forests dominated by Swiss stone pine (*Pinus cembra* L.; PICE), mountain pine (*Pinus montana* Miller; PIMO) or European larch (*Larix decidua* L.; LADE) have only rarely been the focus of scientific research (Brang

1989, Piussi 1994, De Mas and Piutti 1994, Krüsi and Moser 2000). Therefore, little is known about stand structure and stand development of these communities. Since the percentage of forested areas in mountain regions has increased over the past two decades due to land abandonment (Price 1995, Bäntzing 1996, Piussi 2000), it is important to gain knowledge about stand structure and stand development of all subalpine forest types and how these forests will develop in the future. However, it is difficult to assess the natural long-term development of mountain forests in Western Europe, since there are few areas with a history of no or little management.

The Swiss National Park (SNP) is one of the few areas in Western Europe that was not influenced directly by humans during most of the 20th century. Consequently, the Park provides the rare opportunity to investigate changes in stand structure and stand development. Since an extensive database exists for the SNP's forests from the year 1957 (Kurth et al. 1960), we have the opportunity to investigate stand development during 45-years without human interference. The Park's forests are composed of five conifer species. PIMO, PICE, and LADE are the dominant species, while Scots pine (*Pinus sylvestris* L.; PISY) and PIAB are less important (Zoller 1995). PISY is not competitive in the cold climate at high-elevations in the SNP (Keller et al. 1998), and PIAB is not well adapted to the central alpine climate with relatively low rainfall, and mean annual temperatures lower than 1.5°C (Ellenberg 1996). Today, stands dominated by PIMO occupy large parts of the Park, while some other areas are covered with forests comprised of PICE, a mixture of PICE and LADE or mixed species stands. As an analysis of successional pathways revealed (Risch et al. 2003), PIMO dominated forests are the early- to mid-successional forest type of the area, developing into mid-successional mixed species stands, and further to PICE/LADE stands. Since the Middle Ages, large parts of the PIMO forests in the SNP (but also elsewhere) were clear-cut on short rotations for energy supply, but PICE and LADE forests were left standing until they were approximately 250 years old. Single trees were then cut selectively and used for construction purposes and furniture manufacture (cf. Parolini 1995). The clear-cut patches regenerated with PIMO forests. The date of the last clear-cuts is not known with certainty, but likely occurred in the middle of the 19th century. After the last clear-cuts, selective timber extraction for some species was maintained up to 1914, but these activities were also stopped entirely after the founding of the Park (Parolini 1995).

Objectives

The objective of this study was to examine stand structure and stand development in the no longer managed subalpine conifer forests of the SNP. In particular, we investigated how the species composition of (a) living trees, (b) dead trees, and (c) saplings, as well as (d) stand density and (e) dead wood biomass changed in three different stand types over this period.

Study area and methods

The SNP is located in the southeastern part of Switzerland and covers an area of approximately 170 km^2, 50 km^2 of which are covered with forests. The elevation of the area ranges from 1350 to 3170 meters above sea level (m a.s.l.), and the mean annual precipitation and mean annual temperature are 925 ± 162 mm and 0.2 ± 0.7 °C, respectively.

Historical data and present data sampling design

Kurth et al. (1960) established a sampling design for the entire forested area of the SNP using a systematic grid of 143 m x 143 m. This resulted in an database in which all information on saplings (21 to 130 cm tall), trees (>130 cm) and dead trees was aggregated to the stand level. For trees >130 cm, diameter at breast height (DBH; 130 cm) was recorded (Kurth et al. 1960). Today, only the stand-level data are available, but not the individual plot-level (grid-point level) information. This database forms the historical basis for our study.

In 2001 and 2002 (01/02), we re-sampled 19 of the 131 stands delineated by Kurth et al. (1960). They were located within an area of approximately 80 km^2 in the center of the Park at elevations ranging from 1700 to 2200 m a.s.l. The stands were randomly selected in proportion to their abundance in 1957 (Kurth et al. 1960), and were then divided into stand types based on their species composition, tree and stand density in 1957: (1) stands dominated by PIMO (hereafter referred to as "mountain pine"); (2) stands dominated by PIMO but with considerable amounts of all other species ("mixed"); and (3) stands dominated by PICE ("stone pine"). These three groups contained six, six, and seven stands, respectively.

We sampled 16 points in each stand with the point-centered quarter method (Greig-Smith 1983) on a systematic grid of 70 m x 70 m or 40 m x 40 m, depending on stand size. Four trees taller and four trees shorter than 130 cm were sampled separately at each of the points. Species name, distance to the midpoint of the sampling location (m), DBH (cm), condition of the tree (dead/alive; browsed/unbrowsed for saplings only), and tree height (m) (using a clinometer) were recorded. At each of the 16 points, canopy closure was measured with a densiometer, taking four measurements around the center of each sampling point in all cardinal directions (Lemmon 1957).

At the stand center we conducted a woody residue survey to estimate the amount of laying dead wood (t/ha), using the planar intersect method described by Brown (1974). Three transects, each 15.2 m long, were laid out dividing 360 degrees around the stand center into three equal sections. Woody debris on the forest floor and soil wood (main longitudinal axis buried below the forest floor surface) were measured along each transect. Woody debris was divided into four diameter classes: 0.6-2.5 cm, 2.5-7.6 cm, >7.6 cm 'sound', and >7.6 cm 'rotten'. Diameter of 'sound' and 'rotten' woody residue was measured. 'Rotten' was defined as over 50% of the area of the stem showing advanced decay. Soil wood was categorized in brown and white rot decay classes, width and depth were measured. Woody residue was also measured in 1957, but the stand level data is not available. Kurth et al. (1960), however, gave estimates of woody residue for certain regions of the SNP. These values ranged from 0.01 to less than 5 m^3.

Numerical analyses

We calculated tree density (number of stems/ha) for different DBH classes for the living trees (0 = 1 – 4 cm; 1 = 5 – 9 cm; 2 = 10 – 19 cm; 3 = 20 – 29 cm; 4 = 30 – 49 cm; 5 => 50 cm) per species and stand, sapling density per species and stand as well as dead tree density per stand. To get an estimate for stand density we calculated a stand density index (SDI) for the living trees by using the midpoint of each DBH class weighed by the tree density in a particular DBH class (Long and Daniel 1990). For the DBH class > 50 cm, the average of all trees with a DBH > 50 cm was used.

The data were then averaged for each of the three stand types ("mountain pine", "mixed", and "stone pine"). Since Kurth et al. (1960) distinguished between three different tree health conditions ('alive', 'dead' and 'condition unknown' [=heavily damaged, most likely dead]), we pooled the data for the dead trees and the trees of unknown condition

from the year 1957. We then calculated the total biomass of standing dead trees in 1957, by multiplying the volume (m³) of standing dead trees per stand (available from the historical data; Kurth et al. 1960), with the specific wood density for each species (PIMO: 0.8 g/cm³, PICE: 0.44 g/cm³, LADE: 0.55 g/cm³, PIAB: 0.43 g/cm³; PISY: 0.43 g/cm³; Trendlenburg and Mayer-Wegelin 1955, Guggenbühl 1962, Stiftung Arbeitskreis Schreinermeister 1991). Standing dead tree volume for 01/02 was calculated using allometric biomass equations for the different tree species (Kaufmann 2002). Total biomass per hectare was then calculated by multiplying biomass with specific wood density, same as for the 1957 data.

Variance analyses were conducted for each of the three stand types to evaluate if living tree and stand density, sapling density, standing dead tree density, and standing dead tree biomass significantly changed over time. The same analyses were applied to evaluate stand type differences in canopy closure. The significance level was 0.05 for all statistical analysis, differences between stand types were tested using the Bonferroni post-hoc test.

Results

Stand development: living trees and saplings

Between 1957 and 01/02 significant decreases in total tree density were found for all stand types ("mountain pine": -45%; "mixed": -57%; "stone pine": -56%; Table 1), and shifts to larger DBH-classes were detected (Figure 1). Changes in total tree density within all three stand types were strongly related to decreases in the number of PIMO trees, while the tree density of the other species did not reveal significant changes (Table 1). Total stand density (results given as SDI) only significantly changed in the "mixed" and "stone pine" stand type, but not in the "mountain pine" type (Table 2). Despite the significant decreases of PIMO (stems/ha) in all three stand types, PIMO-SDI only changed significantly within the "stone pine" stand type. In the "stone pine" stand type the SDI of PICE also increased significantly, while a significant increase in the SDI of LADE and PIAB was observed in the "mixed" type (Table 2, Figure 1). Between 1957 and 01/02 species composition (%), both in terms of stems/ha and SDI changed markedly in the "mixed" and "stone pine" stand types, but only showed minor changes in the "mountain pine" stand type (Table 1, Table 2). Canopy closure, measured in 01/02, was lowest in the stand type with the lowest total SDI ("mountain pine": 43.1%), and

significantly differed from the values measured in the other two stand types ("mixed": 58.9%, "stone pine": 67.2%; p = 0.0047).
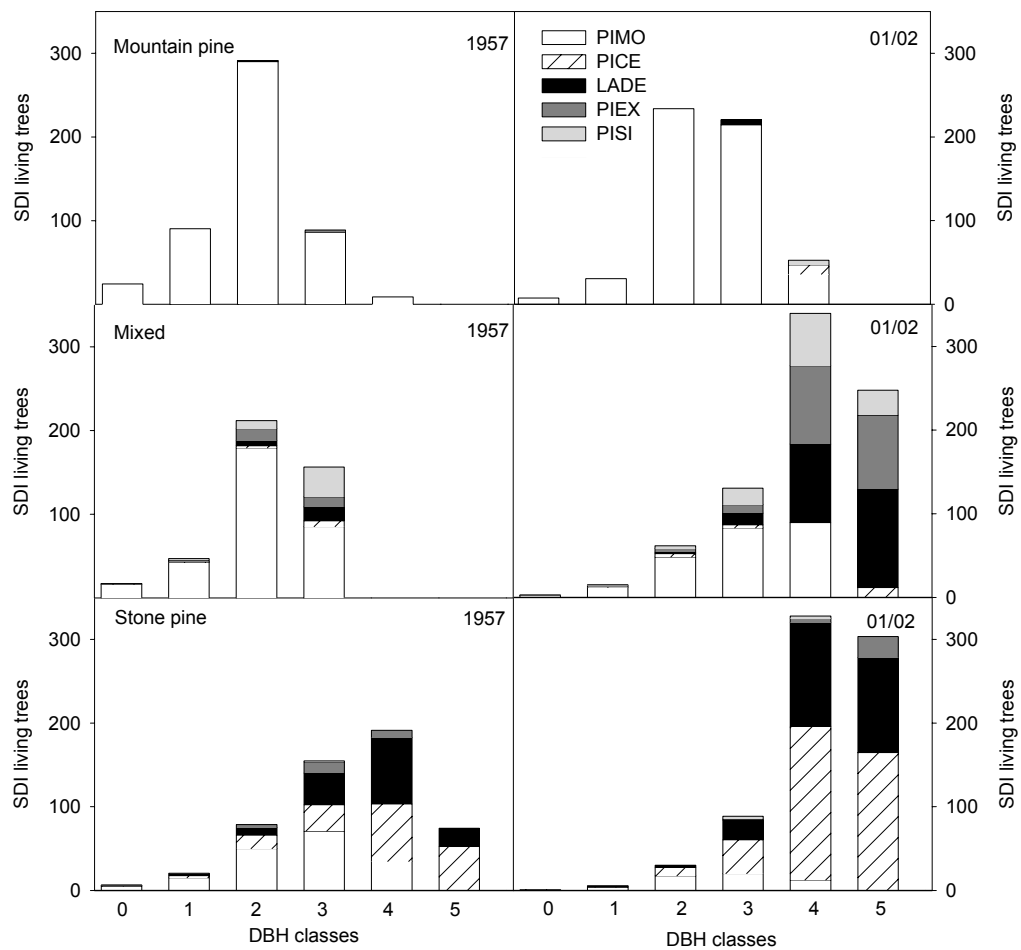

Figure 1: Species composition and SDI of all living trees >130 cm for the different forest stand types in 1957 and 01/02. Each bar shows the sum of SDI for all 5 species for each DBH class. DBH classes: 0 = 1 – 4 cm; 1 = 5 – 9 cm; 2= 10 – 19 cm; 3= 20 – 29 cm; 4 = 30 – 49 cm; 5 = > 50 cm.

Table 1: Tree density (stems/ha), and relative importance of the different tree species (%) in 1957 and 01/02 per stand type. Standard errors are given in parentheses; differences between the two sampling years were tested separately for each stand type using ANOVA (significance level α = 0.05).

	Tree density (stems/ha)								
Species	Mountain pine			Mixed			Stone pine		
	1957	2001	p-value	1957	2001	p-value	1957	2001	p-value
PIMO	2431 (195)	1335 (225)	*<0.01*	1497 (142)	426 (68)	*<0.01*	529 (128)	114 (40)	*0.01*
PICE	0 (-)	6 (6)	*0.34*	24 (21)	32 (17)	*0.63*	167 (27)	214 (29)	*0.25*
LADE	4 (3)	7 (7)	*0.71*	38 (17)	93 (12)	*0.12*	141 (36)	131 (29)	*0.84*
PIAB	2 (2)	0 (-)	*0.34*	82 (26)	118 (30)	*0.91*	37 (28)	9 (9)	*0.38*
PISY	2 (2)	3 (3)	*0.7*	73 (21)	69 (25)	*0.90*	1 (1)	5 (5)	*0.46*
Total	**2439 (196)**	**1351 (227)**	*<0.01*	**1714 (139)**	**738 (69)**	*<0.01*	**875 (113)**	**473 (55)**	*0.01*

	Distribution (%)					
Species	Mountain pine		Mixed		Stone pine	
	1957	2001	1957	2001	1957	2001
PIMO	99.7	98.8	87.3	57.7	60.5	24.1
PICE	-	0.5	1.4	4.3	19.1	45.2
LADE	0.2	0.5	2.2	12.6	16.1	27.7
PIAB	<0.1	-	4.8	16.0	4.2	1.9
PISY	<0.1	0.2	4.3	9.4	0.1	1.1

Table 2: Stand density and relative importance of stand density expressed as SDI and % SDI, respectively, for each stand type for both sampling periods. Standard errors are given in parentheses; differences between the two sampling years were tested separately for each stand type using ANOVA.

	Stand density (SDI)								
Species	Mountain pine			Mixed			Stone pine		
	1957	2001	p-value	1957	2001	p-value	1957	2001	p-value
PIMO	499 (42)	522 (79)	*0.81*	323 (44)	235 (85)	*0.38*	176 (41)	54 (19)	*0.02*
PICE	0 (-)	11 (11)	*0.31*	10 (8)	20 (12)	*0.44*	172 (26)	400 (54)	*<0.01*
LADE	2 (1)	6 (6)	*0.49*	23 (13)	227 (44)	*<0.01*	151 (35)	265 (68)	*0.16*
PIAB	2 (2)	0 (-)	*0.34*	29 (9)	199 (38)	*<0.01*	26 (35)	31 (31)	*0.91*
PISY	1 (1)	6 (6)	*0.40*	47 (13)	116 (35)	*0.09*	1 (1)	6 (6)	*0.43*
Total	**503 (196)**	**545 (5)**	*0.67*	**432 (55)**	**798 (93)**	*<0.01*	**526 (55)**	**756 (68)**	*0.02*

	Distribution (%)					
Species	Mountain pine		Mixed		Stone pine	
	1957	2001	1957	2001	1957	2001
PIMO	99.2	95.8	74.8	29.5	33.5	7.1
PICE	-	2.0	2.3	2.5	32.7	52.9
LADE	0.4	1.1	5.3	28.5	28.7	35.1
PIAB	0.4	-	6.7	25.0	4.9	4.1
PISY	0.2	1.1	10.9	14.5	0.2	0.8

Same as total tree density, total sapling density (saplings/ha) significantly decreased during the 45 years of observation within all three stand types ("mountain pine": -65%; "mixed": -76%; "stone pine": -64%; Table 3). Sapling composition (%), however, only changed in the "mixed" stand type (Table 3). In the stand type with lowest canopy closure ("mountain pine"), the highest sapling density was observed. In 01/02, the tallest saplings were those of PIMO, while PISY were the smallest (Table 3). Both PIAB and LADE

were browsed heavily (apical shoots), while PIMO and PISY were less frequently subject to browsing (Table 3).

Stand development: dead trees and woody residue

The density of standing dead trees decreased significantly over the 45 years of observation in all three stand types ("mountain pine": -72%; "mixed": -94%; "stone pine": -79%; Figure 2, Table 4). However, the biomass of standing dead trees (t/ha) significantly changed in the "stone pine" stand type only (Table 4). PIMO had the highest fraction of all standing dead trees in the two PIMO dominated stands ("mountain pine": 1957 – 99.5%, 01/02 – 99%; "mixed": 1957 – 93.5%, 01/02 – 85.5%), while PIMO, LADE, and PICE all contributed to the standing dead biomass in the "stone pine" type (Figure 2). The percentages of dead trees of total standing trees (living and dead) in 1957 were 31%, 49%, and 29% for "mountain pine", "mixed" and "stone pine", respectively, while the values in 01/02 were 19%, 11%, and 14%, respectively.

Table 3: Sapling density (saplings/ha) and relative importance of sapling density (%) in each stand type for both sampling periods, height and percentage of browsed saplings (apical shoots) in 01/02. Number of saplings per species to calculate averages: PIMO = 598, PICE = 352, LADE = 37, PIAB = 150, PISY = 4. Standard errors are given in parentheses; differences between the two sampling years were tested separately for each stand type using ANOVA.

Species	Sapling density (saplings/ha)								
	Mountain pine			Mixed			Stone pine		
	1957	2001	*p-value*	1957	2001	*p-value*	1957	2001	*p-value*
PIMO	3897 (682)	1307 (445)	*0.01*	2187 (311)	278 (75)	*<0.01*	238 (95)	82 (23)	*0.14*
PICE	85 (54)	95 (34)	*0.88*	168 (129)	93 (48)	*0.60*	765 (187)	275 (69)	*0.03*
LADE	0 (-)	0 (-)	-	32 (17)	2 (2)	*0.12*	107 (33)	33 (12)	*0.06*
PIAB	0 (-)	2 (2)	*0.34*	155 (51)	232 (37)	*0.33*	16 (7)	21 (21)	*0.82*
PISY	0 (-)	0 (-)	-	0 (-)	6 (4)	*0.16*	0 (-)	0 (-)	-
Total	**3982 (722)**	**1404 (445)**	***0.01***	**2541 (327)**	**611 (134)**	***<0.01***	**1127 (232)**	**411 (100)**	***0.02***

Species	Distribution (%)						Sapling condition	
	Mountain pine		Mixed		Stone pine		Height	Browsed saplings
	1957	2001	1957	2001	1957	2001	(cm)	(%)
PIMO	97.9	93.1	86.1	45.5	21.1	20.0	62.6	18.6
PICE	2.1	6.8	6.6	15.2	67.9	66.9	50.4	36.6
LADE	-	-	1.2	0.3	9.5	8.0	51.9	81.1
PIAB	-	0.1	6.1	38.0	1.5	5.1	58.3	83.3
PISY	-	-	-	1.0	-	-	49.3	0

High amounts of non-standing dead wood (woody residue, t/ha) were found in all three stand types (Table 4). Our survey detected the highest amount in the "mixed" stand type where we also observed a decrease in standing dead wood biomass, suggesting that many of the dead trees that were still standing in 1957 tipped over in the past 45 years (Table 4).
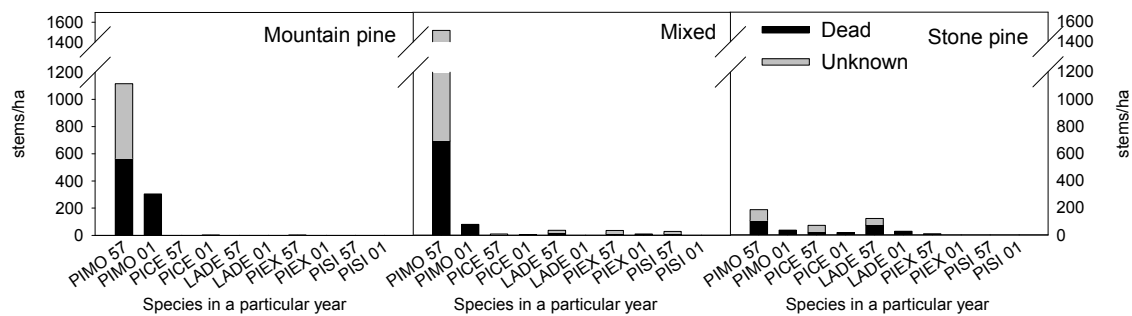

Figure 2: Tree density (stems/ha) of dead trees and trees of unknown condition > 130 cm per hectare for the three forest stand types in 1957 and 01/02. The density for each species is represented by one bar. Dead and unknowns are added up.

Table 4: Standing dead tree density (dead trees/ha), standing dead tree biomass (t/ha) for 1957 and 01/02, as well as woody residue (t/ha) and total dead wood biomass (t/ha) for 01/02. Standard errors are given in parentheses; differences between the two sampling years were tested separately for each stand type using ANOVA.

	Mountain pine			**Mixed**			**Stone pine**		
	1957	**2001**	*p-value*	**1957**	**2001**	*p-value*	1957	2001	*p-value*
Standing dead tree density (stems/ha)	1121 (176)	307 (41)	*<0.01*	1618 (238)	94 (13)	*<0.01*	369 (55)	79 (13)	*<0.01*
Standing dead wood biomass (t/ha)	14.1 (3.4)	17.9 (4.6)	*0.52*	18.0 (3.9)	9.7 (2.7)	*0.07*	6.8 (1.5)	13.7 (2.4)	*0.03*
Woody residue (t/ha)	na[*]	33.1 (12.8)	-	na[*]	57.4 (17.7)	-	na[*]	22.3 (4.2)	-
Total dead wood (t/ha)	na	50.9 (15.6)	-	na	67.1 (97.3)	-	na	36.0 (5.5)	-

[*] Kurth et al. (1960) gave values of 0.1 to less than 5 m³ (or 0.08 to 4 t/ha, assuming wood density of the most frequent tree species PIMO: 0.8 g/cm³) for different areas in the SNP, but no stand data is available.

Discussion

The three tree species dominating in the SNP, PIMO, PICE and LADE have different life history strategies. Understanding their ecological differences is important in order to grasp the development of high-elevation forest communities in this part of the European Alps. Both PIMO and LADE are wind-dispersed, shade-intolerant pioneer species (Richardson and Rundel 1998, Bergès and Chevalier 2001). However, LADE can reach ages of 300 to 800 years (McComb 1955, Riou-nivert 2001) and will therefore be able to

dominate over long periods of time, whereas an early-successional stage dominated by PIMO is relatively short-lived. Seeds of both pioneer species require open mineral soil to germinate: PIMO seedlings are competitive in small openings (few cm), while LADE seedlings need larger patches caused by clear-cuts, avalanches, flooding or fire to establish successfully (Schloeth 1998). Once established, LADE trees generally grow faster than other conifer species and quickly outgrow other pioneer species under favorable conditions (Gower and Richards 1990, Schloeth 1998, Krüsi and Moser 2000). PICE, in contrast, is a shade-tolerant species whose seeds are mainly dispersed by the European thickbilled nutcracker (*Nucifraga caryocatactes caryocatactes*) (Lanner 2000). PICE grows slowly but steadily once established. Although this species has, on average, a lower annual growth rate than LADE, its annual DBH and height increments equal those of PIMO under favorable conditions. Under low-light conditions the increments of PICE are, however, considerably higher than those of both PIMO and LADE (Krüsi and Moser 2000).

While the survival of saplings is mostly determined by competition for light, competition for water, nutrients and space becomes more important once the trees have successfully established (Oliver and Larson 1996, Barnes et al. 1998). After pioneer cohort establishment, natural self-thinning (intraspecific competition) followed by vertical and horizontal stratification (interspecific competition) takes place. Eventually, the pioneer cohort will be lost and a late-successional or old-growth stage will be reached (Spies and Franklin 1996, Franklin et al. 2002).

In our case, we found high sapling density of PIMO in the early-successional stages, where canopy closure was lowest. After pioneer cohort establishment, PIMO loses its competitive advantage in the sapling layer and shade-tolerant PICE saplings start to establish in the PIMO dominated forests. LADE, which under favorable conditions (large openings in the mineral soil) establishes simultaneously with PIMO, is growing much faster than PIMO, and therefore typically is present in the overstory at the time PICE reaches this stratum. LADE will then remain a co-dominant species in the forest community, even in the late-successional stage dominated by PICE. With ongoing succession, less light penetrates to the lower strata due to higher canopy closure, and PICE becomes the most frequent species in the sapling layer. In our study area, the successional changes during stand development were not affected by a considerable

increase in the number of wild ungulates, especially red deer (*Cervus elaphus* L.), since 1940 (Schütz et al. 2000), even though these ungulates were found to browse more heavily on PICE and PIAB saplings compared to pioneer PIMO saplings.

The lack of change in species composition and stand density over the time of observation, the decrease of tree density and shift towards larger DBH classes between 1957 and 01/02 as well as the high density of dead trees indicate that the development within the "mountain pine" stand type is still dominated by self-thinning processes (Oliver and Larson 1996). A further indication that these stands are still in an early-successional phase is that the sapling layer still is composed of mostly PIMO. However, the slight increase in relative abundance of PICE saplings in the understory indicates that compositional changes will likely take place in the future. Yet, on the whole, these stands have not yet entered the understory reinitiation phase, suggesting that they are still largely even-aged.

In contrast, it is likely that self-thinning processes were completed in the "mixed" stand type already in 1957 as indicated by the high density of standing dead trees and the increased tree species diversity compared to the "mountain pine" stand type. Vertical and horizontal stratification were the main processes taking place in this forest type between 1957 and 01/02, as indicated by the increase in tree species diversity with a slow drop-out of PIMO. The "mixed" stand type forests therefore are in a mid-successional stage today. Finally, in the "stone pine" stand type, many of the PIMO trees that were alive in 1957 died in the 45 years of observation due to vertical and horizontal stratification. This forest type has developed from a mid-successional stage, dominated by PIMO, LADE, and PICE, into a late-successional stage, where PICE is dominating, and LADE is a significant stand component. The approximately 50% decrease in tree density in all our stand types corresponds with the values reported in yield-tables for mono-culture forest stands of the same tree species (Landesforstverwaltung Baden-Württemberg 1966).

In agreement with the 50% decrease in tree density we observed a strong increase in non-standing woody residue [1957: 0.1 to 5 m^3, or 0.08 to 4 t/ha (assuming wood density of the most frequent tree species PIMO: 0.8 g/cm^3); 01/02: 36.0 – 67.1 t/ha]. In contrast, standing dead wood biomass only changed slightly over the period of observation, even though standing dead tree density decreased markedly: In 1957 most of the dead trees had

low DBH (0.5 to 4 cm; Kurth et al. 1960), while in 01/02 they belonged to much bigger DBH classes.

Our results elucidated the successional development of continental subalpine forests after abandonment, and our findings therefore mirror stand structural changes that might take place in similar mountain regions in the coming decades. However, we can only estimate how much time elapses until a pioneer stand dominated by PIMO reaches the late-successional stage. Since the youngest stand type already was approximately 120 years old in 1957, and since 45 years were not enough to proceed from "mountain pine" to "mixed" and from "mixed" to "stone pine", respectively, we assume that the successional development in the SNP most likely takes longer than 250 years.

Acknowledgements

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Section II
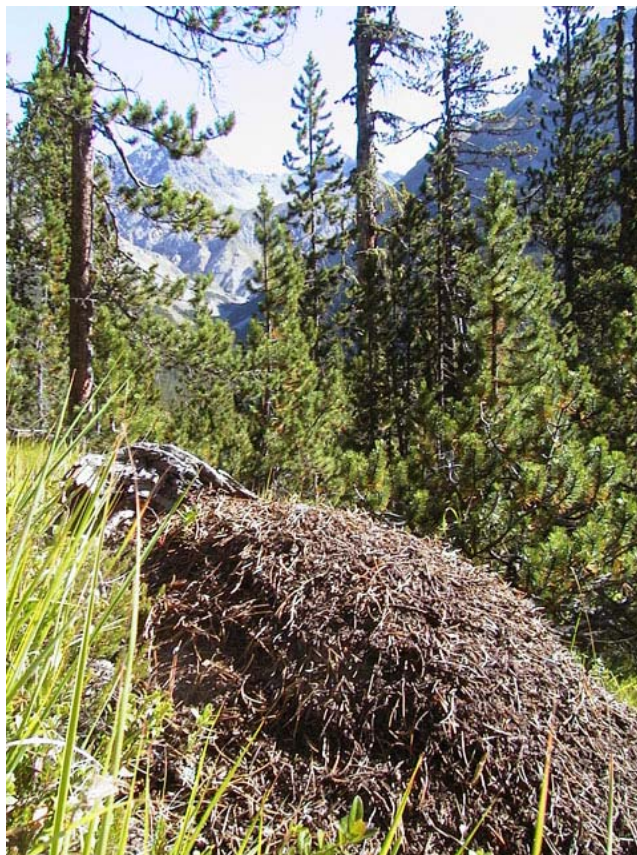
Changes in carbon and nutrient pools during secondary succession in subalpine conifer forests

Paper IV
Above- and belowground carbon and nutrient pools during secondary succession
following land use change in subalpine ecosystems of the Central European Alps

Paper V
Red wood ants (*Formica rufa* group): Their contribution to soil C and N pools, and CO_2
emissions in subalpine forests

Paper IV

Above- and belowground carbon and nutrient pools during succession following land use change in subalpine ecosystems of the Central European Alps

Submitted as:

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Abstract

Traditional agricultural and silvicultural land use are unlikely to be continued in many high-elevation areas of Europe, which could have major impacts on carbon (C) sequestration in these areas. However, little is known about the development of above- and belowground C and nutrient pools following land abandonment in high-elevation ecosystems. Our objectives were to i) determine above- and belowground biomass, C and nutrient pools of five subalpine ecosystems in the Swiss National Park representing different succession stages following land abandonment (i.e., agricultural graslands), and to ii) assess how these pools develp over time. We selected, in successive order, short-grass pastures, tall-grass pastures, mountain pine (*Pinus montana* Miller), mixed-conifer, and stone pine (*Pinus cembra* L.) forests for our study.

Aboveground biomass, C and nutrient pools increased from short-grass pastures to mixed forest stands, but remained unchanged from mixed- to stone pine forests. Changes in nutrient pools were not found to have major impacts on ecosystem productivity.

Decreases in mineral soil organic matter and C pools detected during secondary forest succession resulted in similar total biomass and C pools in all ecosystems studied. These findings contrasted results from studies conducted at low-elevation that reported increasing belowground C pools during forest succession. Thus, high-elevation forests potentially act differently in terms of C sequestration during forest succession than previously expected, which would be important for estimating regional, national or global C pools. In addition, as our results show, high-elevation ecosystems potentially store high amounts of C compared to low-elevation ecosystems, which would also be important for e.g. large-scale C assessments. However, since this study is one of the first field-data based investigations on the development of C and nutrient pools in abandoned, high-elevation ecosystems, we suggest that more studies are needed to assess their importance for C sequestration.

Keywords

high-elevation, carbon and nutrient budgets, secondary succession, land abandonment, pasture, coniferous forest, ericaceous shrubs, nitrogen, phosphorus, cations

Introduction

Recent changes in European economic polices indicate that traditional agricultural and silvicultural practices are unlikely to continue in many high-elevation regions (e.g. Bäntzing 1996, Price 2003). The percentage of forest area and the amount of woody biomass have been reported to increase in Europe as farmland, pastures and forests are abandoned (Kuusela 1994, Brassel and Brändli 1999). Thus, changes in land use practices could have a major impact on carbon (C) sequestration in high-elevation European ecosystems.

Aboveground and total ecosystem C pools in European low-elevation forests have been reported to increase due to reforestation of abandoned farmland (e.g. Kauppi et al. 1992, Thuille et al. 2000, Vesterdal et al. 2002), thus confirming the generally expected increase in biomass during secondary succession following disturbance (e.g. Odum 1969, Bormann and Likens 1979, Peet 1981). The fate of belowground C during succession following land abandonment seems to be more controversial. Increases (Alriksson and Olsson 1995, Smith et al. 1997, Thuille et al. 2000, Poulton et al. 2003), decreases (Jackson et al. 2002), or insignificant changes (Guo and Gifford 2002, Vesterdal et al.

2002) in belowground C pools have been reported during succession from farmland or pasture to forest, while increasing total belowground C pools were generally found during secondary forest succession (e.g. Peet 1981, Barnes et al. 1998). Most of these studies were conducted in low-elevation ecosystems, and little is known about the successional development of belowground C pools after land abandonment at higher elevations. A modeling approach has indicated that high-elevation soils likely would act as C sinks as forest stand basal area (BA) and forest cover increase, and therefore could become increasingly important for C sequestration (Perruchoud et al. 1999). In order to assess whether this model prediction is accurate, field studies on changes in C pools following land abandonment in high-elevation ecosystems are needed. Information is also needed on changes in above- and belowground nutrient pools, since they affect ecosystem productivity and therefore impact C sequestration.

As one of the few areas in Western Europe that has not been directly impacted by humans during most of the 20th century, the Swiss National Park (SNP) provides an opportunity to study how C and nutrient pools develop after land abandonment. Large parts of the subalpine forests (defined as the vegetation belt between 1500 and 2400 m above sea level (m a.s.l) in this part of the Alps; Landolt 1992) were clear-cut between the 16th and 19th century, while some areas were selectively harvested. The majority of the clear-cut stands regenerated to mountain pine (*Pinus montana* Miller) forests, while selectively cut stands remained in mid- to late-successional (mixed conifer and Swiss stone pine/European larch (*Pinus cembra* L./*Larix decidua* Miller) forest stages (Parolini 1995). Some easily accessible sites were converted to grasslands for agricultural use after clear-cut (Parolini 1995).

Red deer (*Cervus elaphus* L.) started to use these grasslands as grazing lawns after the Parks foundation in 1914. As a consequence, these areas developed into short-grass pastures dominated by *Festuca rubra* L., *Carex verna* Chaix, and *Briza media* L. as Schütz et al. (2000) and Wildi and Schütz (2000) found based on time series analysis of 150 permanent plots (up to 85 year series; Figure 1). When grazing stops, the short-grass pastures are replaced by tall-grass pastures dominated by *Carex sempervirens* Vill., *Nardus stricta* L., and *Elyna myrosuroides* (Vill.) Fritsch, which in turn are replaced by mountain pine forests later in succession (Schütz et al. 2000, Wildi and Schütz 2000). Analysis of long-term forest data (45-year time series; Risch et al. 2003b) showed that the mountain pine forests develop into mixed-conifer stands (containing mountain pine,

Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), larch, and stone pine), which are in turn replaced by the late-successional stone pine/larch stands (Risch et al. 2003a,b; Figure 1). The estimated time frame for short-grass pasture to mountain pine forest covers approximately 250 years (Schütz et al. 2000), while an estimated 650 years pass during succession from mountain pine to stone pine/larch forest (Risch et al. 2004; Figure 1).

These five ecosystems of different successional age after land abandonment are still found within the SNP today. The objectives of this study were to i) determine total above- and belowground biomass, C, and nutrient pools for the two pasture and three forest types, and to ii) assess how these pools change during succession following land abandonment.
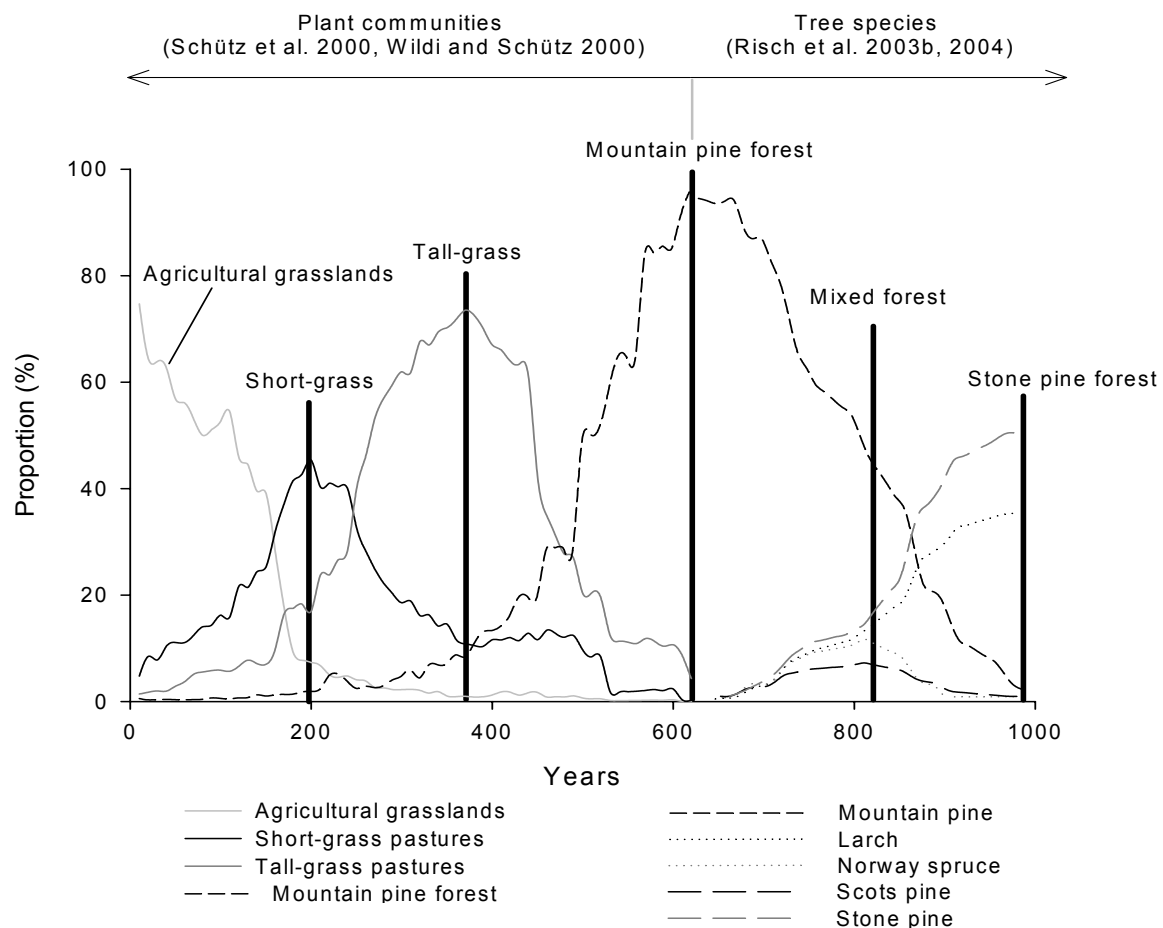

Figure 1: Successional development from agriculturally used grasslands to stone pine forest in the SNP. The development is based on the analysis of time series data (space-for-time approach; Schütz et al. 2000, Wildi and Schütz 2000: meadow to mountain pine forest / Risch et al. 2003b, 2004: mountain pine forest to stone pine forest).

Methods

Study area

The SNP is located in the southeastern part of Switzerland, and covers an area of 170 km^2. Fifty km^2 are forested, 3 km^2 occupied by subalpine grasslands, and the rest covered by alpine grasslands, ice, snow and rocks. The Park is located between 1350 and 3170 m a.s.l. and has 925 $\pm$ 162 mm and 0.2 $\pm$ 0.7°C mean annual precipitation and temperature (average $\pm$ standard deviation, measured at the Park's weather station in Buffalora, 1980 m a.s.l.).

Sampling design

Three short-, two tall-grass pastures, and 18 forest stands from the three successional stages (mountain pine, mixed, stone pine/larch) were selected for study. The number of tall-grass pastures was restricted to two, since all other subalpine pastures are intensively grazed and thus have short-grass vegetation. All sites are part of larger studies on ecosystem productivity or long-term forest succession (Egenter 2001, Pierik and Roetemeijer 2001, Risch et al. 2003a,b). The underlying parent material of all pastures, six mountain pine stands, five mixed stands, and three stone pine/larch stands is calcareous moraines and rubble (Trümpy et al. 1997). Four stone pine/larch stands were found on acid verrucano-dominated moraines and rubble. No mixed and mountain pine stands can be found on this parent material, since forests growing on these acid sites are fairly inaccessible. Consequently, these stands have not been clearcut, and still are in the late-successional stone pine forest stage.

Field sampling

Pastures

Aboveground plant biomass [further referred to as understory vegetation (UV)] was estimated on 50 plots per pasture by clipping all vegetation to 2 cm height on a 48 x 28 cm area (Egenter 2001, Roetemeijer and Pierik 2001). Before clipping, vegetation relevées were conducted, and the cover (%) of each species recorded; species names followed Lauber and Wagner (2001). Mineral soil and surface organic matter (OM) samples were collected on systematic grids in all pastures; the number of samples was stratified by pasture size. The surface organic layer (SOL) was sampled on a 10 x 10 cm area. Due to the high rock content in the subsoil, mineral soil samples were taken only to

a depth of 20 cm. Soil bulk density was determined with the polyurethane foam technique (Page-Dumroese et al. 1999).

Forest stands

Species composition, stand density, age and height were determined for each of the 18 forest stands using the following method: Trees (> 130 cm tall, living and dead) and saplings (21 – 130 cm tall) were sampled with point-centered quarter method (Greig-Smith 1983) on 16 points located on systematic grids of 70 x 70 m or 40 x 40 m, depending on stand size. Species, DBH (diameter at breast height = 130 cm), and height were recorded for the four closest trees and saplings at each point. Stem increment cores were taken from two of the four trees to determine stand age. For more detailed descriptions see Risch et al. (2003a,b). Canopy closure was measured with a densiometer taking four measurements around the center of each of the 16 sampling points in all cardinal directions (Lemmon 1957). A vegetation relevée was conducted on a 10 x 10 m plot established at the center of each stand, and the cover (%) of each species recorded. Species names followed Lauber and Wagner (2001). Stand elevation was measured with an altimeter at the stand center.

All UV and surface OM (including pine cones) were removed from three 700 cm^2 circular plots located on three sides of the 10 x 10 m plot. Mineral soil samples were again excavated to a depth of 20 cm at the three surface OM/vegetation-removal plots, and bulk density estimated using the polyurethane foam technique (Page-Dumroese et al. 1999).

The amount of non-standing dead biomass [woody residue (WR)] was measured in each stand using a planar intersect method (three transects; Brown 1974), as described in detail in Risch et al. (2003a). WR with diameter < 0.6 cm was not sampled, but included in the SOL samples.

Five stem increment cores and five foliage samples of each tree species and ten WR samples (five solid and five rotten) were collected in the different stand types. In addition, seven saplings of each species (10 – 100 cm) were collected to establish regression equations for calculating sapling biomass.

Laboratory analyses
Tree and sapling stem/foliage, WR, and SOL samples were oven-dried at 65 °C, and fine-ground to pass a 0.5 mm screen. The UV samples were dried at 65 °C, weighed, and all

forest samples and samples from one short- and one tall-grass pasture were fine ground for chemical analysis. All samples were analyzed for total C and N on a LECO induction furnace at 1000 °C (LECO Corp., St. Joseph, MI). Samples were were ashed in a muffle furnace and extracted with 2 N HNO_3 for analyses of total Ca, Mg, K, and P. Total Ca and Mg were analyzed by atomic absorption spectrophotometry, total K by flame emission, and total P with a Rapid Flow Analyzer (OI Analytical FS3000).

Mineral soil samples were oven dried at 105 °C, weighed, and passed through a 2 mm sieve. Roots were separated from the > 2 mm material, weighed, ground to pass a 0.5 mm screen, and analyzed for total C, N, P, K, Mg, and Ca as the other organic samples. Mineral soil C and N of the acid soils were measured on a LECO induction furnace at 1000 °C. The alkaline soils (containing high amounts of carbonates) were first treated with a 50% hydrochloric acid solution, dried for 1-2 hrs, and then also analyzed on the LECO C-N analyzer (LECO Corp. St. Joseph, MI). Available mineral soil P was determined with the Bray II or Olson method depending on mineral soil pH (Kuo 1996). Exchangeable Ca, Mg, and K were extracted using the ammonium acetate method (Sumner and Miller 1996). Exchangeable Ca and Mg were determined using atomic absorption techniques, and K by flame emission techniques. Mineral soil and SOL OM concentration was determined by loss-of-ignition (Ben-Dor and Banin 1989). Mineral soil pH was determined on a 2:1 (water:soil) paste (Thomas 1996). Soil texture was determined using the hydrometer method (Gee and Bauder 1986).

Biomass calculations for living and dead trees, branches, foliage, roots, and saplings
Since the study was performed in a National Park, we were unable to destructively sample trees (> 130 cm height) for biomass determination. Therefore, we used species-specific allometric equations for high-elevation forests obtained from Swiss forest inventory data (all trees with DBH > 7.5 cm) and the formula of a paraboloid (all trees with DBH < 7.5 cm) to calculate stem (living and dead trees) and branch biomass for each of the 18 forest stands (Kramer 1992, Kaufmann 2002; Appendix A). Allometric equations were also used to calculate foliage and coarse root (CR) biomass for all trees with DBH > 0.5 cm (Perruchoud et al. 1999, Kaufmann 2001; Appendix A). Fine root (R) biomass was estimated using the weights of root biomass obtained from the mineral soil bulk density samples. Sapling biomass for each species was calculated using regression equations developed for the SNP.

Calculation of C and nutrient pools

We calculated total C and nutrient pools for each pasture and forest site by multiplying total biomass with the respective C or nutrient concentration for mineral soil, SOL, R, WR and UV (Appendix B). Species-specific C and nutrient concentrations for tree and sapling stem/foliage were used to calculate total living tree pools (Appendix B). Carbon and nutrient concentrations of solid WR were used to calculate total standing dead tree pools (Appendix B). Since we were not allowed to sample CR and branches for C and nutrient analysis, we used literature values from European studies to calculate our pools (Appendix B). The results of each pool size were then averaged for the two pasture types (short- and tall-grass) and for each of four forests types (further referred to as "mountain pine", "mixed", "stone pine – alk." and "stone pine - acid").

Statistical analyses

Differences in soil physical and chemical properties as well as above-, belowground and ecosystem biomass, C and nutrient pools among the different ecosystems were tested using a 1-way ANOVA followed by a LSD post-hoc test for pair-wise comparison (significance level: $p = 0.05$) for untransformed data.

Results

Aboveground pools

While grasses and herbs dominated the red deer-grazed short-grass pastures, sedges become more important when grazing stops and tall-grass pastures develop (Table 1). All aboveground C and nutrient pools were higher in the tall-grass pastures (more biomass), but only N and K pools differed significantly (Table 2). Not surprisingly, all aboveground pools were much lower in the pastures than in the mountain pine stands (Table 2). Basal area (BA) and stand height, and thus biomass, C and nutrient pools were significantly lower in the mountain pine dominated stands compared to the stands dominated by the later successional species (Table 3). No further increase in BA or stand height, and thus C and nutrient pools, was detected during succession from mixed conifer to stone pine forests (Table 3). While most of the forest biomass and C was stored in stems, nutrient contents were higher in branches and foliage (Table 2). Since sapling biomass was so small (between 20 and 145 kg/ha), sapling biomass, C and N pools were not included in the totals.

Paper IVEricaceous shrubs (ES) dominated the UV in the mountain pine stands, but were less important on the late-successional stone pine sites, where mosses and needle litter occupied larger areas of the forest floor surface (Table 1). Parent material did not seem to influence aboveground productivity, as we found no differences in pool sizes between the alkaline and acid stone pine forests (Table 2).

Table 1: Pasture and forest understory composition, open ground, needle litter surface cover, and moss occurrence.

Ecosystem type	Herbs	Grasses	Sedges	Ericaceous shrubs			Mosses	Open ground	Needle litter
				Total	*E. carnea* Cover %	others[1]			
Short-grass	50 (7)^a	38 (9)^a	11 (7)^b	0 (0)^c	0 (0)^b	0 (0)	0 (0)^c	0 (0)^b	0 (0)^b
Tall-grass	54 (4)^a	21 (6)^a	31 (7)^a	0 (0)^c	0 (0)^b	0 (0)	0 (0)^c	0 (0)^b	0 (0)^b
Mountain pine	6 (1)^b	5 (1)^b	5 (2)^b	67 (5)^a	52 (8)^a	15 (2)	9 (4)^b	7 (1)^{ab}	0 (0)^b
Mixed	10 (3)^b	30 (17)^a	<1 (<1)^b	54 (15)^b	44 (17)^a	10 (5)	2 (1)^b	13 (5)^a	0 (0)^b
Stone pine (alk.)	11 (3)^b	39 (8)^a	11 (10)^b	8 (6)^c	3 (3)^b	5 (3)	1(<1)^b	7 (7)^{ab}	12 (7)^b
Stone pine (acid)	4 (1)^b	4 (2)^b	0 (0)^b	23 (8)^c	0 (0)^b	23 (8)	19 (7)^a	3 (1)^b	35 (10)^a
p-value	*<0.001*	*0.037*	*0.002*	*<0.001*	*0.003*	*0.10*	*0.003*	*0.02*	*<0.001*

a,b,c = averages with the same letter are not significantly different at p = 0.05
[1]*Vaccinium myrtillus, V. vitis-idea, Rhododendron ferrugineum*

Table 2: Aboveground biomass, C, N, P, Ca, Mg, and K pools (t/ha) and their distribution (in %) within each ecosystem. LT = living trees, BR = branches, SDT = standing dead trees, FL = foliage, UV = understory vegetation. Standard error in parentheses.

Ecosystem type	LT	BR	FL	SDT	UV	Total	LT	BR	FL	SDT	UV
Biomass											
			Pools (t/ha)						Distribution (%)		
Short-grass	-	-	-	-	<1 (<1)[c]	<1 (<1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	3 (1)[bc]	3 (1)[c]	-	-	-	-	100
Mountain pine	106 (156)[b]	12 (2)[b]	4 (1)[b]	19 (5)	5 (1)[a]	146 (14)[b]	73	8	3	13	3
Mixed	234 (32)[a]	16 (3)[ab]	7 (<1)[a]	10 (3)	4 (1)[ab]	271 (36)[a]	86	6	3	4	1
Stone pine (alk.)	259 (56)[a]	23 (4)[a]	5 (<1)[b]	11 (3)	1 (<1)[c]	299 (62)[a]	87	8	2	4	<1
Stone pine (acid)	258 (35)[a]	22 (2)[a]	6 (1)[a]	11 (3)	2 (1)[bc]	299 (41)[a]	86	7	2	4	1
p-value	*0.006*	*0.04*	*0.02*	*0.37*	*0.01*	*<0.001*					
C											
			Pools (t/ha)						Distribution (%)		
Short-grass	-	-	-	-	<1 (<1)[c]	<1 (<1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	1 (1)[abc]	1 (1)[c]	-	-	-	-	100
Mountain pine	54 (8)[b]	6 (1)[b]	2 (<1)[c]	9 (2)	2 (<1)[a]	73 (7)[b]	73	8	13	3	3
Mixed	116 (16)[a]	8 (2)[ab]	4 (<1)[a]	5 (2)	2 (<1)[ab]	135 (18)[a]	86	6	4	3	1
Stone pine (alk.)	131 (27)[a]	11 (2)[a]	3 (<1)[bc]	6 (2)	1 (<1)[bc]	152 (30)[a]	87	8	4	2	<1
Stone pine (acid)	131 (17)[a]	11 (1)[a]	3 (1)[ab]	6 (2)	1 (<1)[bc]	152 (21)[a]	86	7	4	2	1
p-value	*0.005*	*0.04*	*0.02*	*0.37*	*0.005*	*<0.001*					
N											
			Pools (kg/ha)						Distribution (%)		
Short-grass	-	-	-	-	4 (2)[c]	4 (2)[d]	-	-	-	-	100
Tall-grass	-	-	-	-	46 (16)[a]	46 (16)[c]	-	-	-	-	100
Mountain pine	70 (10)[b]	57 (8)[b]	41 (6)[b]	30 (7)	39 (7)[ab]	237 (17)[b]	30	24	17	13	16
Mixed	142 (17)[a]	69 (13)[ab]	94 (4)[a]	16 (6)	37 (4)[a]	358 (35)[a]	40	19	26	4	10
Stone pine (alk.)	160 (31)[a]	97 (16)[a]	80 (9)[a]	18 (5)	16 (3)[bc]	371 (55)[a]	43	26	22	5	4
Stone pine (acid)	165 (22)[a]	98 (9)[a]	92 (17)[a]	18 (5)	27 (10)[ab]	400 (54)[a]	41	25	23	5	7
p-value	*0.005*	*0.05*	*0.001*	*0.37*	*0.02*	*<0.001*					
P											
			Pools (kg/ha)						Distribution (%)		
Short-grass	-	-	-	-	<1 (<1)	<1 (<1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	2 (1)	2 (1)[c]	-	-	-	-	100
Mountain pine	2 (<1)[b]	7 (1)[b]	3 (<1)[b]	<1 (<1)	2 (<1)	15 (2)[b]	15	48	17	8	11
Mixed	6 (1)[a]	13 (3)[ab]	5 (<1)[a]	<1 (<1)	2 (<1)	27 (4)[a]	21	50	20	2	6
Stone pine (alk.)	6 (1)[a]	20 (5)[a]	5 (1)[a]	<1 (<1)	1 (<1)	33 (6)[a]	18	62	15	2	2
Stone pine (acid)	6 (1)[a]	18 (3)[a]	5 (1)[a]	<1 (<1)	1 (<1)	31 (5)[a]	19	57	17	2	4
p-value	*0.002*	*0.02*	*0.004*	*0.37*	*0.09*	*0.002*					
Ca											
			Pools (kg/ha)						Distribution (%)		
Short-grass	-	-	-	-	1 (1)	1 (1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	14 (5)	14 (5)[c]	-	-	-	-	100
Mountain pine	22 (3)	37 (5)[b]	6 (1)[b]	4 (1)	17 (5)	86 (9)[b]	26	43	7	4	19
Mixed	34 (4)	48 (10)[ab]	12 (<1)[a]	2 (1)	13 (3)	109 (14)[ab]	31	44	11	2	14
Stone pine (alk.)	31 (4)	69 (12)[a]	11 (1)[a]	2 (1)	5 (2)	118 (16)[a]	26	59	9	2	2
Stone pine (acid)	36 (6)	68 (7)[a]	13 (2)[a]	2 (1)	6 (3)	125 (14)[a]	30	56	11	2	1
p-value	*0.13*	*0.04*	*0.002*	*0.37*	*0.08*	*<0.001*					
Mg											
			Pools (kg/ha)						Distribution (%)		
Short-grass	-	-	-	-	<1 (<1)[b]	<1 (<1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	5 (2)[ab]	5 (2)[c]	-	-	-	-	100
Mountain pine	4 (1)[c]	24 (4)[b]	2 (<1)[b]	1 (<1)	7 (2)[a]	38 (4)[b]	11	64	6	2	17
Mixed	46 (2)[a]	32 (6)[a]	6 (<1)[a]	1 (<1)	4 (1)[ab]	89 (7)[a]	52	36	6	1	5
Stone pine (alk.)	26 (7)[b]	46 (8)[a]	4 (1)[a]	1 (<1)	1 (<1)[b]	77 (16)[a]	33	59	6	1	2
Stone pine (acid)	31 (9)[b]	45 (4)[a]	5 (1)[a]	1 (<1)	1 (1)[b]	83 (14)[a]	38	54	6	1	2
p-value	*<0.001*	*0.04*	*0.004*	*0.37*	*0.02*	*<0.001*					
K											
			Pools (kg/ha)						Distribution (%)		
Short-grass	-	-	-	-	2 (1)[b]	2 (1)[c]	-	-	-	-	100
Tall-grass	-	-	-	-	17 (6)[a]	17 (6)[c]	-	-	-	-	100
Mountain pine	9 (1)[b]	10 (1)[a]	9 (1)[b]	14 (3)	17 (4)[a]	59 (3)[b]	15	17	15	23	30
Mixed	15 (2)[a]	15 (3)[ab]	27 (1)[a]	7 (3)	20 (5)[a]	84 (9)[a]	18	18	32	9	23
Stone pine (alk.)	15 (3)[a]	22 (5)[a]	22 (3)[a]	8 (2)	10 (1)[ab]	77 (11)[ab]	19	29	28	11	13
Stone pine (acid)	16 (2)[a]	21 (3)[a]	25 (5)[a]	8 (2)	8 (2)[ab]	78 (12)[ab]	20	27	32	11	10
p-value	*0.04*	*0.02*	*<0.001*	*0.37*	*0.04*	*<0.001*					

a,b,c = averages with the same letter are not significantly different at p = 0.05

Table 3: Age, height, basal area (BA), canopy closure and tree species composition of the four forest types studied. Standard error in parentheses.

Ecosystem type	Age	BA	*Pinus montana*	*Pinus cembra*	*Larix decidua*	*Picea abies*	*Pinus sylvestris*	Stand height	Canopy closure
	(years)	(m²/ha)			% of total BA			(m)	(%)
Mountain pine	156 (10)	25 (4)^b	96 (3)	2 (2)	1 (1)	- (-)	1 (1)	13 (<1)^b	43 (4)^c
Mixed	187 (5)	42 (2)^a	17 (1)	1 (1)	32 (7)	34 (9)	16 (6)	24 (2)^a	54 (3)^{bc}
Stone pine (alk.)	223 (24)	44 (3)^a	7 (4)	49 (13)	44 (10)	- (-)	- (-)	23 (1)^a	70 (7)^a
Stone pine (acid)	223 (18)	50 (8)^a	4 (2)	60 (10)	30 (12)	6 (6)	1 (1)	25 (1)^a	65 (3)^{ab}
p-value		*0.006*						*<0.001*	*<0.001*

a,b,c = averages with the same letter are not significantly different at p = 0.05

Belowground pools

Soil bulk density, rock content and available water-holding capacity did not significantly differ between the six ecosystem types (Table 4). Mineral soil organic matter (SOM) concentration was highest in the pastures and mountain pine stands, decreased in the mixed and alkaline stone pine forests, and was lowest in the acid stone pine stands. As expected, soil pH was lowest in the late-successional acid stone pine stands (Table 4).

Table 4: Mineral soil physical properties, pH, available water-holding capacity, and OM content. Standard error in parentheses.

Ecosystem type	Texture	Bulk density	Rock content	OM	pH	Available water
		(g/cm³)	(%)	(%)		(g/100 g soil)
Short-grass	Loamy sand	1.0 (0.1)	22 (6)	14.9 (2.7)^a	6.5 (0.3)^a	9.4 (1.6)
Tall-grass	Loamy sand	1.1 (0.1)	27 (12)	10.6 (0.9)^{ab}	5.6 (1.5)^{ab}	8.3 (1.3)
Mountain pine	Sandy loam	1.3 (0.1)	32 (4)	13.5 (1.5)^a	6.2 (0.1)^a	11.5 (1.5)
Mixed	Loamy sand	1.4 (0.1)	30 (3)	7.3 (0.8)^b	5.5 (0.5)^{ab}	12.2 (1.7)
Stone pine (alk.)	Sandy loam	1.1 (0.1)	21 (2)	8.1 (0.8)^b	5.3 (0.4)^{ab}	14.5 (1.2)
Stone pine (acid)	Sand	1.6 (0.1)	37 (7)	3.2 (0.7)^c	3.1 (0.2)^b	10.6 (1.3)
p-value		*0.08*	*0.31*	*<0.001*	*0.001*	*0.3*

a,b,c = averages with the same letter are not significantly different at p = 0.05

Mineral SOM pools were significantly lower in the acid stone pine stands, but did not differ among the other ecosystems. Mineral soil C pools were similar among the pastures and the mountain pine forests (Table 5). A significant decrease was however detected, when the mixed- and stone pine forests replaced the mountain pine stands. Decreases in mineral soil C pools during secondary forest succession were correlated with decreasing cover of ES, which in turn was correlated to increasing canopy closure (Figure 2). A change in ES species composition related to soil pH differences was also found. *Erica carnea* L. comprised 80% of the ES cover in the mountain pine and mixed stands, and

40% in the alkaline stone pine forest, while *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., and *Rhododendron ferrugineum* L. dominated the ES community in the acid stone pine stands (Table 1). *E. carnea,* which is associated with alkaline soils, forms an extensive root system in both the mineral soil and SOL (Braun-Blanquet et al. 1954), and therefore would add recalcitrant litter to the SOL and mineral soil, while ES associated with acid soils have their main rooting zone in the F/H-horizon (e.g. Persson 1983). Thus, both the decrease in ES cover and changes in ES species composition likely affected our mineral SOM and C pools during secondary forest succession.

In contrast to the changes in mineral SOM and C pools, roots, SOL, and WR biomass and C pools did not change during succession in the ecosystems studied, but CR pools increased in response to increased aboveground tree biomass (Table 5). Total belowground biomass and C pools were not significantly different among the six ecosystem types studied.

Total belowground N pools were highest in the short-grass pastures, and significantly lower in the forest ecosystems compared to the two pasture types (Table 5). Even though CR and WR pools were present in the forests but not in the pastures, they were not large enough to make up for low N amounts in the mineral soil and SOL. Belowground N pools were lowest in the stone pine stands growing on the acid soils.

The high belowground N contents in the short-grass pastures likely are related to historical land use in the SNP, as former meadows have often been fertilized with liquid manure (Schütz et al. 2003). The low N pools in forest mineral soil is likely due to high N-leaching losses, and replacement of N-rich pasture litter (grasses) with tree and ES litter of lower N content (Table 2, Appendix B, Table B2). Also, more N-fixing legumes are present in the UV of the pastures (short-grass: 10 % cover, tall-grass: 6 %) compared to the forests (< 1 %), and could add N to the pasture soils.

Total belowground P and K pools showed no trend during succession (Table 5). Since mineral soil P is usually held as Ca-, Fe-, and/or Al-phosphates, leaching losses are very low (Hilal et al. 1973). Magnesium and Ca pools were related to soil pH and were significantly lower in the acidic stone pine stands.

Table 5: Belowground biomass, C, and N pools (t/ha) and their distribution (in %) within each ecosystem. MS = mineral soil, SOL = surface organic layer, R = roots obtained from the soil cores, CR = coarse roots, WR = woody residue. Standard error in parentheses.

Ecosystem type	MS*	SOL	R	CR	WR	Total	MS	SOL	R	CR	WR
					Biomass						
			Pools (t/ha)					Distribution (%)			
Short-grass	156 (12)[a]	53 (20)	11 (4)	-	-	220 (17)	71	24	5	-	-
Tall-grass	109 (15)[a]	46 (15)	5 (2)	-	-	160 (2)	69	28	3	-	-
Mountain pine	138 (19)[a]	43 (9)	4 (1)	19 (3)[b]	33 (13)	237 (27)	58	18	2	8	14
Mixed	112 (18)[a]	29 (11)	7 (2)	68 (8)[a]	60 (22)	276 (24)	40	10	3	25	22
Stone pine (alk.)	101 (2)[a]	34 (16)	7 (2)	73 (9)[a]	21 (7)	236 (21)	43	14	3	31	9
Stone pine (acid)	46 (3)[b]	41 (18)	6 (5)	89 (15)[a]	26 (6)	208 (20)	22	20	3	43	12
p-value	*0.005*	*0.84*	*0.67*	*<0.001*	*0.34*	*0.15*					
					C						
			Pools (t/ha)					Distribution (%)			
Short-grass	84 (5)[ab]	27 (9)	4 (2)	-	-	115 (7)	73	24	3	-	-
Tall-grass	66 (2)[ab]	23 (8)	2 (1)	-	-	91 (8)	73	25	2	-	-
Mountain pine	91 (13)[a]	23 (5)	2 (<1)	9 (2)[b]	17 (7)	142 (17)	64	16	1	7	12
Mixed	54 (6)[bc]	16 (6)	3 (1)	34 (4)[a]	31 (11)	138 (10)	39	11	2	25	23
Stone pine (alk.)	54 (5)[bc]	19 (9)	3 (1)	36 (4)[a]	11 (3)	123 (11)	44	15	2	30	9
Stone pine (acid)	29 (3)[c]	20 (7)	3 (2)	45 (7)[a]	14 (3)	110 (11)	26	18	3	41	12
p-value	*0.003*	*0.88*	*0.80*	*<0.001*	*0.27*	*0.22*					
					N						
			Pools (kg/ha)					Distribution (%)			
Short-grass	7660 (701)[a]	1932 (665)[a]	86 (35)[a]	-	-	9678 (353)[a]	79	20	1	-	-
Tall-grass	4768 (353)[b]	1369 (553)[ab]	30 (9)[b]	-	-	6167 (896)[b]	77	22	<1	-	-
Mountain pine	3273 (450)[bc]	530 (125)[bc]	16 (2)[b]	15 (2)[b]	59 (24)	3893 (490)[c]	84	14	<1	1	1
Mixed	2661 (542)[c]	350 (113)[c]	25 (6)[b]	54 (16)[a]	111 (35)	3201 (537)[cd]	83	11	1	2	3
Stone pine (alk.)	2992 (58)[bc]	481 (239)[bc]	31 (6)[b]	58 (7)[a]	37 (13)	3599 (206)[c]	83	13	1	2	1
Stone pine (acid)	1170 (83)[d]	529 (171)[bc]	23 (16)[b]	71 (12)[a]	53 (12)	1846 (209)[d]	63	29	1	4	2
p-value	*<0.001*	*0.007*	*0.03*	*<0.001*	*0.27*	*<0.001*					
					P[1]						
			Pools (kg/ha)					Distribution (%)			
Short-grass	8 (1)[b]	85 (32)[a]	5 (2)	-	-	98 (33)[a]	8	87	5	-	-
Tall-grass	5 (<1)[b]	58 (17)[ab]	2 (1)	-	-	65 (17)[ab]	7	90	3	-	-
Mountain pine	5 (3)[b]	22 (5)[bc]	1 (<1)	3 (<1)[b]	2 (1)	33 (5)[b]	15	67	3	8	7
Mixed	5 (2)[b]	14 (5)[c]	1 (<1)	10 (1)[a]	4 (1)	34 (3)[b]	14	41	4	29	12
Stone pine (alk.)	15 (5)[a]	19 (9)[bc]	2 (0.7)	11 (1)[a]	1 (1)	48 (9)[ab]	32	40	3	22	3
Stone pine (acid)	6 (3)[b]	25 (10)[bc]	1 (1.1)	13 (2)[a]	2 (<1)	47 (9)[ab]	12	53	3	28	4
p-value	*0.004*	*0.01*	*0.06*	*<0.001*	*0.29*	*0.02*					
					Ca[2]						
			Pools (kg/ha)					Distribution (%)			
Short-grass	9554 (755)[a]	1096 (292)	72 (31)[a]	-	-	10722 (1027)[a]	89	10	1	-	-
Tall-grass	7479 (3892)[a]	876 (651)	16 (8)[b]	-	-	8371 (4551)[a]	89	10	<1	-	-
Mountain pine	8919 (1343)[a]	690 (212)	28 (8)[b]	2 (<1)[b]	7 (3)	9646 (1380)[a]	92	7	<1	<1	<1
Mixed	5976 (750)[a]	339 (116)	22 (9)[b]	7 (1)[a]	14 (4)	6358 (842)[b]	93	5	<1	1	<1
Stone pine (alk.)	6517 (860)[a]	432 (134)	18 (9)[b]	7 (1)[a]	4 (2)	6978 (983)[a]	93	6	<1	1	<1
Stone pine (acid)	1211 (196)[b]	298 (132)	5 (2)[b]	9 (1)[a]	7 (1)	1530 (177)[b]	76	19	<1	4	<1
p-value	*0.006*	*0.20*	*0.04*	*<0.001*	*0.26*	*0.003*					
					Mg[2]						
			Pools (kg/ha)					Distribution (%)			
Short-grass	1961 (152)[bc]	467 (216)	26 (14)	-	-	2454 (245)[a]	80	19	1	-	-
Tall-grass	1055 (350)[c]	318 (279)	9 (5)	-	-	1382 (634)[a]	76	23	1	-	-
Mountain pine	2561 (487)[ab]	180 (64)	8 (2)	11 (2)[b]	2 (1)	2762 (485)[a]	93	7	<1	<1	<1
Mixed	1546 (303)[c]	57 (29)	5 (2)	41 (5)[a]	4 (1)	1653 (323)[a]	93	4	<1	2	<1
Stone pine (alk.)	996 (390)[cd]	89 (42)	5 (3)	44 (7)[a]	1 (1)	1135 (433)[ab]	88	8	<1	4	<1
Stone pine (acid)	263 (73)[d]	30 (11)	2 (1)	54 (9)[a]	2 (<1)	351 (48)[b]	75	9	1	15	<1
p-value	*0.003*	*0.07*	*0.05*	*<0.001*	*0.23*	*0.005*					
					K[2]						
			Pools (kg/ha)					Distribution (%)			
Short-grass	328 (45)	156 (55)[a]	25 (9)	-	-	509 (25)	64	31	5	-	-
Tall-grass	356 (53)	157 (47)[a]	12 (1)	-	-	525 (8)	68	30	2	-	-
Mountain pine	392 (91)	62 (12)[b]	7 (1)	15 (2)[b]	24 (10)	500 (97)	80	13	1	<1	5
Mixed	398 (64)	40 (9)[b]	10 (3)	54 (6)[a]	44 (16)	546 (60)	80	8	2	1	9
Stone pine (alk.)	433 (100)	46 (22)[b]	6 (2)	58 (7)[a]	15 (5)	558 (161)	85	9	1	1	3
Stone pine (acid)	425 (45)	40 (14)[b]	11 (8)	71 (12)[a]	19 (5)	566 (70)	84	8	2	2	4
p-value	*0.98*	*0.009*	*0.17*	*<0.001*	*0.33*	*0.99*					

a,b,c = averages with the same letter are not significantly different at p = 0.05. [1]mineral soil P pools are extractable P, [2]mineral soil Ca, Mg, K pools are exchangable Ca, Mg, K cation pool
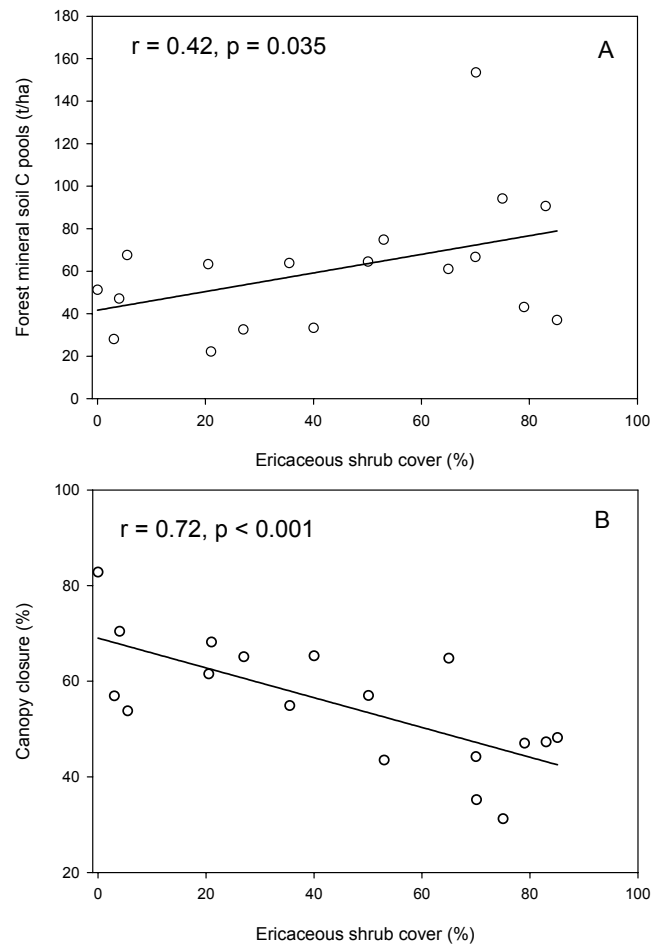
Figure 2. Relationship between ericaceous shrubs (%), canopy closure (%), and mineral soil C pools (t/ha). A: Relationship between mineral soil and ericaceous shrub cover, B: relationship between canopy closure and ericaceous shrub cover.

Ecosystem pools

Ecosystem biomass and C pools were similar in the two pastures and as expected, were significantly lower than in the forested ecosystems (biomass: $p < 0.001$, C: $p = 0.009$). Total biomass was lower in the mountain pine stands, but no difference in total C pools was found among the four forest types (Figure 3). Aboveground OM and C pools were higher in the later successional forest types, but this was offset by lower belowground biomass and C. Nearly all of the pasture biomass and C was belowground, while belowground OM and C pools in the forests ranged from 66 % to 41 % (Figure 3).
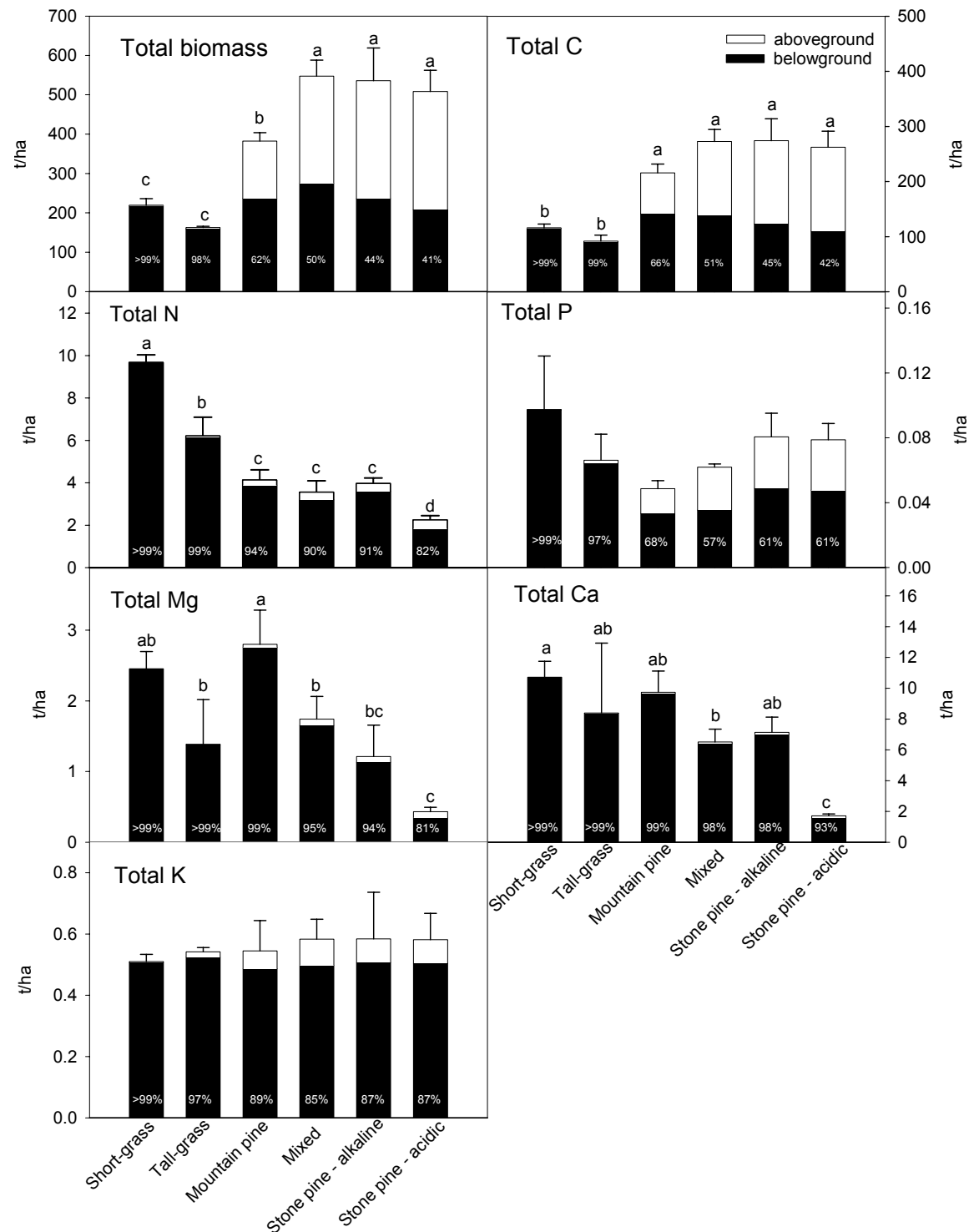
Figure 3. Total above- and belowground biomass, C and nutrient pools for all ecosystems types. a,b,c = averages with the same letter are not significantly different at p = 0.05. Total ecosystem pool standard errors given as error bars. Values in % = Percentage of belowground pools.

The pastures had much higher ecosystem N pools than the forests due high N contents in the mineral soil (historical land use; p = 0.01). No significant differences were found for P and K. Ecosystem Mg and Ca was lowest in the stone pine stands on acid parent

material (Mg: p = 0.008, Ca: p < 0.001; Figure 3). Even though the aboveground N, Mg, and Ca pools increased during succession the increases were too small to make up for belowground differences, thus the ecosystem pools showed decreasing trends during succession. The highest fractions of all nutrients were allocated belowground, most of them in the mineral soil (Figure 3, Table 5).

Discussion

Grassland succession: Development from short- to tall-grass pastures
We were not able to find studies that investigated changes in C and nutrient pools during pasture to pasture succession following land abandonment. However, our total aboveground biomass and C pools of the pastures were comparable to values reported for other high-elevation pastures and hay-meadows (0.7 to 3.6 t/ha; Paulsen 1995). His mineral soil C pools, calculated using soil maps (resolution of 1:200'000), were also similar to our pools, but he did not indicate soil depth nor whether the SOL or roots were included. Two other studies reported similar and lower belowground C pools for meadows/pastures in low-elevation Germany and Denmark, but both sampled to deeper soil depths (no indication if SOL was included; Berthold and Beese 2002, Vesterdal et al. 2002). Our C and N pools were ones reported by Bardgett et al. (2001) for the 0 – 10 cm mineral soil layer in sheep pastures of different grazing intensity in England, while a permanent pasture in Denmark (mineral soil 0 – 25 cm) had comparable belowground N pools (Ritter et al. 2003). Harrison (1978) reported similar above- and belowground P pools in a sheep-grazed *Festuca*-pasture in England. We did not find any studies that investigated Ca, Mg, or K pools.

Pasture to forest succession: Development from tall-grass pastures to mountain pine forests

Biomass and C pools

Very little information is available on above- and belowground pools during succession following abandonment of high-elevation pastures or meadows. Thuille et al. (2000) reported that C pools (trees, SOL) increased during pasture to forest succession in the montane zone of Italy (1130 to 1390 m a.s.l.), but did not find a clear trend in mineral soil C pools. In contrast, Bitterlich et al. (1999) reported increases in mineral SOM content in the A-horizon after larch and spruce trees established on abandoned meadows in the Austrian Alps, but did not indicate if these increases were significant or calculate

belowground C pools. In North America, Prichard et al. (1999) found higher soil C pools in subalpine forests on SW-facing slopes of the Washington Olympic Mountains than in adjacent meadows, but lower C contents on NW slopes. They attributed these results to slower OM decomposition due to longer snow-pack in the more productive, dense forests on the SW-facing sites. Results from other high-elevation studies in North America showed lower soil C pools in forests compared to the adjacent meadows (overview in Bockheim 2003). Most studies in low-elevation ecosystems also reported decreases in mineral SOM and C after natural forest establishment or afforestation of pastures/meadows. This decrease was attributed to greater longevity and slower annual turnover rates of tree roots compared to grass roots (Post and Kwon 2000, Guo and Gifford 2002, Paul et al. 2003).

As shown above, most studies have found decreased soil OM and C pools when pastures and meadows are replaced by forests. The lack of change in belowground OM and C during pasture to mountain pine forest succession in our study may be due to the establishment of ES in the UV of the mountain pine stands. While grass litter and roots generally decompose quite rapidly (Tate 1987), ES leaves and roots decompose very slowly due to high amounts of phenols, lignin, and organic acids, and low N concentrations (Read 1991). This plant group also has mycorrhiza (ericoid), which form dense hyphal mats between the SOL and mineral soil, and contain high fractions of recalcitrant C (Read 1991, Paul and Clark 1996).

Nutrient pools

Similar to our results, Bitterlich et al. (1999) showed that mineral soil N concentration in high-elevation ecosystems in Austria decreased during succession from pasture to forest, but N pools were not calculated. We are not aware of any other study that investigated changes in N pools during natural forest establishment following pasture/meadow abandonment. We also could not find any study that investigated changes in P, Ca, Mg, and K pools during pasture to forest succession.

Forest succession: Development from mountain pine forest to stone pine forests

Forest stand types C and nutrient pools

We are not aware of any field studies that determined biomass, C or nutrient pools in high-elevation forests of Europe. The only study that gives values for above- and

belowground OM and C pools in high-elevation conifer forests is the modeling study by Perruchoud et al. (1999). Their calculated aboveground pools were lower than our results, but they only used forest inventory data for trees with DBH >12 cm. Estimates of belowground pools (based on aboveground forest composition with no differentiation between alkaline and acidic soils) were also much lower than our values, since belowground pools were calculated based on litter input correlated to aboveground biomass. Paulsen (1995) calculated mineral soil C pools for high-elevation Swiss forest soils (1800 – 2200 m a.s.l) based on a soil type map (resolution of 1:200'000). His values were similar to ours, but he did not indicate the soil depth used in his calculations and whether the SOL, WR or roots were included. He only gave average forest biomass for all Swiss forests (low- and high-elevation on all soil types), which was similar to the biomass in our mixed- and stone pine stands.

A comparison of our aboveground, belowground and total biomass, C and N pools with studies conducted in unmanaged, low-elevation European forests is shown in Table 6. The single species stands studied by Helmisaari (1995), Helmisaari et al. (2002) and De Kovel et al. (2000) have similar aboveground pool sizes compared to our mountain pine stand, while our mixed- to stone pine stands have similar aboveground pools as the stand studied by Katzensteiner (2003). The Italian spruce stand had much higher aboveground C pool sizes (Thuille et al. 2000), which could be due to a warmer and moister climate likely found at this site located in northern Italy. The boreal spruce and spruce-pine stands listed in Table 6 have much lower aboveground C pools than our mixed and stone pine stands (Kubin 1983, Perrson et al. 2000, Finér et al. 2003). Reasons for lower pools in the latter two studies likely is a much younger stand age compared to our stands, while the study by Kubin (1983) was conducted at high latitude (> 66°N) where productivity likely is lower than at our sites due to low temperatures, dark winters and long periods of snow coverage.

Our belowground pools are higher than results from most other studies reported in the literature (Table 6). However, all of the studies in Table 6 were conducted on acid soils, and in most of them the soils were sampled to different mineral soil depths. Perrson et al. (2000), who also sampled to 20 cm, found similar belowground biomass, C and N pools to our acid stone pine stands.

Table 6: Number of stands sampled (Nr.) elevation (Elev), forest age, basal area (BA), height (hgt), mineral soil sampling depth (depth) and soil type (type: acid or alkaline) and total above-, belowground and ecosystems biomass (bio), C, and nutrient pools of natural stands studied within Europe.

Ecosystem type	Nr.	Elev	Age	BA	Hgt	Depth	Type	Bio	C	N	P	Ca	Mg	K	Source
		m a.s.l.	yr	m²/ha	m	cm				t/ha					
Total aboveground															
Subalpine															
Mountain pine	6	2010	156	25	13	20	alk.	122	64	0.17	0.01	0.07	0.03	0.03	**This study, Switzerland[1]**
Mixed	5	1790	187	42	24	20	alk.	275	128	0.30	0.03	0.09	0.08	0.06	**This study, Switzerland[1]**
Stone pine (alk.)	3	2040	223	44	23	20	alk.	287	145	0.33	0.03	0.11	0.08	0.06	**This study, Switzerland[1]**
Stone pine (acid)	4	1980	223	50	25	20	acid	286	145	0.35	0.03	0.12	0.08	0.06	**This study, Switzerland[1]**
Montane															
P.abies, some hardwoods	1	1300	140	56	26	-	acid	263	131	0.35	0.03	0.71	0.04	0.11	Katzensteiner 2003, Austria[1]
P.abies, Abies alba	1	1370	130	-	28	3	acid	-	207	-	-	-	-	-	Thuille et al. 2000, Italy[2]
Low-elevation															
P. abies	1	-	250	20	16	100	acid	80	-	0.12	0.02	0.18	0.02	0.07	[†]Kubin 1983, Finland[1]
P. sylvestris	1	145	100	26	20	-	acid	113	-	-	-	-	-	-	[†]Helmisaari et al. 2002, Finland[1]
P. abie, P. sylvestris	1	220	140	-	-	60	acid	-	80	0.28	-	-	-	-	[†]Finér et al. 2003, Finland[1]
P. sylvestris	1	145	100	26	20	30	acid	121	-	0.19	0.04	0.13	0.04	0.09	[†]Helmisaari 1995, Finland[3]
P. sylvestris, P. abies	1	175	180	-	-	20	acid	-	74	0.36	-	-	-	-	[†]Persson et al. 2000, Sweden[1]
P. sylvestris	1	10	121	-	-	10	acid	97	~60	~0.2	-	-	-	-	De Kovel et al. 2000, Netherlands[1]
Total belowground															
Subalpine															
Mountain pine	6	2010	156	25	13	20	alk.	204	125	3.8	0.03	9.6	2.8	0.5	**This study, Switzerland[4]**
Mixed	5	1790	187	42	24	20	alk.	216	107	3.1	0.03	6.3	1.6	0.5	**This study, Switzerland[4]**
Stone pine (alk.)	3	2040	223	44	23	20	alk.	215	119	3.5	0.05	7.0	1.1	0.5	**This study, Switzerland[4]**
Stone pine (acid)	4	1980	223	50	25	20	acid	182	97	1.8	0.05	1.5	0.4	0.5	**This study, Switzerland[4]**
Montane															
-	-	-	-	-	-	-	var.	-	62	-	-	-	-	-	Perruchoud et al. 2001, Switzerl.[5]
P.abies, A. alba	1	1370	130	-	28	3	acid	-	65	-	-	-	-	-	Thuille et al. 2000, Italy[6]
Colline															
P. abies	1	-	250	20	16	100	acid	250	-	4.3	1.7	5.7	54.3	15.5	[†]Kubin 1983, Finland[4]
P. sylvestris, P. abies,	1	175	180	-	-	20	acid	216	69	1.5	-	-	-	-	[†]Persson et al. 2000, Sweden[4]
P. abies, P. sylvestris	1	220	140	-	-	60	acid	-	80	2.4	-	-	-	-	[†]Finér et al. 2003, Finland[7]
P. sylvestris	1	145	100	26	20	30	acid	-	-	2.1	1.1	0.9	1.1	0.4	[†]Helmisaari 1995, Finland[4]
P. abies	1	-	~100	-	-	30	acid	354	-	6.7	-	-	-	-	Gundersen et al. 1998, Denmark[4]
P. sylvestris	1	10	121	-	-	10	acid	161	~80	~2.4	-	-	-	-	De Kovel et al. 2000, Netherlands[4]
-	-	-	-	-	-	100	var.	-	23-177	-	-	-	-	-	Callesen et al. 2003, Scandinavia[6]
-	-	-	-	-	-	100	var.	-	88-146	5.1-6.0	-	-	-	-	Vejre et al. 2003, Denmark[6]

Table 6: Continued.

Ecosystem type	Nr.	Elev m a.s.l.	Age yr	BA m²/ha	Hgt m	Depth cm	Type	Bio	C	N t/ha	P	Ca	Mg	K	Source
Total ecosystem															
Subalpine															
Mountain pine	6	**2010**	**156**	**25**	**13**	**20**	alk.	**326**	**189**	**4.0**	**0.04**	**9.7**	**2.8**	**0.5**	**This study, Switzerland**[8]
Mixed	5	**1790**	**187**	**42**	**24**	**20**	alk.	**491**	**235**	**3.4**	**0.06**	**6.4**	**1.7**	**0.6**	**This study, Switzerland**[8]
Stone pine (alk.)	3	**2040**	**223**	**44**	**23**	**20**	alk.	**502**	**264**	**3.8**	**0.06**	**7.1**	**1.2**	**0.6**	**This study, Switzerland**[8]
Stone pine (acid)	4	**1980**	**223**	**50**	**25**	**20**	acid	**468**	**242**	**2.2**	**0.08**	**1.6**	**0.5**	**0.6**	**This study, Switzerland**[8]
Montane															
P.abies, A. alba	1	1370	130	-	28	3	acid	-	272	-	-	-	-	-	Thuille et al. 2000, Italy[9]
Colline															
P. abies	1	-	250	20	16	100	acid	330	-	4.4	1.7	5.9	54.3	15.6	†Kubin 1983, Finland[8]
P. abies, P. sylvestris	1	220	140	-	-	60	acid	-	160	2.7	-	-	-	-	†Finér et al. 2003, Finland[10]
P. sylvestris	1	145	100	26	20	30	acid	-	-	2.5	1.1	1.0	1.1	0.5	†Helmisaari 1995, Finland[8]
P. sylvestris	1	10	121	-	-	10	acid	258	~140	~2.6	-	-	-	-	De Kovel et al. 2000, Netherlands[8]

† boreal forests (Latitude > 60° N)
1 stem wood, branches/twigs, foliage
2 stem wood only
3 stem wood, branches/twigs, foliage, bark, cones, dead branches
4 forest floor, mineral soil, roots
5 mineral soil
6 forest floor, mineral soil
7 forest floor, mineral soil, roots, stumps
8 stem wood, branches, foliage, forest floor, mineral soil, roots
9 stem wood, forest floor, mineral soil
10 wood, branches, foliage, forest floor, mineral soil, roots, stumps

Changes in pool sizes during succession

Studies in unmanaged, low-elevation European forests have reported increased biomass and C pools with increasing stand age (Thuille et al. 2000, Helmisaari et al. 2002). However, no information is available on total ecosystem pool changes during secondary forest succession (shift in tree species composition). The same holds true for plantation forests in these areas (e.g. Mund et al. 2002, Vucetich et al. 2000, Vesterdal et al. 2002), and for unmanaged and planted forests in high-elevation.

Implications of land use change on C and nutrient pools in high-elevation forests
Our study shows that forest establishment on former subalpine pastures in the SNP leads to a significant increase in ecosystem biomass and C pools. Given the ongoing changes in high-elevation agriculture, the abandonment of pastures could become increasingly important for C storage. Stopping forest management (often resulting in secondary forest succession) does not seem to affect C sequestration in the high-elevation forests studied. This contrasts the generally expected increase in ecosystem biomass during secondary succession (Bormann and Likens 1979, Barnes et al. 1998) as well as the simulated results for high-elevation forests of Perruchoud et al. (1999). They predicted increasing belowground and total forest ecosystem C pools over time due to greater litter inputs and higher CR pools as stands increased in BA. We also found increased aboveground C pools over time, but the decreasing amount of ES cover and change in species composition resulting in decreasing mineral soil biomass and C pools offset changes CR pools. Thus, our results suggest that high-elevation ecosystems where ES are abundant (Landolt 1992, Legros 1992) could act differently in terms of C storage during succession than other ecosystems. In particular, this holds true for areas with calcareous soils, where the deeper rooting *E. carnea* is predominant (Braun-Blanquet et al. 1954). ES likely would also have a strong impact on high-latitude ecosystem C pools. In these ecosystems on mostly acid soils, *V. myrtillus, V. vitis-idea* and *Calluna vulgaris* (L.) Hull dominate the UV (e.g. Ellenberg 1996). However, since they predominately root in the F/H-horizon (e.g. Persson 1983), their effect on belowground C pools might not be as distinct as the one of *E. carnea* on alkaline soils.

Carbon pools in our forests were generally higher than those reported from low-elevation European forests, mainly due to higher amounts of C stored in the mineral soils studied. Thus, high-elevation forests have the potential to store high amounts of C, and could be

critical for national C assessments. This is especially important for countries such as Switzerland, where a large proportion of the land is high-elevation (above 1500 m a.s.l.).

Phosphorus, and not N is limiting in the ecosystems studied (Krapfenbauer 1969, Dietl 1994). Thus, since P pools did not significantly change, successional changes in nutrient pools probably do not have major impacts on C sequestration in the pasture and forest ecosystems studied.

However, since the present study is one of the first field data based investigations on total C and nutrient pools in abandoned, high-elevation ecosystems it might not represent other high-elevation ecosystems. Further studies are needed in order to gain knowledge on how much C and nutrients are stored in these ecosystems and how they are affected by successional processes following land abandonment.

Acknowledgements

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Appendix A

Stem biomass ($Bio_{stem > 7.5}$) was calculated for both standing living and dead trees separately with equation (1) according to Kaufmann (2002). For trees with DBH between 0.5 and 7.5 cm ($Bio_{stem < 7.5}$), we used equation (2) for a paraboloid (Kramer 1982). Total branch biomass was calculated by adding branch and twig biomass calculated with equation (3) (Kaufmann 2001). Total foliage biomass (Bio_{foli}) for each stand was estimated with equation (4) (Kaufmann 2001). Formula (5) was used for calculating coarse root biomass (Perruchoud et al. 1999, Kaufmann 2001).

$$Bio_{stem > 7.5} = \sum_{i,j} \left\{ \left(a_{0i} + a_{1i} * DBH_{i,j}{}^2 * H_{i,j} + a_{2i} * DBH_{i,j}{}^3 * H_{i,j} \right) * stems_{i,j} * sg_i \right\} \tag{1}$$

$$Bio_{stem < 7.5} = \sum_{i,j} \left(\frac{1}{2} * \pi * \frac{1}{2} DBH^2{}_{i,j} * H_{i,j} * sg_i \right) * stems_{i,j} \tag{2}$$

$$Bio_{branches\ and\ twigs} : \ln\left(\frac{p_i}{1 - p_i} \right) = b_0 + b_1 * DBH_i + b_2 * h1_i + b_3 * h2_i \tag{3}$$

$$Bio_{foli} = \sum_{i,j} \left\{ \left(a_i + b_i * DBH_{i,j}^2 + c_i * DBH_{i,j}{}^4 \right) * stems_{i,j} \right\} \tag{4}$$

$$Bio_{root} = \sum_{j} \left\{ \left(a_3 + a_4 * DBH_j^3 + a_5 * DBH_j^4 + 48.796249 * wtyp \right) * stems_j \right\} \tag{5}$$

i = tree species, $DBH_{i,j}$ = mean diameter of species i in diameter class j in cm, $H_{i,j}$ = mean height of species i in diameter class j in cm, $stems_{i,j}$ = number of stems of species i in diameter class j, a_{0i}, a_{1i}, a_{2i}, a_i, b_i, c_i = regression parameters, sg_i = specific gravity of species i (Table A1), a_3 = -0.371467, a_4 = 0.003077, a_5 = -0.000005217, and $wtyp$ = 0.

Table A1: Regression parameters for equations (1), (2), (3), and (5) from Kaufmann (2001, 2002). sg-values from Trendlenburg and Mayer-Wegelin (1955), Guggenbühl (1962), Stiftung Arbeitskreis Schreinermeister (1991).

Species i	a_{0i}	a_{1i}	a_{2i}	sg_i	a_i	b_i	c_i
Mountain pine	0.00978	0.37868	-0.09278	0.80	1.13880	0.00791	8.8691E-9
Scots pine	0.00978	0.37868	-0.09278	0.49	1.13880	0.00791	8.8691E-9
Larch	0.02362	0.37185	-0.10275	0.55	1.13880	0.00791	8.8691E-9
Swiss stone pine	0.01850	0.40625	-0.12512	0.44	1.13880	0.00791	8.8691E-9
Norway spruce	0.00926	0.42407	-0.17402	0.43	1.41370	0.02418	-1.0670E-6
	$^1b_{0i}$	$^1b_{1i}$	$^1b_{2i}$	$^1b_{3i}$	$^1h_{1i}$	$^1h_{2i}$	
Mountain pine	-7.71477	0.07229	0	0	0	1	
Scots pine	-7.71477	0.07229	0	0	0	1	
Larch	-5.88712	0.01082	0	0	0	1	
Swiss stone pine	-7.71477	0.07229	0	0	0	1	
Norway spruce	-	-	-	-	-	-	
	$^2b_{0i}$	$^2b_{1i}$	$^2b_{2i}$	$^2b_{3i}$	$^2h_{1i}$	$^2h_{2i}$	
Mountain pine	-1.71524	-0.01391	0	0	0	1	
Scots pine	-1.71524	-0.01391	0	0	0	1	
Larch	-2.27729	-0.00672	0	0	0	1	
Swiss stone pine	-1.71524	-0.01391	0	0	0	1	
Norway spruce	-1.20641	-0.01918	0	0.44296	0	1	

[1] branches (no merchantable branches for Norway spruce), [2] twigs

Appendix B

C and nutrient concentrations

Concentrations of stem wood and foliage of each species as well as solid and rotten WR are shown in Table B1, concentrations of mineral soil, SOL, R, and UV for each succession stage in Table B2.

Concentrations for CR for all tree species and branches for Scots pine (as a surrogate for all pine species) and Norway spruce were taken from the literature (Kimmins et al. 1985; Table B3). Since no Mg value was available for CR we assumed a 5:1 Ca:Mg-ratio based on values for pine and spruce species given in Kimmins et al. (1985). We we were not able to find literature values for larch branches, so we assumed larch stem:branch ratios of 1:6, 1:4, 1:5, 1:5, and 1:3, for N, P, K, Ca, and Mg based on (Kimmins et al. 1985) to calculate branch pools for larch.

Table B1: C, N, P, Mg, Ca, K, C/N for stem wood, foliage and WR. Values are averages from five samples each. Standard error in parentheses.

	C	N	C:N	P	Ca	Mg	K
	(%)	(%)		(mg/kg)	(g/kg)	(g/kg)	(g/kg)
Stem wood							
P. montana	50.5 (0.8)	0.07 (<0.01)	767 (35)	21.8 (4.2)	0.21 (0.02)	0.08 (0.01)	0.04 (0.01)
P. cembra	52.7 (1.5)	0.07 (<0.01)	771 (54)	22.7 (5.7)	0.19 (0.05)	0.07 (0.02)	0.06 (0.01)
L. decidua	48.7 (0.2)	0.06 (<0.01)	897 (65)	21.9 (3.7)	0.06 (0.02)	0.04 (<0.01)	0.14 (0.02)
P. abies	48.7 (0.1)	0.07 (<0.01)	753 (74)	37.6 (7.4)	0.15 (0.04)	0.06 (0.01)	0.52 (0.33)
P. sylvestris	50.6 (0.9)	0.06 (<0.01)	917 (111)	14.6 (2.6)	0.23 (0.04)	0.09 (0.01)	0.05 (0.01)
Foliage							
P. montana	51.5 (0.3)	0.99 (0.07)	53 (4)	650.7 (20.5)	1.44 (0.23)	0.56 (0.1)	2.18 (0.53)
P. cembra	50.3 (0.2)	1.34 (0.02)	38 (1)	827.3 (62.2)	2.33 (0.45)	0.55 (0.05)	2.91 (0.75)
L. decidua	50.3 (0.4)	2.05 (0.12)	25 (1)	1145.4 (175.3)	2.24 (0.35)	1.36 (0.05)	6.62 (0.68)
P. abies	50.5(0.2)	1.05 (0.10)	50 (5)	556.1 (21.7)	1.40 (0.61)	0.52 (0.14)	3.40 (0.40)
P. sylvestris	51.4 0.2)	1.25 (0.05)	41 (1)	731.3 (34.6)	1.43 (0.33)	0.92 (0.03)	2.00 (0.78)
WR							
Solid	50.9 (0.4)	0.16 (0.02)	335 (55)	65.1 (13.2)	0.19 (0.07)	0.05 (0.01)	0.73 (0.04)
Rotten	56.0 (1.3)	0.29 (0.06)	248 (67)	93.9 (25.8)	0.37 (0.05)	0.13 (0.03)	0.76 (0.06)

Table B2: Average contents of C, N, P, Mg, Ca, K, C/N ratio for mineral soil, SOL = surface organic layer, R = roots, UV = understory vegetation per stand type. Standard error in parentheses

Stand type	C (%)	N (%)	C:N	P (mg/kg)	Ca (g/kg)	Mg (g/kg)	K (g/kg)
				UV			
Short-grass	44.2 (-)[b]	1.7 (-)[a]	27 (-)[b]	696.3 (-)[ac]	4.6 (-)	1.7 (-)[a]	6.9 (-)[b]
Tall-grass	45.0 (-)[ab]	1.5 (-)[a]	29 (-)[b]	669.9 (-)[ac]	6.9 (-)	1.7 (-)[a]	5.8 (-)[b]
Mountain pine	49.9 (0.9)[a]	0.88 (0.09)[b]	59 (4)[a]	386.4 (51.2)[b]	3.3 (0.4)	1.3 (0.19[ab]	4.1 (0.7)[b]
Mixed	49.6 (1.2)[a]	1.04 (0.12)[b]	50 (6)[b]	476.3 (79.7)[bc]	3.5 (0.7)	1.1 (0.2)[bc]	5.1 (0.8)[b]
Stone pine (alkaline)	48.0 (0.4)[a]	1.76 (0.15)[a]	28 (2)[b]	792.7 (108.3)[a]	3.4 (0.9)	1.4 (0.2)[ab]	11.6 (2.3)[a]
Stone pine (acid)	49.2 (1.0)[a]	1.40 (0.14)[a]	36 (3)[b]	642.7 (79.6)[ac]	2.9 (0.3)	0.7 (0.1)[c]	5.4 (1.3)[b]
P-value	*0.006*	*<0.001*	*<0.001*	*0.007*	*0.215*	*0.003*	*0.004*
				Mineral soil			
Short-grass	8.3 (1.5)[a]	0.73 (0.07)[a]	16 (3)[b]	7.3 (0.6)[b]	9.3 (1.8)[a]	1.8 (0.2)[a]	0.3 (<0.1)
Tall-grass	6.0 (1.0)[ab]	0.47 (0.12)[b]	24 (9)[b]	4.2 (1.1)[b]	6.9 (4.4)[ab]	0.9 (0.4)[bc]	0.3 (<0.1)
Mountain pine	8.6 (1.3)[a]	0.31 (0.03)[bc]	45 (5)[a]	4.7 (1.2)[b]	8.6 (1.2)[a]	2.2 (0.2)[a]	0.3 (0.2)
Mixed	3.6 (0.3)[bc]	0.16 (0.01)[de]	28 (4)[b]	2.9 (1.2)[b]	4.2 (0.9)[b]	1.0 (0.2)[b]	0.3 (<0.1)
Stone pine (alkaline)	4.2 (0.3) [bc]	0.22 (0.03)[cd]	28 (5)[b]	13.5 (5.0)[a]	4.9 (0.1)[b]	0.7 (0.3)[bc]	0.3 (<0.1)
Stone pine (acid)	2.0 (0.4)[c]	0.08 (0.02)[e]	26 (2)[b]	3.0 (1.2)[b]	0.9 (0.3)[a]	0.2 (0.1)[c]	0.2 (<0.1)
P-value	*0.001*	*<0.001*	*0.006*	*0.006*	*<0.01*	*<0.01*	*0.74*
				SOL			
Short-grass	28.4 (1.1)[b]	2.08 (0.28)[a]	15 (2)[b]	844.6 (71.8)[a]	12.6 (3.0)	3.7 (1.5)	1.5 (0.2)[ab]
Tall-grass	27.0 (1.7)[b]	1.62 (0.25)[a]	17 (1)[b]	687.7 (19.5)[b]	9.2 (5.5)	3.21 (2.6)	1.9 (0.1)[a]
Mountain pine	40.0 (1.4)[a]	0.89 (0.04)[b]	47 (3)[a]	373.8 (24.7)[c]	13.8 (2.7)	3.1 (0.6)	1.1 (0.1)[bc]
Mixed	36.2 (3.2)[a]	0.81 (0.04)[b]	45 (5)[a]	357.6 (18.1)[c]	8.1 (1.5)	1.3 (0.4)	1.1 (0.1)[bc]
Stone pine (alkaline)	36.4 (1.5)[a]	0.94 (0.1)[b]	39 (3)[a]	445.4 (67.7)[c]	15.2 (2.2)	2.4 (0.8)	1.0 (0.05)[c]
Stone pine (acid)	36.2 (3.9)[a]	0.95 (0.06)[b]	39 (4)[a]	462.7 (24.7)[c]	5.6 (0.7)	0.6 (<0.01)	0.8 (0.04)[c]
P-value	*0.007*	*<0.001*	*<0.001*	*<0.001*	*0.146*	*0.184*	*0.003*
				R			
Short-grass	37.5 (1.3)[b]	0.80 (0.10)[a]	51 (8)[c]	381.5 (49.2)[a]	5.5 (1.2)	2.6 (1.1)	2.3 (0.2)[ab]
Tall-grass	37.2 (0.5)[b]	0.65 (0.05)[ab]	59 (1)[bc]	353.1 (44.9)[a]	4.9 (3.6)	2.4 (1.8)	2.9 (0.4)[a]
Mountain pine	45.6 (0.5)[a]	0.37 (0.02)[bc]	123 (7)[a]	210.6 (13.6)[b]	6.9 (2.2)	1.9 (0.5)	1.7 (0.2)[bc]
Mixed	39.5 (1.8)[b]	0.38 (0.03)[bc]	108 (14)[a]	213.1 (33.3)[b]	3.1 (0.7)	0.7 (0.1)	1.5 (0.1)[bc]
Stone pine (alkaline)	40.8 (1.4)[bc]	0.44 (0.09)[b]	100 (21)[ab]	217.5 (40.2)[c]	3.2 (1.4)	0.8 (0.5)	0.7 (0.1)[c]
Stone pine (acid)	44.9 (1.7)[ac]	0.44 (0.08)[b]	111 (17)[a]	198.4 (20.3)[b]	2.1 (1.3)	0.7 (0.4)	1.7 (0.5)[bc]
P-value	*0.005*	*<0.001*	*0.012*	*0.003*	*0.364*	*0.140*	*0.009*

a,b,c = averages with the same letter are not significantly different at p = 0.05.

Table B3: Average contents of C, N, P, Mg, Ca, K, C/N ratio for brances and CR. Source: Kimmins et al. (1985).

	C (%)	N (%)	P (%)	Ca (%)	Mg (%)	K (%)
			Branches			
Pine	50	0.47	0.06	0.3	0.08	0.2
Spruce	50	0.76	0.06	0.3	0.07	0.25
Larch	50	0.36	0.12	0.3	0.12	0.7
			CR			
All species	50	0.08	0.015	0.06	0.012	0.08

Paper V

Red wood ants (*Formica rufa* group): Their contribution to soil C and N pools, and CO₂ emissions in subalpine forests

Anita C. Risch[1] , Martin F. Jurgensen[2], Martin Schütz[1], and Deborah S. Page-Dumroese[3]. Red wood ants (*Formica rufa* group): Their contribution to soil C and N pools, and CO₂ emissions in subalpine forests. *Ecology*

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Abstract

Red wood ants (RWA) (*Formica rufa* group) build large mounds consisting primarily of organic detritus and are found in many conifer and mixed conifer-hardwood forests of Europe. While much is known on RWA biology, behavior, and distribution, very little information is available regarding their impact on soil carbon (C) and nitrogen (N) cycling in forest ecosystems. Therefore, the objectives of this study were to estimate how much RWA mounds contribute to total forest soil C and N pools and C fluxes. We found that RWA mound density (number per ha) was linked to forest tree species composition, slope aspect, and canopy closure. The size of RWA mounds was positively correlated with successional age of the stands, resulting in largest RWA mounds in the oldest stands, where also RWA mound C and N pools were highest (990 kg/ha C and 21 kg/ha N). Carbon and N concentrations of mound material were significantly higher than in the forest floor, while C:N ratios were not. RWA mound C and N pools, in contrast, were found to be significantly lower than in the forest floor. The same pattern was found for

CO$_2$ emissions from RWA mounds. Even though the emissions from the mounds were found to be 12.4 (July) to 3.5 (September) times higher than from the forest soil, and RWA mounds therefore CO$_2$ "hot spots", they only contributed between 0.7 and 2.5% to the total forest soil CO$_2$ emission. Consequently, the contribution of RWA to total forest soil C and N pools and forest CO$_2$ emission is minor and likely not important when calculating or modeling C and N pools or C fluxes.

Keywords
mound density, high-elevation conifer forests, carbon and nutrient stores, carbon dioxide, Swiss Alps, forest floor, mineral soil, closed chamber system, "hot spots"

Introduction
Red wood ants (RWA) (*Formica rufa* group) are commonly found in many conifer and mixed conifer-hardwood forests of Europe (e.g. Gösswald 1989a,b). Because of their wide occurrence, this group of ants has been the focus of extensive research on their social structure (Gösswald 1989a), geographical distribution and density (e.g. Kissling 1985), population dynamics and behavior (Klimetzek 1981), and and their impact on biodiversity (Laakso and Setälä 2000). RWA have also been found to impact tree growth by feeding on leaf defoliators or protecting sap-sucking leaf aphids (Laakso and Setälä 2000; Smith and Schowalter 2001).

RWA build large above-ground nests (mounds) composed of litter collected from the surrounding forest floor (Wisniewski 1976; Gösswald 1989a,b). Many studies have reported mound density (number of mounds per ha) or mound size in European forests: Austria (Eichhorn 1963), Belgium (Ceusters 1979), Czech Republic (Frouz et al. 1997), Finland (Laasko and Setälä 2000), France (Torossian et al. 1979), Germany (Travan 1998), Great Britain (Sudd et al. 1977), Ireland (Breen 1979), Italy (Pavan 1962), Spain (Ceballos and Ronchetti 1965), and Sweden (Lenoir et al. 2001). However, many of these RWA studies from a wide range of forest ecosystems did not have extensive mound inventories or gave detailed information on stand age and tree species composition. Some individual RWA mound sizes and volumes were reported, but these measurements were not the main focus of most studies (Sudd et al. 1977; Torossian et al. 1979; Ceusters 1979; Coenen-Stass et al. 1980; Frouz et al. 1997).

Although mound density of RWA can be high in certain forest types (Raignier 1948; Ceballos and Ronchetti 1965; Gris and Cherix 1977; Cherix and Bourne 1980), very little

is known on the contribution of these mounds (composed of organic material) to forest soil carbon (C), nitrogen (N) pools and soil processes. The chemical composition of RWA mound material differs considerably from surrounding mineral soil (Frouz et al. 1997; Laakso and Setälä 1998; Lenoir et al. 1999) and forest floor (Lenoir et al. 2001). Higher numbers of soil microorganism are present in RWA mounds compared to the forest floor and mineral soil (Gösswald 1989a; Laasko and Setälä 1998), which could produce more CO_2 than the surrounding soil. Respiration from RWA living in mounds, estimated to range from 200 to 10'000 ants per dm^3 mound material (Kneitz 1964, Coenen-Stass et al.1980) or 500'000 to 1'000'000 or more ants per mound (Rosengren et al. 1987, Gösswald 1989a), may also be an important source of CO_2 emissions. However, no information is available on total C and N contents in RWA mounds or CO_2 emissions from these mounds. Consequently, studies on belowground C and N pools (e.g. Perruchoud et al. 1999; Vucetich et al. 2000; Ritter et al. 2003) and CO_2 emissions in European conifer forests (e.g. Widén 2002; Pumpanen et al. 2003; Subke et al. 2003) did not consider the contribution of RWA mounds in their calculations. Therefore, the objectives of our study were to: i) determine RWA mound density (numbers per ha) and mound volume in four different conifer forest stand types in the Central European Alps, ii) estimate the contribution of RWA mounds to soil C and N pools in these forests, and iii) compare CO_2 emissions from RWA mounds to the surrounding soil surface.

Site description

This study was conducted in the Swiss National Park (SNP), located in the southeastern part of Switzerland. The Park covers an area of 170 km^2 with elevations ranging from 1350 to 3170 m above sea level (m a.s.l.). Mean annual precipitation and temperature are 925 $\pm$ 162 mm and 0.2 $\pm$ 0.7°C (average $\pm$ standard deviation, measured at the Park's weather station in Buffalora, 1980 m a.s.l.). Fifty km^2 of the SNP are covered with forests, which are composed of mountain pine (*Pinus montana* Miller), Swiss stone pine (*Pinus cembra* L.), European larch (*Larix decidua* Miller), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). Pure stands of mountain pine are the early-successional forests, which are replaced by mixed-conifer stands at mid-succession. Most of the mixed stands contain all five conifer species, but stands dominated by larch/mountain pine are also found. The mixed stands are replaced by stone pine or stone pine/larch stands in late-succession (Risch et al. 2003a,b).

As part of a study on long-term forest dynamics, 16 forest stands were selected in proportion to their abundance in a 1957 forest inventory (Kurth et al. 1960; for more detail see Risch et al. 2003a,b). Six stands were dominated by mountain pine, two by larch/mountain pine, five contained all five tree species ("mixed"), and three were comprised of Swiss stone pine/larch ("stone pine"). A description of the stands studied is presented in Table 1. More detailed information to stand and soil sampling can be found in Risch et al. (2003a,b, 2004).

Table 1: Description of the four forest types studied in the Swiss National Park (in order from early to late successional stage). Part A: Forest stand properties, Part B: Slope and mineral soil properties. PIMO = *Pinus montana*, PICE = *Pinus cembra*, LADE = *Larix decidua*, PIAB = *Picea abies*, PISY = *Pinus sylvestris*, OM = organic matter.

A

Stand type	Nr. of stands	Tree species composition (% of total basal area)					Forest stand properties				
		PIMO	PICE	LADE	PIAB	PISY	Canopy closure	Stand height	Stand age	Basal area	Stand density
	n						%	m	years	m²/ha	stems/ha
Mountain pine	6	96	2	1	-	1	43	14	165	25	1659
Larch/mountain pine	2	35	-	62	1	2	46	19	168	34	1275
Mixed	5	17	1	32	34	16	54	25	200	42	784
Stone pine	3	3	63	25	8	1	63	27	236	54	577

B

Slope and mineral soil[1] properties

Stand type	Slope exposure	Slope-angle	Texture	Rock content	pH	Avail. water	OM	Bulk density	C pools	N pools
		°		%		g/100 g soil	%	g/cm³	t/ha	t/ha
Mountain pine	S	21	Sandy loam	32	6.2	12.2	15	1.3	139	3.3
Larch/mountain pine	ESE	14	Sandy loam	33	6.6	6.8	12	1.2	100	2.9
Mixed	SSE	20	Loamy sand	30	5.5	11.5	7	1.4	69	2.7
Stone pine	NNW	24	Sand	37	3.1	10.6	3	1.6	28	1.2

[1]Measured in the surface 20 cm of mineral soil

Methods

RWA mound and forest floor sampling

In each stand RWA mounds were tallied in a 20 m radius circle around 16 systematically distributed sampling points (systematic grid of 70 x 70 m or 40 x 40 m depending on stand size). Mound volume and surface area were calculated from height and two perpendicular diameters measured on each mound using the equation of half an ellipsoid (Sudd et al. 1977; Ceusters 1979, Gösswald 1989b).

Ant mound samples for bulk density determination and chemical analyses were collected at six average sized mounds per stand type (total of 24 mounds). At each mound one 150 cm^3 sample (core diameter 6.5 cm) was taken at 0 – 10 cm and at 10 – 20 cm from the top. Since extensive RWA mound disturbance is restricted in the SNP, we were only able to collect a 150 cm^3 sample near the mound center (40 – 50 cm from top) from every second mound. Three circular 700 cm^2 forest floor samples were collected at the center of each stand (Figure 1). All RWA mound and forest floor samples were oven dried at 65°C, fine-ground to pass a 0.5 mm mesh screen, and analyzed for total C and N on a LECO induction furnace at 1000 °C. Sub-samples were dried at 105 °C to correct bulk density calculations. Organic matter (OM) content was determined by loss of ignition (Ben-Dor and Banin 1989).
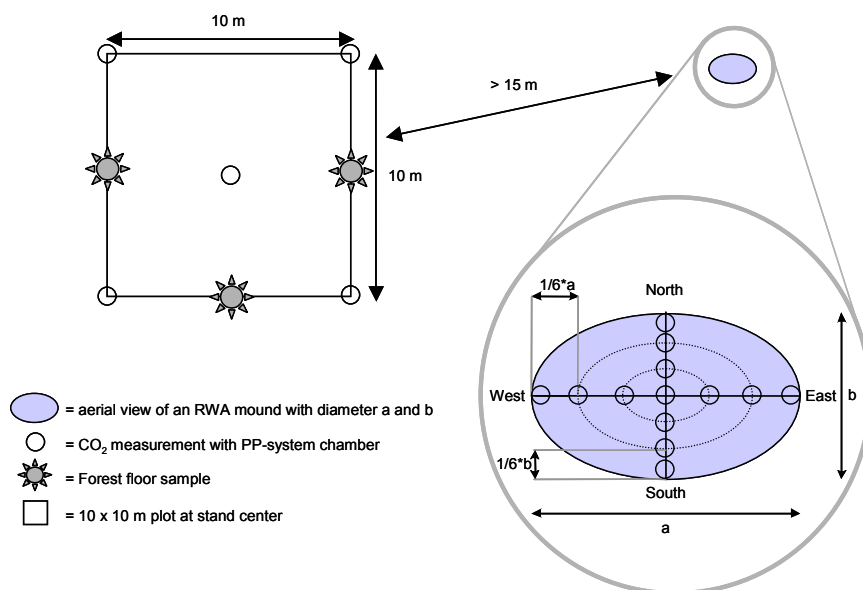
Figure 1: Forest floor and CO_2 sampling design.

CO$_2$ emissions

We measured CO$_2$ emissions with a PP-System EGM-4 infrared gas analyser on four mounds nearest to the stand center in each forest type (total of 16 mounds). Thirteen measurements were taken on two transects across each mound (Figure 1) every second week from late June till mid-September (6 sampling periods) when it was not raining. Soil CO$_2$ emission from the soil surface was also measured in each stand using the EGM-4 infrared gas analyzer on PVC collars inserted at five locations after snowmelt (Figure 1).

Statistical analyses

Differences in number of ant mounds, RWA mound bulk densities, RWA mound and forest floor C and N concentrations, and pools among the different stand types were tested using a 1-way ANOVA followed by a LSD post-hoc test for pair-wise comparison (significance level: p = 0.05). Because RWA mounds from the same stand may not be independent from each other, we used a nested ANOVA (stand within stand type) followed by LSD pairwise comparison to test whether individual mound parameters (height, diameter, volume) differed between the four stand types. Number count data (RWA mounds/ha) were square root transformed, and height, diameter, and volume log transformed before analysis to increase normality and to reduce heterogeneity of variance. Differences between forest floor and RWA mound C and N concentration and pools were tested using 1-way ANOVA for each stand type. Differences between average RWA mound and forest floor CO$_2$ emission of the four stand types were tested with t-test for pairwise comparison using the data pairs for each measuring period. Overall differences in CO$_2$ emissions of RWA mounds and forest floor among stand types was analyzed using repeated measure ANOVA. Pairwise comparison (t-test) was used to test differences in emissions from the individual 16 mounds (over all six measuring periods) and differences in emissions dependent on sampling location (top, 1/3, 2/3, and bottom in all caridinal directions; total of 13 locations). CO$_2$ emission data was log transformed for all analyisis to assure equal variance. Regression analysis was used to assess the correlation between RWA mound CO$_2$ emission and mound size (volume and surface area).

Results and Discussion

RWA mound density, size and volume

A total of 242 RWA mounds were recorded within the 16 forest stands studied. The number of mounds per hectare differed significantly among the forest types (Table 2). The highest numbers were found in mixed-conifer forests, which also had the highest tree species diversity of the four stand types (Table 1). Higher tree species diversity has been reported to favor the development of RWA mounds by increasing the number and type of leaf aphids and other RWA food sources (Laine and Niemelä 1989; Gösswald 1989a,b). Mixed stand types were also located on SSE-exposed slopes (Table 1), which generally provide more suitable temperature and moisture conditions for RWA colonization (Forel 1920; Klimetzek 1970; Bretz 1971; Sossna 1973; Travan 1998). The low RWA mound numbers in south-facing mountain pine stands were likely due to a combination of minimal tree species diversity and high stand temperatures associated with relatively low canopy closure (Adlung 1966; Kissling 1979; Travan 1998). In contrast, dense canopy closure in the north-exposed stone pine stand type would give considerably lower air temperature, which likely results in fewer RWA mounds per hectare (Klimetzek 1970; Sossna 1973).

While RWA mound height (p = 0.057) and diameter (p = 0.066) were not significantly different among our four stand types, individual mound volumes in stone pine stands were more than five times larger (p = 0.035) than mounds in the other three stand types (Table 2). However, when calculated on a hectare basis, total RWA mound volumes did not significantly differ among the stand types (p = 0.135). Stone pine stands were located on north-facing slopes and had the highest canopy closure (Table 1), site conditions that generally lead to larger RWA mounds (Gösswald 1989a). The stone pine stands also were the oldest stands studied in our study (Table 1), and would likely contain older RWA mounds than younger, early-successional forests. RWA mounds usually increase in size as colonies become older (Wellenstein 1928; Gösswald 1989b), but little is known on the relationship of mound size to stand age in different forest types. Only a few studies have reported the age of forests in which the RWA mounds were located (Sudd et al. 1977; Cherix 1980; Punttila 1996).

Table 2: Number/ha and size of RWA mounds in high-elevation conifer forests in the SNP, and in other European forest types. Dominant tree species in bold, otherwise species listed alphabetically. - = not available, ± = standard deviation, ( ) = standard error in parentheses.

Forest composition	Elevation (m a.s.l.)	Nr. of mounds per ha	Nr. of mounds in study	Height (cm)	Diam (cm)	RWA mound Average volume (m³)	RWA mound Total volume (m³/ha)	Source
This study								
P. montana*	**2006 (28)**	**6.4 (0.3)[c]**	**62**	**46 (3)**	**83 (5)**	**0.29 (0.05)[b]**	**1.8 (0.3)**	
L.decidua, P. montana*	**1850 (30)**	**10.9 (0.1)[b]**	**51**	**43 (3)**	**95 (7)**	**0.36 (0.06)[b]**	**3.9 (0.7)**	
P. abies, L. decidua, P. montana, P. sylvestris*	**1792 (25)**	**13.3 (0.4)[a]**	**100**	**53 (3)**	**102 (5)**	**0.44 (0.06)[b]**	**5.5 (0.7)**	
P. cembra, L. decidua*	**1963 (32)**	**6.0 (0.3)[c]**	**29**	**83 (10)**	**155 (17)**	**2.17 (0.7)[a]**	**13.3 (4.9)**	
Other studies								
Mixed conifer forests								
L. decidua, P. abies, Abies alba,	1100 – 1700	5.6	-	-	-	-	-	Eichhorn 1963, Austria
L. decidua, P. cembra, P. abies	1500 – 2150	5.6	-	-	-	-	-	
P. sylvestris, Pinus nigra, Larix leptolepis, Pinus contorta, Picea sitkaensis (plantation)	150	1.6	324	27±18	54±35	0.6 – 0.9	-	Sudd et al. 1977, Great Britain
P. abies, P. sylvestris	-	-	1	94	-	-	-	Rosengren et al. 1987, Finland
Single species conifer forests								
P. sylvestris	-	1 - 10	-	-	-	-	-	Lenoir et al. 2001, Sweden
P. abies	-	2.0[1] 13.8[2]	-	-	-	-	-	Punttila 1996, Finland
P.abies (plantation)	380	5	1	-	-	1 – 3	-	Frouz et al. 1997, Czech Republic
P. abies (plantation)	260 - 500	1.2 –6.1	44 - 266	75 - 85	130 - 230	0.5 – 2.2	-	Ceusters 1979, Belgium
P. abies	~70	-	9	10 – 80	60 -250	-	-	Heimann 1963, Germany
P. abies	-	16.6	-	-	-	-	-	Rosengren et al. 1987, Finland

Table 2: Continued

Forest composition	Elevation (m a.s.l.)	Nr. of mounds per ha	Nr. of mounds in study	Height (cm)	Diam (cm)	RWA mound Average volume (m^3)	Total volume (m^3/ha)	Source
Mixed conifer-hardwood forests								
Fagus sylvatica, P. abies, A. alba	950[3]	3	3	25	73 – 75	-	-	Eichhorn 1964, Austria
	1050[3]	12	5	39	82 – 87	-	-	
	1240[4]	6	6	31	100 – 126	-	-	
P. sylvestris, *Betula pubescens*	80 – 330	3 – 6	6	80	160	-	-	Laine and Niemelä 1989, Finland
Betula pendula, P. abies, P. sylvestris	-	1 – 10	-	-	-	-	-	Lenoir et al. 2001, Sweden
B. pendula, P. abies, P. sylvestris,	-	9	10	43±11[5]	103±24[5]	-	-	Laasko and Setälä 1998, Finland
A. alba, F. sylvatica, L. decidua, P. abies, P. sylvestris, Quercus spp.	332 – 637	<0.1 – 0.2	-	-	-	-	-	Wellenstein 1967, Germany
Quercus spp., Pinus spp.	-	-	1	-	-	0.57	-	Coenen-Stass et al. 1981, Germany
P. abies, , *Acer pseudoplatanus, F. sylvatica, Salix grandifoli, Sorbus aucuparia*[6]	1050	17.1	-	-	-	-	-	Cherix 1980, Switzerland
Hardwood forests								
F. sylvatica, Quercus spp,	332 – 637	<0.1	-	-	-	-	-	Wellenstein 1967, Germany
F. sylvatica	600 - 800	0	-	-	-	-	-	Eichhorn 1963, Austria
Forest composition uncertain								
A. alba, F. sylvatica, L. decidua, P. abies, P. cembra, P. montana[7]	1500 – 2000	4 – 67	4 - 67	-	-	0.4 – 7.4	0.4 – 11.2	Toroissian et al. 1979, France
Mixed conifer	-	3.0 - 4.8	-	-	-	-	-	Travan 1998, Germany
Mixed conifer/hardwood	-	4.4 – 4.5	-	-	-	-	-	
Unknown composition	700 – 1800	0.3 – 17.8	-	-	-	-	-	
Black forest[8]	300 – 700	<0.1 – 0.2	298	35±5 - 40±7	76±10 - 106±21	-	-	Klimetzek 1981, Germany
7 different stand types	500 - >1500	-	102 - 295	10 – 79[9]	21 – 187[9]	-	-	Eichhorn 1964, Austria
Corylus spp., Betula spp., L. decidua, P. abies and P. cembra[7]	400 - 1800	<0.1	408	46 – 93	16 - 38	-	-	Kneitz 1965, Germany

* detailed stand description in Table 1, [1] old forest (> 100 years), [2] young forest (14 to 25 years), [3] *F. sylvatica* (40%), *P. abies* (30%), *A. alba* (30%), [4] *F. sylvatica P. abies*, almost no *A. alba*, [5] average mound, [6] age 70 to 90 years, [7] studies in different forest stands, but not well defined which stand had which species composition, [8] Species composition most likely monoculture Norway spruce, [9] mean mound from different stand types, a,b,c, = averages with the same letter are not significantly different at p = 0.05.

Dethier and Chérix (1982) reported that two RWA species (*Formica lugubris* ZETT. and *Formica aquilonia* YARROW) are present in the SNP forests. However, the mound size differences we found among stand types likely are not related to the RWA species distribution, since no correlation has yet been reported between mound size and RWA species (Sossna 1973; Gösswald 1989a).

Comparing our results to other studies is difficult, since very limited information is available on RWA in European subalpine forests (Table 2). Torossian et al. (1979) reported mound numbers for high-elevation forests in France containing both stone pine and mountain pine, but information on tree species composition, slope exposition, and canopy closure in their stands were incomplete or lacking. A similar situation was found in the RWA study by Kneitz (1965) for high-elevation Austrian forests containing stone pine and larch. Eichhorn (1963) gave qualitative descriptions of the stone pine/larch stands he studied in Austria, but again, quantitative stand data was not given. The same lack of stand and site information was found for many RWA studies conducted in other forest types at lower elevations (Table 2).

In general, most studies have shown that RWA prefer conifer forests or mixed conifer-hardwood stands over pure hardwood stands (Gösswald 1989b; Table 2). However, low mound densities found in some low-elevation German and Austrian conifer or mixed conifer/hardwood stands during the 1960/1970 time period (Eichhorn 1963; Kneitz 1965; Wellenstein 1967; Klimetzek 1981) seem to contradict this general pattern. These stands were intensively managed and fragmented during the 19th and 20th century, were subjected to severe air pollution, and experienced extensive RWA mound destruction after the 2nd World War (Kneitz 1965; Gösswald 1989b; Travan 1998). We did not find newer studies from these forests to determine if RWA populations have increased since 1960/70.

RWA mound C and N pools
RWA mound bulk densities (BD) of the 0 – 10 cm, 10 – 20 cm and 40 – 50 cm mound depth were not significantly different within each individual stand type. Therefore, we used an average mound BD to calculate mound C and N pools for each forest type (Table 3). Our BD values are similar to RWA mounds in Finland (L. Finér/T. Domisch, personal communication) and Germany (Coenen-Stass et al. 1980). Gösswald (1989a) reported a

higher RWA mound BD of 210 kg/m^3, but did not give any information on how this value was obtained or the numbers of mounds sampled.

Similar to BD's, C and N concentrations of our mound samples taken at different RWA mound depths did not differ significantly, and so we again used average values to calculate mound C and N pools in each stand type. RWA mounds in the larch/mountain pine stand type had significantly higher C and OM concentrations than mounds in the other stand types, reflecting their lower BD's, but N concentrations and C:N ratios were similar among the stand types (Table 3). Both C and N pools were significantly higher (C: p <0.001; N: p < 0.001) in stone pine stands, but did not differ among the other three stand types.

Carbon concentrations of RWA mounds in the mountain pine and mixed stand types were significantly higher than the surrounding forest floor (Table 3). Significantly higher mound N concentrations were also found in all stand types except the mountain pine. However, C:N ratios of RWA mounds and forest floor were similar. Expressed on an area basis, the amounts of C and N in RWA mounds were only a fraction of C and N stored in the forest floor, ranging from 0.6 to 5% (Table 3). If C and N present in the surface mineral soil (0 − 20 cm) is also included (Table 1), the contribution of RWA mounds to total soil C and N pools is even smaller. RWA mounds also extend into the mineral soil and increase mineral soil C and N contents compared to non-mound soil (Malozemova and Koruma 1973; Hulugalle 1995, unpublished data SNP). However, the volume of soil affected by RWA mounds is so small that it would not change the relationship of RWA mounds to total soil C and N pools.

Very little additional information is available on C and N in RWA mounds. Lenoir et al. (2001) reported variable results for OM, C and N material taken from RWA mounds and forest floor in Sweden (Table 3). In a laboratory experiment they found that decomposition rates of RWA mound material is very slow under moisture conditions similar to the inside of the mound. Frouz et al. (1997) found higher C concentrations in a RWA mound located in a Norway spruce plantation in the Czech Republic than in the forest floor. However, neither Lenoir et al. (2001) nor Frouz et al. (1997) calculated amounts of C and N in RWA mound or estimated the total RWA mounds C and N pools/ha.

Table 3: RWA mound and forest floor bulk density, OM, C and N concentration, C:N ratios, and C and N pools in the SNP in Switzerland and in other studies conducted in Europe. Standard error in parentheses.

Forest type	Bulk density (kg/m³)	RWA mound						Forest floor					
		OM (%)	C (%)	N (%)	C:N ratio	C pool (t/ha)	N pool (kg/ha)	OM (%)	C (%)	N (%)	C:N ratio	C pool (t/ha)	N pool (kg/ha)
This study, Switzerland													
Mountain pine	169 (13)[a]	76 (5)[b]	43.8 (2.3)[b]	1.07 (0.07)	43 (4)	0.13 (0.02)[b]	3.2 (0.6)[b]	74 (3)	40.0 (1.3)	0.89 (0.04)	47 (3)	23 (5)	353 (16)
Larch/mountain pine	108 (4)[c]	92 (1)[a]	51.3 (0.8)[a]	0.99 (0.04)	53 (3)	0.22 (0.04)[b]	4.2 (0.8)[b]	80 (2)	42.5 (1.9)	0.88 (0.03)	48 (1)	24 (10)	376 (31)
Mixed	131 (7)[bc]	79 (3)[b]	46.2 (1.9)[b]	0.97 (0.05)	50 (4)	0.33 (0.05)[b]	7.0 (1.0)[b]	66 (5)	36.1 (3.2)	0.82 (0.04)	50 (3)	16 (6)	300 (30)
Stone pine	150 (10)[ab]	81 (2)[b]	46.3 (1.2)[b]	1.05 (0.04)	45 (5)	0.99 (0.34)[a]	20.9 (7.7)[a]	76 (6)	35.5 (5.4)	0.93 (0.08)	39 (3)	19 (10)	408 (56)
Other studies													
*P. sylvestris	-	79-82	36-45	0.65-0.81	56	-	-	81	44	1.20	36	-	-
*P. sylvestris, P. abies, B. pendula	-	74-86	38-45	1.17-1.21	33-37	-	-	45	25	0.96	28	-	-
**P. abies	-	-	-	39	-	-	-	-	35	-	-	-	-

* Lenoir et al. 2001 (Sweden), ** Frouz et al. 1997 (Czech Republic)
a,b,c = averages with the same letter are not significantly different at p = 0.05

CO_2 emissions

Average CO_2 emission significantly differed between the 16 RWA mounds monitored. The emissions were correlated to mound volume and surface area (r = 0.78, p < 0.001; r = 0.79, p < 0.001), and ranged between 0.8 and 8.6 g $CO_2/m^2/hr$ (season average of the individual 16 mounds) with an average of 3.9 g $CO_2/m^2/hr$ (season average of all mounds). In general, emissions were highest on the mound top and decreased towards the mound bottom regardless of cardinal direction. Average CO_2 emissions (all 16 mounds, all 6 sampling periods) were significantly higher at the mound top compared to all other measurements (Table 4), while CO_2 emissions sampled at 1/3 from the top were significantly higher than the ones taken at 2/3 from the top and at the bottom of the mound (no difference in cardinal directions; Table 4).

Since decomposition rates of OM material in active mounds are very low (Lenoir et al. 2001), we can assume that the contribution of RWA mound decomposition to total CO_2 emissions is neglectable. Also root respiration by vascular plants likely is very small, as RWA are known to quite effectively prevent plant growth on and close to the mound (Gösswald 1989a). Thus, CO_2 emissions measured in our study mainly origin from RWA respiration, the respiration of other organisms living within the mound (microbes and parasites), or tree roots. While no information is available on the amount of tree roots underneath/within RWA mounds, some studies have been conducted on RWA respiration rates and respiration of microbes inhabiting RWA mound material. Respiration of *Formica rufa* L. workers has been reported to be on average $1.14*10^{-5}$ g CO_2/hr per worker (6.5 µl/hr) at temperatures of 25°C (Holm-Jensens et al. 1980). Thus, 100'000 workers would produce 1.14 g CO_2/hr. Given that population sizes range between 500'000 and 1 million (or more) RWA in large mounds (Rosengren et al. 1987, Gösswald 1989a), the highest fraction of the total CO_2 emission measured in this study likely is produced by RWA. Nevertheless, as Frouz (2000) showed, also microbe respiration can contribute to total respiration. He found that microbial respiration was approximately 0.7 CO_2 mg/g/day when incubating mound material (without ants) under moisture and temperature conditions comparable to the inside of RWA mounds (27°C; 10% moisture). Thus, an average SNP RWA mound (volume = 0.6 m^3, bulk density = 139 g/cm^3, surface area = 2.2 m^2) would release approximately 1.1 g $CO_2/m^2/hr$.

Table 4: Pairwise comparison of average CO2 emissions (all 16 mounds, all 6 sampling periods) measured at the 13 different sampling locations. Log transformed data was used. * indicates significant different results, ns = not significant. Significance level $p = 0.05$.

| | | North | | | East | | | South | | | West | | |
		1/3	2/3	bottom	1/3	2/3	bottom	1/3	2/3	bottom	1/3	2/3	bottom
North	**2/3**	*											
	bottom	*	*										
East	**1/3**	ns	*	*									
	2/3	*	ns	*	*								
	bottom	*	ns	ns	ns	*							
South	**1/3**	ns	*	*	*	*	*						
	2/3	*	ns	ns	*	ns	ns	*					
	bottom	*	*	ns	*	*	ns	*	*				
West	**1/3**	ns	*	*	ns	ns	*	ns	*	*			
	2/3	*	ns	ns	*	ns	ns	*	ns	ns	*		
	bottom	*	*	ns	*	*	ns	*	*	ns	*	*	
Top		*	*	*	*	*	*	*	*	*	*	*	*

Given that the largest fraction of CO_2 measured likely origins from RWA, emission rates can be used as surrogates for RWA presence and therefore to explain the spatial differences in emission rates measured at our 13 sampling locations. Since the actual nest (breeding chamber, "heat core") lays within the top part of the RWA mound (Gösswald 1989a), we would have higher numbers of RWA located in this part of the mounds, which is the likely reason for the significantly higher average CO_2 emissions measured at the top and 1/3 from the top of the mound (Table 4). RWA maintain temperatures of 25°C to 30°C in this part of the nest (Frouz 2000) by "bringing" heat from the mound surface into the center using their bodies as "heat-carriers". In particular in spring, large fractions of the colony move between the mound surface and the nest (Rosengren et al. 1987, Gösswald 1989a). Our CO_2 emission measurements mirror this behavior to some extent, as shown for the two mounds with the highest and the lowest emission during the season in Figure 2. Mound A was located on a ESE-facing slope, and had highest emission rates at the S-side of the mound during most of the season (Figure 2A). Mound B, which was located on a S-facing slope had highest emissions on the S-slope in June, while highest values were measured on the N-side between July and early August. On the N-side of the mound temperatures were likely somewhat lower, thus offering better conditions, compared to the top and S-side where temperatures reached up to 60°C on the surface (A. Risch, personal observations). In late August, the RWA were again more evenly distributed in their mound, while they were no longer active (almost no emissions) in early September (Figure 2B).
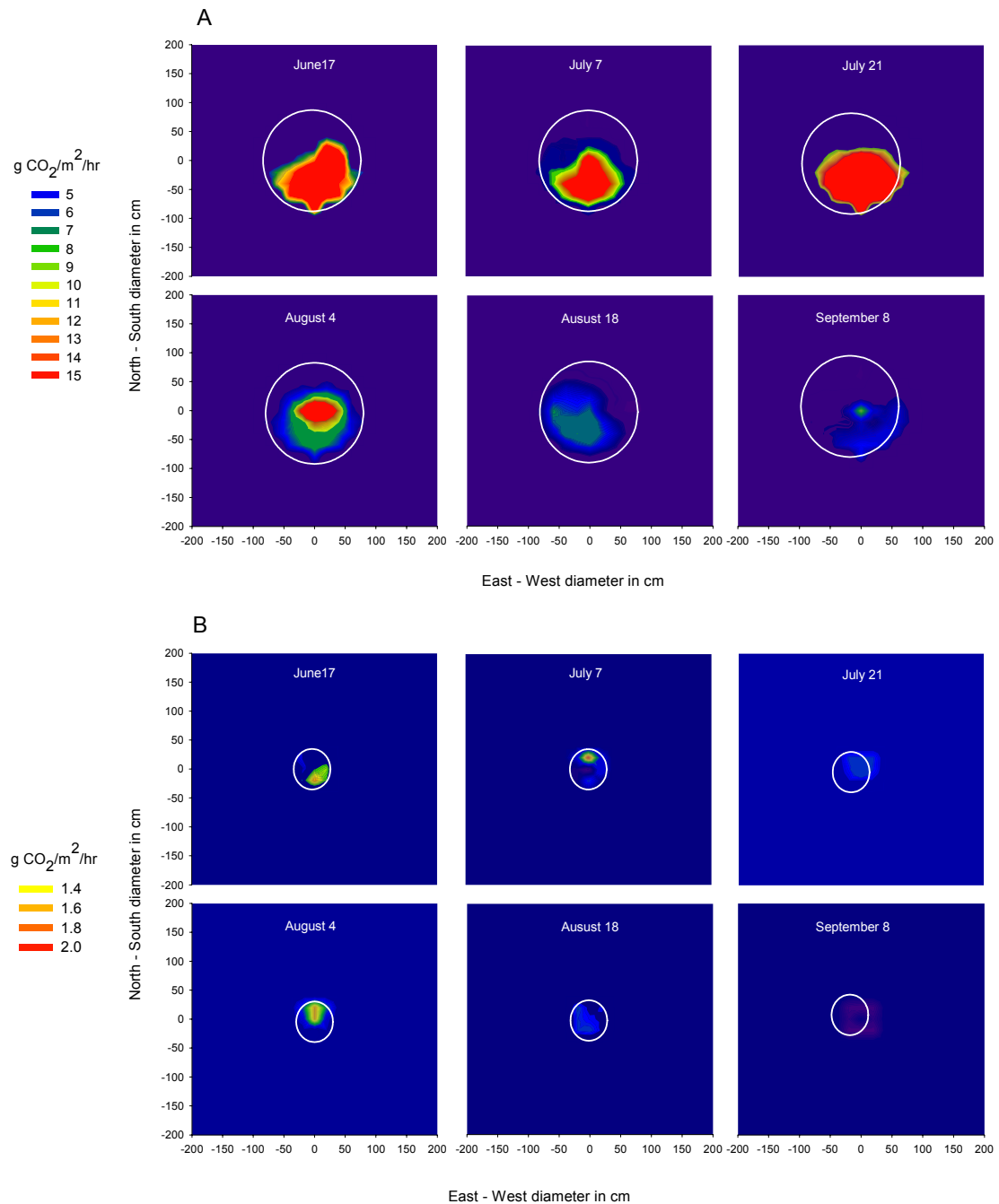
Figure 2: CO_2 emission between June 17 and September 8 of two RWA mounds. The white ellipse indicates the aboveground basal extent of the mounds (aerial view). Data points between the 13 sample locations were calculated by interpolation of the surrounding sample points. A: RWA mound with the highest, B: RWA mound with the lowest CO2 emission during the sampling season.

Besides the spatial differences in RWA mound CO_2 emissions, we also detected a significant trend in emission rates over the sampling season ($p < 0.001$), while no differences were detected among the four stand types ($p = 0.24$). Forest floor emissions differed among the stand types ($p = 0.045$), and also showed a seasonal trend (except mixed stand type, $p > 0.001$). Both RWA mound and forest floor emissions peaked in

July and decreased towards early September (Figure 3). This reduction in RWA mound CO_2 emission is likely associated with decreasing mound temperatures in fall (Heimann 1963, Rosengren et al. 1987; T. Domisch/M. Ohashi, personal communication), when RWA become less active. Changes in temperature (air/soil) were likely also responsible for the seasonal trend found in forest floor emissions.

Overall, RWA mounds were "hot spots" for CO_2 emissions having significantly higher emission rates than the forest floor ($p < 0.001$; Figure 3). The values ranged from 12.4 (mid July; average of all mounds) to 3.5 (early September; average of all mounds) times higher than the forest floor. However, the total surface area of our RWA mounds only averaged 9 to 32 m^2/ha in the different stand types, which is 310 to 1110 times lower than the surface of the forest floor. Consequently, CO_2 emissions from the mounds contributed only 0.7 to 2.5% of the total soil CO_2 emissions during the summer. Thus, RWA mounds likely are not very important sources of CO_2 in the four forest types studied.
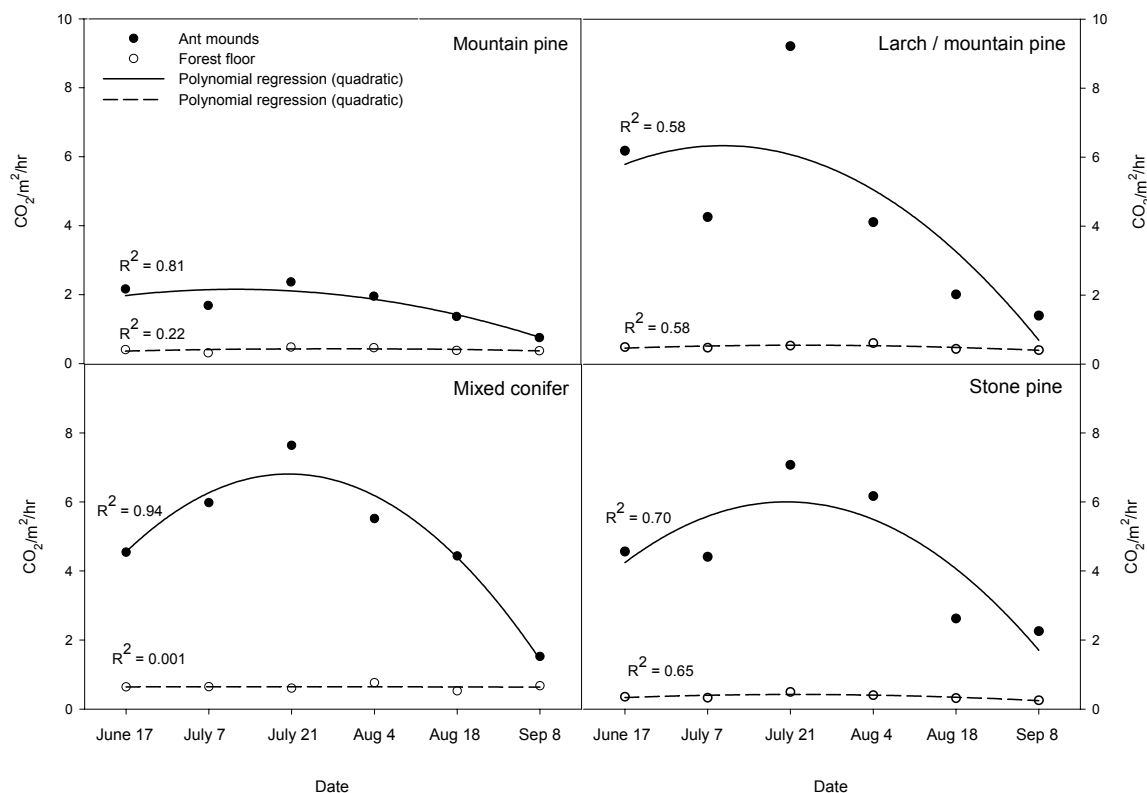
Figure 3: Average stand type specific CO_2 emission rates of RWA mounds and forest floor at six sampling dates between mid June and beginning of September.

We are not aware of any other study that meassured CO_2 emissions from RWA mounds. Bender and Wood (2003) reported higher CO_2 emission from US fire ant mounds than from the soil surface, but similar to our study, the contribution to total ecosystem CO_2 emissions was very small. In contrast to termite nests, which can contribute significant amounts of CO_2 to the environment (Zimmermann et al. 1982, Khalil et al. 1990, Konaté et al. 2003), ant mounds probably do not have to be accounted for when calculating or modeling regional, national, or global CO_2 budgets.

The importance of RWA for forest soil processes

Concerning ecosystem CO_2 emission, RWA do not have a major impact on total ecosystem efflux. The same holds true when analyzing RWA mound C and N pools at one point in time. However, since RWA quite frequently abandon their mounds and since RWA mound material contains more C and N compared to the forest floor, RWA potentially increase total forest ecosystem C and N pools over long time spans. Since no information is available on mound abandonment rates or on how fast the abandoned mounds decompose, we cannot extrapolate our results to acquire an estimate of how RWA influence ecosystem C and N pools over long time periods.

Acknowledgements

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Section III

Modelling the development of subalpine conifer forests in the Central European Alps

Paper VI
Simulating structural forest patterns with a forest gap model: a model evaluation

Paper VII
Using a Markov-chain model to predict succession in subalpine conifer forests in the Central European Alps

Paper VIII
Predicting long-term development of abandoned subalpine conifer forests in the Central European Alps

Paper VI

Simulating structural forest patterns with a forest gap model: a model evaluation

Submitted as:

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Abstract

Forest patch models have been used successfully in forest dynamics research. Up to now, studies have mostly focused on simulating the temporal changes in species composition, comparing the results to potential natural vegetation or forest inventory data. Yet, these models could also be very useful in predicting structural forest patterns (e.g. size distribution) over large time spans. However, little is known on the performance of forest patch models in simulating such features, since the availability of long-term forest stand data is limited. The objective of this study was to test and improve the performance of the forest gap model ForClim in simulating structural features. To this end, we used long-term forest data (45-years) from three different forest types in the Swiss National Park.

Initial simulation runs were conducted with a slightly modified version of the model, but the simulations failed to reproduce the observed structural patterns. A detailed analysis of the growth performance of individual trees led to the conclusion that the height-diameter function implemented in ForClim V2.9 is unrealistic, and should be replaced by an ecologically more robust function. By implementing such a new function, we were able to significantly improve the performance of ForClim in simulating the structural features of the different mountain forest stands. Our results showed close matches between simulated and observed stand data after 45 years. We believe that model evaluation and validation,

such as conducted in this study, could be quite useful for increasing the reliability of simulations performed with this class of models.

Keywords
ForClim, long-term forest data, growth function, forest succession, validation

Introduction
Gap models are individual-tree based, semi-mechanistic simulators designed to study tree population dynamics on small patches of land. These models have been quite successful in research related to forest development and long-term forest succession (e.g. Bugmann 1997, Fischlin and Gyalistras 1997, Bugmann and Fischlin 1996, Kräuchi and Kienast 1993, Prentice et al. 1993, Urban and Shugart 1989, Solomon et al. 1981). Up to now, modeling studies have mostly focused on simulating temporal changes in species composition (Hasenauer et al. 2000), and they have generally been validated by comparing the results with potential natural vegetation (e.g. Lexer 2000) or national forest inventory data (e.g. Löffler and Lischke 2001). Yet, even though gap models could be useful for predicting structural forest patterns (e.g. size distribution), only few studies have been conducted in this context (e.g. Lindner et al. 1997). The main reason for the lack of such research is that appropriate long-term forest data containing structural features are difficult to obtain (Bugmann 1996, Lindner et al. 1997). Thus, little is known on the accuracy of forest patch models in simulating structural features such as tree size distribution. Therefore, the objective of this study was to 1) test and 2) improve the performance of a forest gap model, ForClim (Bugmann 1994), in simulating structural features based on long-term forest data from the Swiss National Park (SNP).

Material and methods

Study site
The SNP is located in the southeastern part of Switzerland and covers an area of approximately 170 km^2, 50 km^2 of which are forested. The area was not influenced directly by humans during most of the 20th century. The elevation ranges from 1350 to 3170 meters above sea level (m a.s.l.), and the mean annual precipitation and mean annual temperature are 925 ± 162 mm and 0.2 ± 0.7 °C (mean ± standard deviation; measured at the weather station in Buffalora located just outside the Park, 1980 m a.s.l.).

The Park's forests are dominated by five conifer species. Mountain pine (*Pinus montana* Miller), Swiss stone pine (*Pinus cembra* L.), and European larch (*Larix decidua* Miller)

are the major species, while Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) are less important (Zoller 1995). Both Scots pine and Norway spruce are not competitive in the cold and dry climate at high elevations in the SNP (Ellenberg 1996, Keller et al. 1998). Today, stands dominated by mountain pine occupy large parts of the Park, while other areas are covered with forests dominated by Swiss stone pine (or a mixture of Swiss Stone pine/larch), and mixed species stands (all five species; Risch et al. 2003a,b).

Long-term forest data

A database for the SNP's forests exists for the year 1957 (Kurth et al. 1960). This database contains information on the number of trees/ha in certain DBH (diameter at breast height = 137 cm) classes sampled on 2050 systematically distributed plots. This information was consolidated to 131 stands (Kurth et al. 1960). Today, only the stand level data are available.

We re-sampled 19 of the 131 stands in 2001 and 2002. They were located within an area of approximately 80 km^2 in the center of the Park at elevations between 1700 to 2200 m a.s.l., and were selected randomly in proportion to their abundance in 1957 (Kurth et al. 1960). The 19 stands were then divided into stand types based on their species composition, tree density and stand density in 1957: (1) stands dominated by mountain pine (hereafter referred to as "mountain pine"); (2) stands dominated by mountain pine but with considerable amounts of all other species ("mixed"); and (3) stands dominated by Swiss stone pine or Swiss stone pine/larch ("stone pine"). These three groups contained six, six, and seven stands, respectively (Risch et al. 2003a).

We sampled 16 points in each stand on a systematic grid of 70 x 70 meters or 40 x 40 meters, depending on stand size using the point-centered quarter method (Greig-Smith 1983). Trees taller than breast height were sampled, and tree density (number of stems/ha) for different DBH classes was calculated per species and stand (for a detailed description see Risch et al. 2003a,b). The numbers of trees/ha per DBH class and species were then averaged for the three different stand types "mountain pine", "mixed", and "stone pine" and both sampling years.

The ForClim model

The horizontally non-explicit forest model used in this study is ForClim. A detailed description of model version 2.9 can be found in Bugmann (1994, 1996), Bugmann and

Cramer (1998) and Bugmann and Solomon (2000). The version used here was a modified version of V2.9. This version features the following modifications compared to the latest published version (Bugmann and Solomon 2000):

- It samples monthly precipitation data from long-term statistical data assuming a log-normal distribution (Eq. 1), as opposed to the normal distribution used in earlier versions of ForClim. This change was introduced because particularly in dry areas, precipitation is not distributed normally around the long-term mean, and assuming a normal distribution leads to a strong overestimation of the frequency of months with very little or even zero precipitation.

$$\frac{1}{\sigma\sqrt{2\pi}}\frac{1}{x}\exp\left\langle -\frac{1}{2}\left(\frac{\log_e\langle x\rangle - \mu}{\sigma}\right)^2\right\rangle \tag{1}$$

where σ is the standard deviation and μ the arithmetic mean of the monthly precipitation sum.

- The tree regeneration routine was changed to account for differences in regeneration strategies of shade-tolerant and shade-intolerant tree species. There is an ecological trade-off in the sense that shade-intolerant tree species often produce more offspring under favorable conditions than shade-tolerant ones (Kimmins 1997). To take this into account, the multiplier *kLa* was included in the calculation of the number of newly established trees in ForClim. *kLa* is a species-specific parameter that describes the light tolerance, ranging from 1 (most shade-tolerant) to 9 (least shade-tolerant). Thus, with this change we effectively assume that shade-intolerant trees produce up to 9 times as much offspring as shade-tolerant trees.

Initialisation of ForClim with measured 1957 data

In ForClim, simulations are performed for small patches ("gaps"), having a standard size of 833 m^2. An initialization of the 1957 forest stand data on a 833 m^2 patch-size scale was therefore necessary. To accomplish this, we used the structure generator (Strugen) of the SILVA model (Pretzsch 1992, 2001, Kahn and Pretzsch 1997). Strugen is powerful in generating detailed forest data based on inventory data (stems/ha in different DBH classes), while simultaneously considering the spatial interactions between trees. We

generated a one-hectare forest patch for each specific forest stand type in a first step (see Figure 1). Since Strugen assigns an x-y-coordinate for each tree when generating the patch, we were able to divide the one-hectare patch into twelve 833 m² sub-patches in a second step (Figure 1). Each of these sub-patches contained a certain number of trees defined by their x-y-coordinates (Figure 1). This procedure was repeated 10 times, resulting in a total of 120 sub-patches. These sub-patches were imported into ForClim for simulation (Figure 1), and the model thus was run for each of these 120 patches.

A

	<5cm	<10cm	<20cm	<30cm	<50cm	>50 cm
Pmon	13	10	54	40	48	5
Pcem	0	8	19	25	39	31
Ldec	0	3	5	6	16	19
Pabi	61	11	0	0	1	0
Psil	11	0	0	0	0	0

D

	<5cm	<10cm	<20cm	<30cm	<50cm	>50 cm
Pmon	1	1	4	3	4	0
Pcem	0	1	2	2	3	3
Ldec	0	0	0	0	1	2
Pabi	5	1	0	0	0	0
Psil	1	0	0	0	0	0
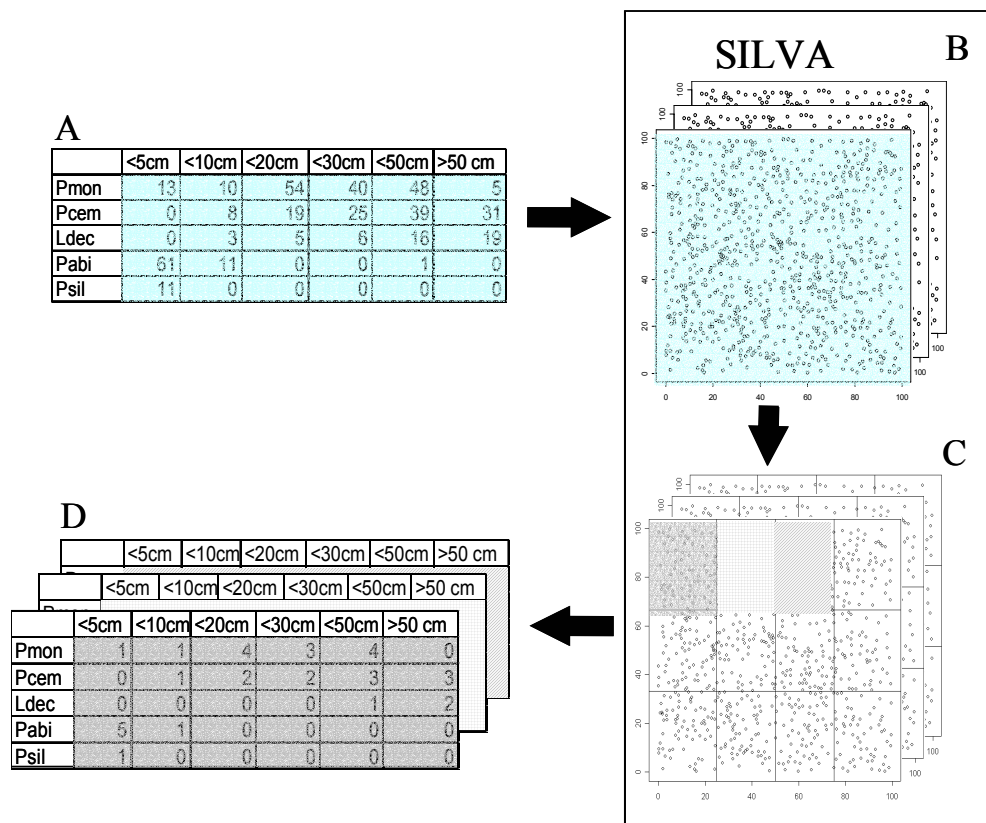
Figure 1: Initialization of 1957 data for the use in ForClim using the structure generator (Strugen) of the SILVA model. A: Forest stand data 1957 (number of stems/ha per species and DBH class). B: Generated one-hectare patches in SILVA. Each tree is assigned an x-y-coordinate. C: Each one-hectare patch is "cut" into 12 sub-patches of 833 m² each. This procedure is repeated 10 times for each stand type. D: Sub-patches to import into ForClim.

A summary of the initialized and the empirical data per stand type can be found in Figure 2. Since ForClim only considers trees with a DBH larger than 1.27 cm, whereas the empirical data contain all trees with a DBH larger than 0.1 cm, the total number of stems/ha in DBH class 0 (0 to 4 cm) is not shown (Figure 2). This DBH class was, however, included for all the simulations.
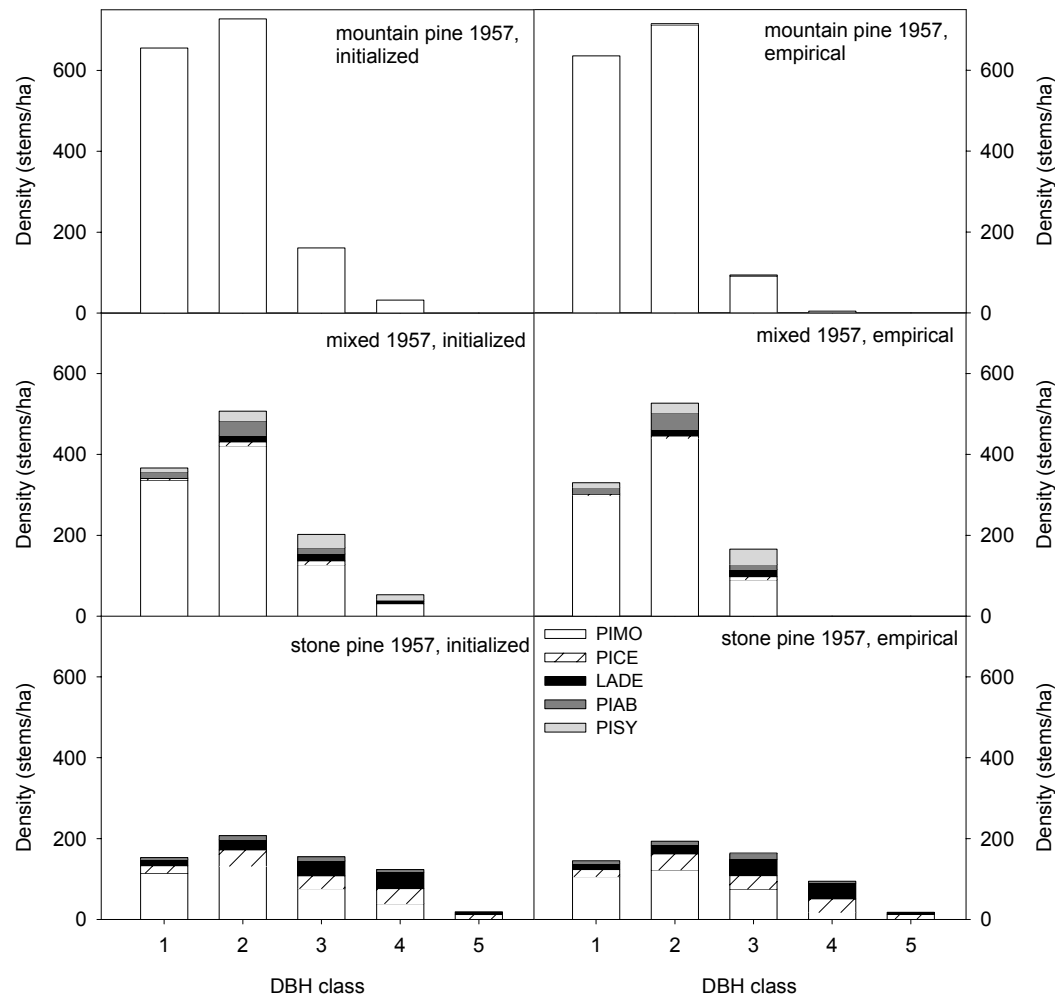
Figure 2: Comparison of initialized and empirical 1957 data for all three stand types. Stems/ha of all species within a certain DBH class are added. DBH classes: 1 = 5 to 9 cm, 2 = 10 to 19 cm, 3 = 20 to 29 cm, 4 = 30 to 49 cm, 5 = > 50 cm. PIMO = mountain pine, PICE = Swiss stone pine, LADE = European larch, PIAB = Norway spruce, PISY = Scots pine.

Simulation of structural features between 1957 and 2001/2002

Using the initialized 1957 data, we simulated the structural development of all three stand types for the time period 1957 to 2001/2002. In a first step, we manually calibrated the model for the mono-species stand type ("mountain pine"), as explained in the "Results" section. Climate data were taken from the weather station Buffalora (1980 m a.s.l.) located just outside the Park. Since most of the "mountain pine" stands were located on south slopes, ForClim was set up to simulate dry conditions (i.e., the parameter for slope/aspect (kSlAsp) was set to +2). Otherwise, the default values of all model parameters were used. The model output after 45 years of simulation (1957 to 2001/2002) was compared with the empirical data. After the model calibration, we simulated and compared the structural development of the other two stand types.

Results

Simulation of the "mountain pine" stand type

Simulation with modified ForClim V2.9.

Simulating the structural development of the "mountain pine" stand type between 1957 and 2001/2002 with the modified version V2.9 yielded poor results. Total number of stems/ha and biomass decreased to almost zero. Analyzing the simulation output revealed that i) most of the trees died shortly after 1957, and ii) no regeneration took place under the canopy of the initial stand. We first suspected that poor parameter estimation procedures for mountain pine were responsible for the observed behavior. In order to improve model behavior, we explored changing the species-specific parameterization of mountain pine [maximum DBH, maximum age, maximum height, degree days, light tolerance of trees and saplings] using empirical data from the SNP. However, these changes did not result in markedly improved model behavior.

In a next step, we therefore analyzed the possible structural reasons for the poor growth of mountain pine in the model, and found that the height to diameter relationship of individual trees was responsible for this artifact. Specifically, most larger trees died soon after 1957, as they were approaching their maximum height. The growth function implemented in ForClim V2.9 is based on a parabolic relationship between tree height and DBH (Botkin et al. 1972). As a result, a tree grows only minimally in diameter when it approaches its maximum height, and therefore dies (Botkin et al. 1972, Bugmann 1994). Since this behavior is questionable from a biological point of view, we decided to replace the existing parabolic growth function with an asymptotic one, which is biologically more plausible (see Lindner et al. 1997).

Implementation of a new height-diameter relationship

The new asymptotic function implies that trees still grow in DBH after reaching their maximum height. The function includes equation (2), following Leemans and Prentice (1989).

$$H = a + b \cdot \left(1 - e^{c \cdot D}\right) \tag{2}$$

where H is the height of a tree, $a = 137$ cm (breast height), $b = H_{max} - a$, $H_{max} =$ maximum height of a certain tree species, $c = -s/b$, where s is a parameter denoting

initial height growth relative to diameter growth, i.e. the "skinniness" of a tree, and D = DBH.

If we assume tree volume V to be proportional to $D^2 \cdot H$ (see Moore 1989), V can be expressed as

$$V = D^2 \cdot \left(a + b \cdot \left[1 - e^{c \cdot D}\right]\right) = (a + b) \cdot D^2 - b \cdot D^2 \cdot e^{c \cdot D} \tag{3}$$

For the derivative of V with respect to D, we find

$$\frac{dV}{dD} = 2 \cdot (a + b) \cdot D - D \cdot b \cdot e^{c \cdot D} \cdot (c \cdot D + 2) = D \cdot \left(2 \cdot H_{max} - b \cdot e^{c \cdot D} \cdot (c \cdot D + 2)\right) \tag{4}$$

Following Moore (1989), we derived a new diameter growth equation, which is given by

$$\frac{dD}{dt} = g \cdot D \cdot \left(\frac{1 - \dfrac{H}{H_{max}}}{2 \cdot H_{max} - b \cdot e^{c \cdot D} \cdot (c \cdot D + 2)} \right) \tag{5}$$

where g = growth rate (cm/year).

We calculated values of the parameter s (skinniness of a tree) for the dominant tree species present in the SNP using empirical data from 1957 (Kurth et al. 1960) and 2001/2002 (Table 1). The implementation of the new growth function (Eq. 5) resulted in version 2.9.3 of ForClim.

Table 1: Linear regressions $H = s \cdot D + 137$ (see Eq. 2) for the five dominating tree species of the SNP. H = tree height, D = tree diameter, n = number of trees.

	s	n	r^2	p value
Pinus montana	41	557	0.55	< 0.001
Pinus cembra	55	100	0.79	< 0.001
Pinus sylvestris	58	100	0.53	< 0.001
Picea abies	59	90	0.82	< 0.001
Larix decidua	62	100	0.78	< 0.001

Simulation runs with ForClim V2.9.3.

Using ForClim V2.9.3 for simulating the structural development of the "mountain pine" stand type from 1957 to 2001/2002 yielded increasing biomass and decreasing total number of stems/ha, as observed in the empirical data (Figure 3). The simulated stand

contained 2113 stems/ha in 1957 and 1191 in 2001/2002. These numbers approximately match the observed values (1957: 2438, 2001/2002: 1350), keeping in mind that the empirical data contained all trees with DBH > 0.1 cm, while the modeled data contained only those with DBH > 1.27 cm. Note that the model was in no way calibrated to achieve these results. They resulted simply from the implementation of the new height-diameter relationship (Eq. 2).

Simulated biomass was overestimated for the year 2001/2002 compared with the empirical value. However, ForClim is known to generally produce high biomass values (Bugmann 1996). In addition, the simulated values represent stem biomass plus foliage biomass, whereas the measured data refer to stem biomass alone; thus, an overestimation of 10 - 20% has to be expected in any case.
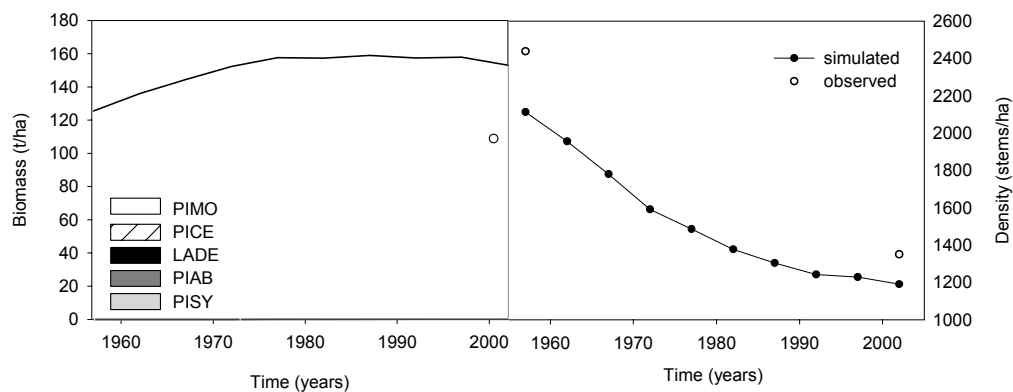
Figure 3: Modeled development of the "mountain pine" stand type between 1957 and 2001/2002, using ForClim V2.9.3. Left: Simulated cumulative biomass (t/ha). The open circle indicates empirical values estimated for this stand type in 2001/2002 (106 t/ha bole biomass, unpublished data). No value for empirical 1957 biomass is available. Right: Simulated total number of stems per hectare (closed circles). The two open circles indicate the empirical number of stems/ha in 2001/2002. PIMO = mountain pine, PICE = Swiss stone pine, LADE = European larch, PIAB = Norway spruce, PISY = Scots pine.

A comparison between the simulated and empirical structural features for the year 2001/2002 [density (stems/ha) and basal area (BA; m^2/ha) of different DBH classes] can be found in Figure 4, Model run 1. While the number of stems/ha was slightly higher than the one of the empirical data, BA was found to be much too high. A closer analysis of the output showed that too many large trees survived. In order to improve model behavior, we changed the age-related mortality factor kDeathP (Bugmann 1994) from 4.605 to 9.21 in a first approach (Figure 4, Model run 2). The default value of kDeathP is 4.605, which implies that 1% of all established saplings (DBH = 1.27 cm) survive to their species-specific maximum age (Bugmann 1994), whereas a value of kDeathP of 9.21 reflects the

assumption that only 1‰ of the new trees reach their maximum age, which may be more realistic. The output of Model run 2 yielded slightly too few stems/ha, but total BA was much closer to the empirical observations (Figure 4, Model run 2).

A second approach to decrease the number of trees was conducted by changing the two general parameters "browsing" (kBrow) and "seedling establishment" (kEstP) based on site-specific observations from the SNP (note that the default value of the parameter kDeathP, 4.605, was used). These two changes i) increased stress-induced seedling mortality and ii) decreased the number of saplings, especially of non-wind-dispersed species. The estimation for browsing pressure was obtained from the empirical data (2001/2002), whereas for seedling establishment we assumed 10 times lower establishment rates for the bird-distributed Swiss stone pine compared to the four other species, which are wind-dispersed. As can be seen in Figure 4 (Model run 3), these two changes were only effective in reducing the number of Swiss stone pine and Norway spruce trees in DBH class 1, but they did not considerably change total number of stems/ha or BA compared to model run 1. However, the reduction of Swiss stone pine and Norway spruce trees in DBH class 1 still yielded results closer to the empirical data. We therefore combined the changes made in Model run 3 with the ones made in Model run 2. The results can be found in Figure 4, Model run 4. Using this modified model setup, the simulated number of stems/ha was lower than observed, but BA was comparable to the empirical data, although the simulated trees appear to be growing faster than in reality. In addition, in this simulation run some larch trees were able to establish, as observed in the empirical data.

Overall, when comparing the four model runs (1 through 4) conducted for the "mountain pine" stand type, we found that ForClim was fairly robust in simulating species composition. Only the species composition in DBH class 1 was affected by the different model setups. The structural features, however, showed some differences. The number of stems/ha in DBH class 1 were generally underestimated in all model runs, while they were slightly too high in DBH classes 4 and 5. Yet, overall, we conclude that the model can be considered fairly robust to changes in model parameters when simulating stand structural features.

Since Model run 4 yielded the results closest to the observed data, we used this modified setup of ForClim V2.9.3 for simulating the structural development of the "stone pine" and "mixed" stand types.
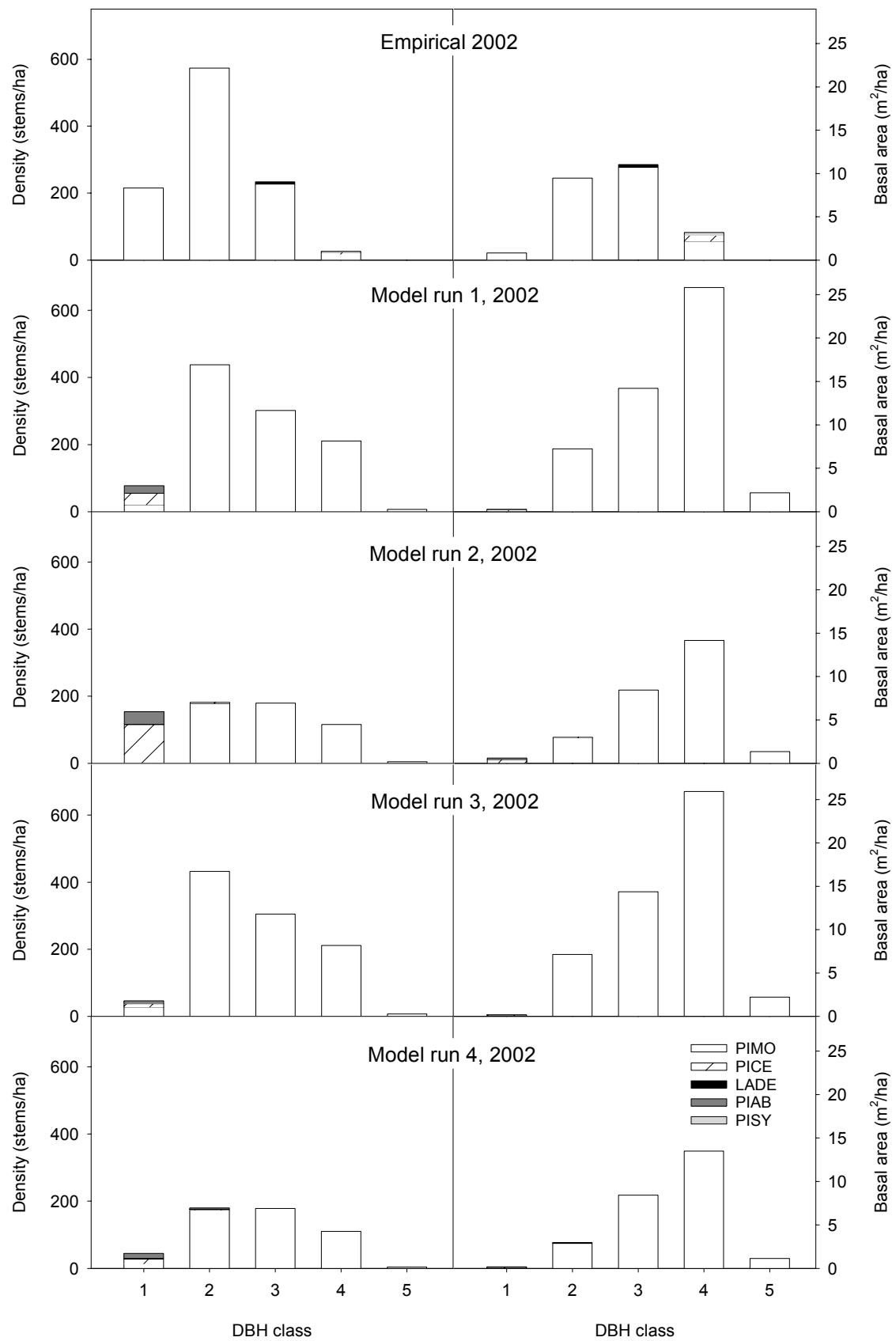
Figure 4: Empirical and simulated number of stems/ha and BA per DBH class in the "mountain pine" stand type in 2001/2002. Simulations were conducted with four different model setups of ForClim V2.9.3. Model run 1: no changes, Model run 2: kDeathP 9.21 instead of the default value 4.605, Model run 3: kEstP, kBrow adjusted, Model run 4: kEstP, kBrow and kDeathP changed.

Simulation runs for the stand types "stone pine" and "mixed"

The comparison between simulated and empirical structural features for the year 2001/2002 of the "stone pine" stand type can be found in Figure 5. Using the modified model version 2.9.3 (with revised values of the parameters kEstP, kBrow and kDeathP as described above), the simulation resulted in an underestimation of number of trees/ha, in particular of the larch, Swiss stone pine and Norway spruce trees in the highest two size classes (Figure 5, Model run 4 south). BA was too low in all DBH classes. Since most of the sampled "stone pine" forest stands were located on north slopes, we decided to adjust the slope aspect parameter in the model in order to better match the environmental conditions. The parameter kSlAsp was therefore changed from +2 (south slope) to –2 (north slope). These changes resulted in a higher number of simulated stems/ha, and a BA distribution much closer to the empirical data (Figure 5, Model run 4 north). In contrast to the simulation assuming south slope conditions, the number of Norway spruce trees was now overestimated in DBH classes 1 and 2. Yet, these trees did not contribute much to the BA in either of these two DBH classes. The number of larch trees increased considerably when assuming north-slope conditions, while the one of Swiss stone pine did not change markedly.
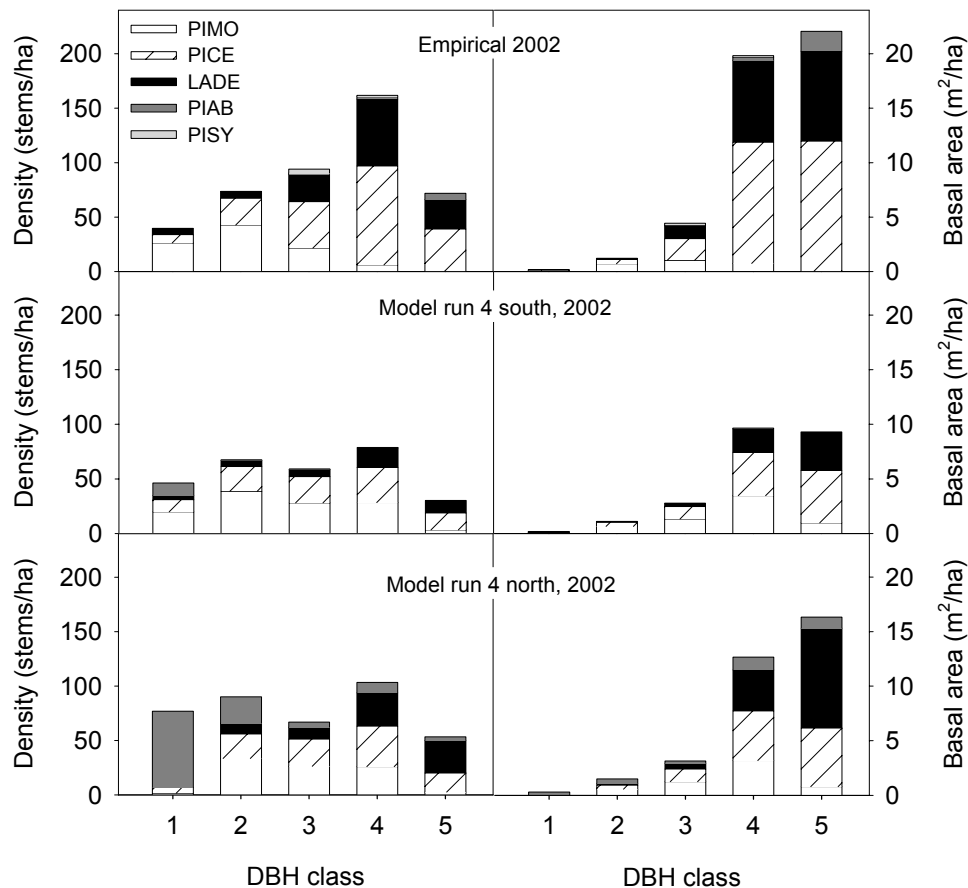
Figure 5: Empirical and simulated number of stems/ha and BA per DBH class in the "stone pine" stand type in 2001/2002. Simulations were conducted with two different model setups (ForClim V2.9.3). Model run 4, south, was run for dry south slope conditions, Model run 4, north, for north slope conditions (kSlAsp = +2 and –2, respectively).

Simulating the structural development within the "mixed" stand type under both south and north slope conditions, we again detected that model accuracy increased when slope aspect (kSlAsp) was changed to reflect the more realistic north slope conditions under which these stands were growing (Figure 6). However, comparing the empirical and simulated results yielded major differences. Our observations in the Park revealed high numbers of large Scots pine and larch trees. In the model, Scots pine was not able to establish at all, and only a few larch trees were detected after 45 years of simulation. Again, too many Norway spruce trees were simulated for small DBH classes. Further, mountain pine trees seemed to survive much better in the model than actually observed. Overall, the simulations of the mixed stand type yielded the poorest results when comparing empirical and simulated data.
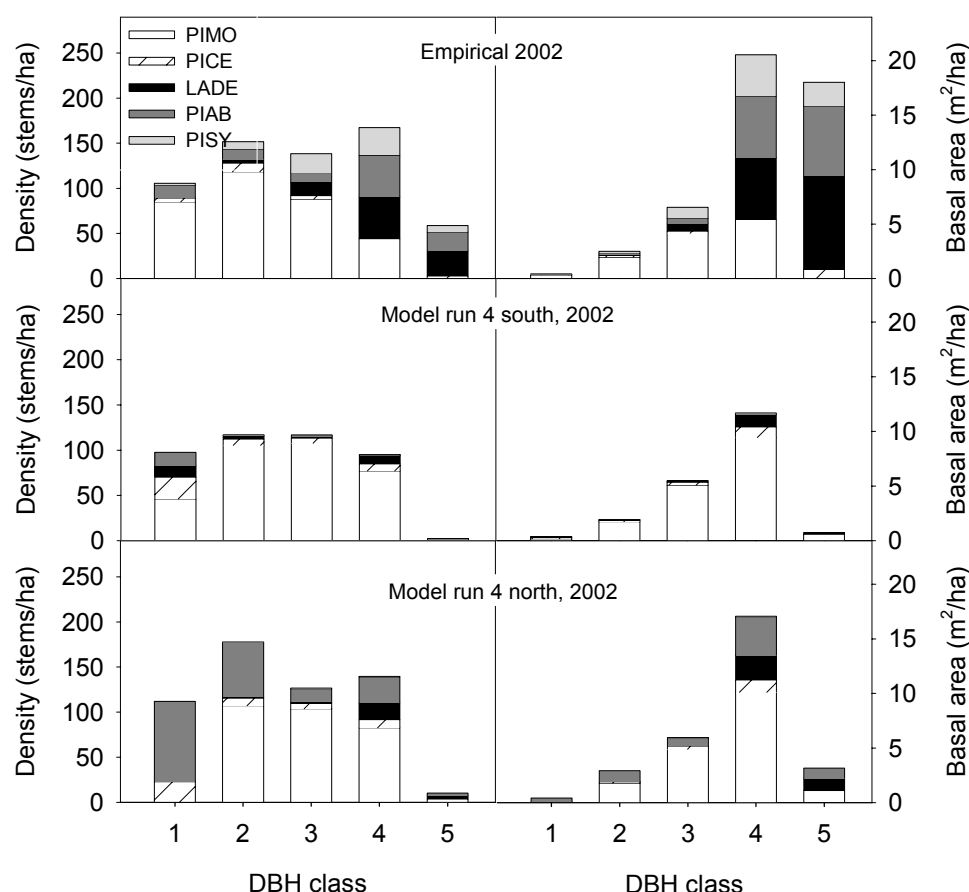
Figure 6: Empirical and simulated number of stems/ha and BA per DBH class in the "mixed" stand type in 2001/2002. Simulations were conducted with two different model setups (ForClim V2.9.3). Model run 4, south, was run for dry south slope conditions, Model run 4, north, for north slope conditions (kSlAsp = +2 and –2, respectively).

Discussion

The aim of this study was to test and improve the performance of the ForClim model in simulating forest structural features. After replacing the parabolic height-diameter relationship used in model version V2.9 by an asymptotic function (resulting in ForClim version V2.9.3), we were able to simulate long-term stand structural development in the SNP that closely matches empirical observations. The remaining differences between simulated and observed data could result from errors in both the empirical data source and the model. The empirical data might contain some error originating from the relatively low number of samples per stand type in 2001/2002 (six, six and seven, respectively; see Methods section), the different sampling schemes, or different sampling areas in 1957 vs. 2001/2002. The most conspicuous example for these problems is evident from the large numbers of larch and spruce trees in size classes 4 and 5 in the data set sampled in 2001/2002, compared to the much lower number of these species found in 1957 (Figure 6).

Potential errors originating from the model are discussed below.

With regard to the simulations of the three different stand types, we found that in the "mountain pine" type the number of small trees (DBH classes 1 and 2) was underestimated. A potential reason for these findings could be that in the model too large tree crowns are assigned to mountain pine trees (see Bugmann 1994). In the SNP, most mountain pines have very small crowns, which leads to fairly open stands (canopy closure around 45%) in which regeneration is abundant (Risch et al. 2003). Thus, competition for light is most likely much lower than in stands with higher canopy closure (Oliver and Larson 1996), and regeneration therefore should be more numerous. ForClim, in its current setup, does not account for such local differences that may affect regeneration, and therefore the model tends to underestimate the number of small trees in the SNP. In order to further improve model behavior, the parameterization of mountain pine should be adjusted for the study area, i.e. the model should account for the small crown sizes. The slight overestimation of number of trees/ha in the DBH classes 4 and 5 most likely results from small discrepancies in the number of trees (simulated vs. observed in 1957) in the initialization data set, which are due to the method used.

In the "stone pine" stand type, the most evident differences between simulated and empirical data after 45 years were the high number of simulated Norway spruce trees in DBH classes 1 and 2 (north-slope conditions). Naturally, Norway spruce would not be competitive in the inner-alpine climate with low precipitation and temperatures (Ellenberg 1996, Keller et al. 1998), and therefore this species would regenerate poorly even on moist north slopes (A. Risch, personal observations). Changing the value of the slope/aspect parameter led to moisture conditions that are favorable for Norway spruce growth, even though the model was run using temperature data too low to allow this species to be competitive in higher size classes (Ellenberg 1996, Keller et al. 1998). Our results suggest that the way Norway spruce is parameterized in ForClim may make this species overly sensitive to changes in soil water availability, while temperature seems to be less limiting. In further studies, the parameterization of Norway spruce should be evaluated in more detail, especially when the model is used to simulate forest development in inner-alpine dry regions.

The "mixed" stand type yielded the poorest results. While again the number of stems/ha and BA were somewhat too low, the modeled species composition did not match the observed data. Especially the lack of Scots pine in the simulated data is evident. A

possible reason for these differences could be that most of these stands were found on sites where the local micro-climate most likely was different from the one measured at the weather station used for the simulations. These stands were either found in narrow canyons, where it is moister, or on west-slopes at somewhat lower elevation (Kurth et al. 1960). Both these microclimates may lead to conditions that allow Scots pine to establish. To improve the simulation output in ForClim, climatic data that are characteristic of this stand type would need to be collected.

Overall, we found that ForClim yielded fairly good results in predicting long-term structural changes in different forest stands. The model behavior could potentially be improved further by implementing a light-dependent value of the s parameter, as Lindner et al. (1997) did for long-term simulations with the forest gap model FORSKA. Also, changes in the parameterization of the tree species present in the SNP, or increasing the number of samples in the field surveys may lead to a better match between simulated and measured data. Despite the fairly good results found in this study, gap models do not yield results of comparable accuracy to simulations conducted with forest stand models such as e.g. SILVA (Pretzsch 1992, 2001, Kahn and Pretzsch 1997), as Lindner et al. (1997) pointed out. Nevertheless, the validation of gap models with long-term data could be quite useful, and may lead to insights into model problems that need to be and can be corrected. Once these models are validated, it will be possible to provide more reliable answers to applied research questions, such as those dealing with the long-term development of forest stands in mountain regions under specific management regimes, the impacts of climate change on these stands, or assessments of carbon storage in forest ecosystems.

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Paper VII

Using a Markov-chain model to predict the successional development of subalpine conifer forests in the Central European Alps

Manuscript (not intended for publication):

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Abstract

A Markov-chain model is a straightforward formalization, free of many technical assumptions that other dynamic models normally make. The objective of this study was to develop and test a Markov-chain model of the successional development of subalpine conifer forests in the Swiss National Park (SNP). We calculated three different scenarios using parameters for the transition between the successional stages expected to occur in the SNP that were estimated based on expert knowledge (minimum, average and maximum solution). Two additional scenarios were calculated based on a parameter calibration with measured data (formal and heuristic solution). Applying these approaches, we were able to simulate the general successional development within the Park's forests. The heuristic approach was found to best represent successional development within the study area. Based on this scenario, a distribution close to the equilibrium will be reached around the year 2400. The forests will then be comprised of 19% early- to mid-successional mountain pine stands, 18% mixed stands and 63% late-successional and old-growth stone pine/larch stands. The simulated successional development could potentially be improved further by using a more complex successional scheme or a larger data set (e.g. forest inventory data).

Keywords

Succession, high elevation forests, Markov-chain

Introduction

A simplified Markov-type model represents a view on successional dynamics that is
largely non-mechanistic, but computationally very efficient. Markov models of forest
succession have been used and analysed for several decades (see e.g. Horn 1975, Usher
1979, 1981). They formalize the course of succession as a random chain of transitions
among successional states prescribed by a fixed conceptual scheme of succession. The
core of a Markov-chain model is represented by the transition probability matrix, which
often is assumed to be constant across time, and whose pattern mirrors the successional
scheme. The numerical values of the parameters in the transition matrix can be estimated
from field data or from 'general literature knowledge', which is inherently uncertain.

A Markov-chain model is a straightforward formalisation, free of many technical
assumptions that other dynamic models normally must make. Therefore, this type of
model logically complements other modelling approaches such as gap models, landscape
models, etc., and provides a synoptic view of successional processes. The objective of
this study was i) to develop a Markov-chain model for the successional development of
subalpine conifer forests in the Swiss National Park (SNP), ii) to compare the modelled
short-term (1957 – 2001) development with empirical data, and iii) to model the long-
term forest development within the SNP.

Methods

Study area

The SNP is located in the southeastern part of Switzerland and covers an area of
approximately 170 km^2, 50 km^2 of which are forested. The area was not influenced
directly by humans during most of the 20th century. The elevation ranges from 1350 to
3170 meters above sea level (m a.s.l.), and the mean annual precipitation and mean
annual temperature are 925 ± 162 mm and 0.2 ± 0.7 °C, respectively (measured at the
park's weather station in Buffalora, 1980 m a.s.l). The dominating tree species in the
study area are mountain pine (*Pinus montana* Miller), Swiss stone pine (*Pinus cembra*

L.), European larch (*Larix decidua* Miller), Norway spruce (*Picea abies* L.), and Scots pine (*Pinus sylvestris* L.; see Risch et al. 2003a,b,c; Papers I - III).

Successional forest development in the SNP

The successional development of the forests in the SNP has been investigated in a previous study, resulting in a general scheme of successional changes (Figure 1, Risch et al. 2003c; Paper II).
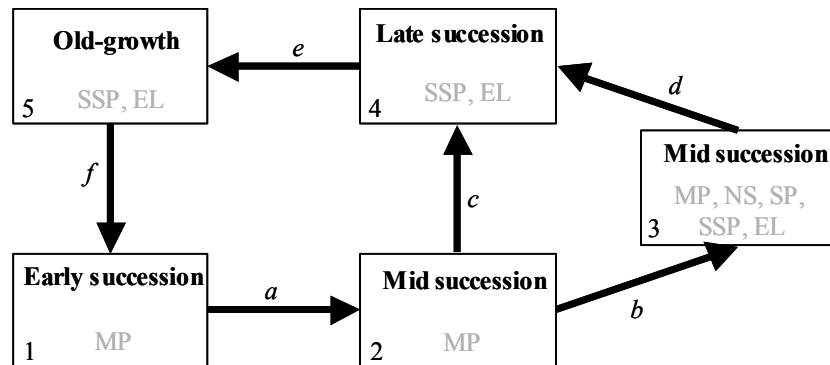
Figure 1. Conceptual scheme of succession in the SNP. Numbers indicate different successional stages; *a, b, c, d, e*, and *f* indicate the rates of transitions. MP = mountain pine, SSP = Swiss stone pine, EL = European larch, NS = Norway spruce, SP = Scots pine.

The average duration of each successional stage shown in Figure 1 was estimated based on expert knowledge and literature data (Table 1).

Table 1. Minimum and maximum stage durations estimated from expert knowledge and literature data. Stage names and numbers refer to the names and numbers shown in Figure 1.

Stage name	Stage number	Duration of stage	Remarks
Mountain pine (early succ.)	1	80 to 120 years	Mountain pines do not get much older than 250 years {Therefore the maximum duration of stage 1 and 2 together was set as 270 years}
Mountain pine (mid succ.)	2	80 to 150 years	
Mixed (mid succ.)	3	80 to 150 years	
Stone pine/larch (late succ.)	4	50 to 150 years	Mountain pines do not get much older than 250 years, therefore the assumption is made that late-successional stages will be reached after 300 to an absolute maximum of 600 years. Piussi (1994) and De Mas and Piutti (1994) reported similar ages for late-successional stages in the Italian Alps.
Stone pine/larch (late succ.)	5	400 to 600 years	Stone pine and larch can become 400 to 1200 years (Mayer 1992, Richardson and Rundel 1998) and 400 to 800 years old, respectively (McComb 1955, Mayer 1992). Therefore this stage could persist for an additional 400 to 600 years. This is based on the assumption that the old-growth stage is reached between 50 to 150 years after the late-successional stage is reached.

Development of the Markov-chain model

Using the information embedded in Figure 1 and Table 1, we constructed a Markov-chain model for succession in the SNP that has the form

$$x(t+1) = P\,x(t) \tag{1}$$

The vector x(t) can be interpreted as the area distribution among the specified stages after t time steps. *P* is the transition probability matrix.

$$P = \begin{bmatrix} 1-a & 0 & 0 & 0 & f \\ a & 1-b-c & 0 & 0 & 0 \\ 0 & b & 1-d & 0 & 0 \\ 0 & c & d & 1-e & 0 \\ 0 & 0 & 0 & e & 1-f \end{bmatrix} \tag{2}$$

with *a, b, c, d, e* and *f* denoting the probabilities of the corresponding transitions in a given time step (see Figure 1).

Parameter estimation based on expert knowledge

From Table 1, two vectors, $\boldsymbol{m}_{min}$ and $\boldsymbol{m}_{max}$, can be derived, indicating the minimum and maximum durations of the stages in the units of the time step (here, let $\Delta t = 10\text{yr}$):

$$\boldsymbol{m}_{min} = [\,8\ \ 8\ \ 8\ \ 5\ \ 40\,], \ \boldsymbol{m}_{max} = [\,12\ \ 15\ \ 15\ \ 15\ \ 60\,]. \tag{3}$$

Note that Figure 1 contains two alternative transitions from Stage 2. Based on personal observations, we assumed that the likelihood ratio is *b:c* = 7:2. Therefore, according to the method of calculation substantiated by Logofet and Lesnaya (2000), the transition matrices were the following for the minimum (P_{min}) and maximum stage duration (P_{max}):

$$P_{min} = \begin{bmatrix} \tfrac{7}{8} & 0 & 0 & 0 & \tfrac{1}{40} \\ \tfrac{1}{8} & \tfrac{7}{8} & 0 & 0 & 0 \\ 0 & \tfrac{7}{72} & \tfrac{7}{8} & 0 & 0 \\ 0 & \tfrac{2}{72} & \tfrac{1}{8} & \tfrac{4}{5} & 0 \\ 0 & 0 & 0 & \tfrac{1}{5} & \tfrac{39}{40} \end{bmatrix} \qquad P_{max} = \begin{bmatrix} \tfrac{11}{12} & 0 & 0 & 0 & \tfrac{1}{60} \\ \tfrac{1}{12} & \tfrac{14}{15} & 0 & 0 & 0 \\ 0 & \tfrac{7}{135} & \tfrac{14}{15} & 0 & 0 \\ 0 & \tfrac{2}{135} & \tfrac{1}{15} & \tfrac{14}{15} & 0 \\ 0 & 0 & 0 & \tfrac{1}{15} & \tfrac{59}{60} \end{bmatrix} \tag{4}$$

Calibration of parameters using measured data

Since data were available on the distribution of the stand types in both 1957 and 2001 (for detailed information on sampling methods see Risch et al. 2003b; Paper III), we used the 1957 data as the initial probability vector (at time t_0) for model calibration. The calibration was conducted following Logofet and Korotkov (2002). By using the 1957 data as the initial probability vector, we chose model parameters producing minimal differences between the model results for 2001 and the observed data for 2001 ('formal' solution). The data from the model for the year 2001 needed for this optimisation were obtained by linearly interpolating between time steps t_4 = 1997 and t_5 = 2007. The goal function that was minimized in this procedure was the sum of squared differences between measured and modelled data (using the Newton method). The calibration was performed using Microsoft Excel 2000 for Windows. Based on this 'formal' solution, we also calculated a 'heuristic' solution by taking the nearest boundary of the expert-derived interval between the minimum and maximum solution (Table 1) where the values of the formal solution lay outside this interval. Parameters for all estimation procedures can be found in Table 2.

Once the model was calibrated for the 1957 to 2001 time span (short-term development), we modelled the development from 1957 to 2400 (long-term development). Percentage similarity coefficients (PS) were calculated to compare the model results with the measured 2001 results, as well as to compare the long-term simulations among each other (Bugmann 1997).

Table 2: Parameters resulting from the different estimation procedures.

Parameter	Min duration	Average duration	Max duration	Formal calibration	Heuristic calibration
a	0.125	0.104	0.083	0.115	0.115
b	0.097	0.075	0.052	0.402	0.097
c	0.028	0.021	0.015	0.010	0.015
d	0.125	0.096	0.067	0.008	0.067
e	0.200	0.133	0.067	0.105	0.105
f	0.025	0.021	0.017	0.086	0.025

Results

Short-term development (1957 – 2001)

Using the general succession scheme and the estimated duration times, we were able to develop a Markov-chain model that describes the general successional development within the study area. A comparison of the modelled and empirical data 2001 (in %) is shown in Table 3. We found that all modes of calibration except for the formal one overestimated the percentage of mid-successional mountain pine forests, while the percentage of mid-successional mixed species stands was underestimated. The formal scenario showed simulated results matching the empirical data (percentage similarity coefficient = 1). The heuristic approach yielded slightly better results than the minimum, average and maximum approach, revealing 84% similarity between simulated and observed data.

Table 3: Measured distribution in 1957 and 2001, and distribution of different stand types using the five procedures for parameter estimation (Table 1). Deviation from the empirical 2001 distribution is given in parentheses. PS = percentage similarity coefficient between observed and simulated data 2001.

Stage name	Stage nr.	Distribution of selected 16 stands (%)		Min duration (%)	Average duration (%)	Max duration (%)	Formal calibration (%)	Heuristic calibration (%)
		1957	2001	2001	2001	2001	2001	2001
Mountain pine (early succ.)	1	62.5	37.5	35 (-2.5)	39 (+1.5)	43 (+5.5)	37.5 (0)	37 (-0.5)
Mountain pine (mid succ.)	2	6.3	12.5	25 (+12.5)	24 (+11.5)	22 (+9.5)	12.5 (0)	25 (+12.5)
Mixed (mid succ.)	3	12.5	31.2	13 (-17.2)	12 (-18.2)	12 (-19.2)	31.2 (0)	15 (-16.2)
Stone pine/larch (late succ.)	4	18.8	12.5	13 (+0.5)	15 (+2.5)	18 (+5.5)	12.5 (0)	16 (+3.5)
Stone pine/larch (old-growth)	5	0	6.3	13 (+6.7)	10 (+3.7)	5 (-1.3)	6.3 (0)	8 (+1.7)
PS				*0.79*	*0.81*	*0.80*	*1.00*	*0.84*

Calculating the residence times of the various different stages for each of the five scenarios, we found that the formal approach revealed an unrealistically low value for the transition time from the mountain pine mid-successional stage to the mixed mid-successional stage (25 years, Table 4). In contrast, the residence time for the mid-successional stage was unrealistically high (54589 years; see Table 4).

Table 4: Average residence times (years) for the different successional stages as predicted by the different parameter sets.

Stage name	Stage nr.	Min duration	Average duration	Max duration	Formal calibration	Heuristic calibration
Mountain pine (early succ.)	1	80	96	120	89.5	89.5
Mountain pine (mid succ.)	2	80	104	150	25	89.5
Mixed (mid succ.)	3	80	104	150	54589	150
Stone pine/larch (late succ.)	4	50	75	150	106	106
Stone pine/larch (old-growth)	5	400	480	600	330	400

Long-term development (1957 – 2400)

The different long-term development scenarios using minimal, maximal, average, formal and heuristic residence times are shown in Figure 2. The minimum and average scenario suggest that equilibrium will be reached towards the year 2400 and 2470 (changes between two time steps <0.5%), respectively (Table 4). Using these scenarios, approximately 23% and 22% of the forest are projected to be in early- and mid-successional mountain pine, 9% and 11% mid-successional mixed, and 68% and 67% late-successional and old-growth stands after 450 years of succession (Figure 2). The maximum scenario seems to approach a similar distribution, but no equilibrium is reached in the year 2400 yet (Table 4). The heuristic approach yields 19% early- and mid-successional mountain pine, 18% mid-successional mixed and 63% late-successional and old-growth stands in 2400, but it also will reach equilibrium later (Figure 2, Table 5). Using the formal approach, equilibrium is reached in 2390, but the distribution of the different forest stands is strongly different from the one predicted by the other four scenarios. Overall, all but the formal scenario predict that the Park's forest will be dominated by late-successional and old-growth stone pine / larch stands in the future (Figure 2).

Table 5: Year the equilibrium is reached as predicted by the different parameter sets. Distribution of the different stages at time of equilibrium is also shown.

Stage name	Min duration (%)	Average duration (%)	Max duration (%)	Formal calibration (%)	Heuristic calibration (%)
Mountain pine (early succ.)	12	11	10	6	11
Mountain pine (mid succ.)	11	12	12	2	10
Mixed(mid succ.)	9	10	10	79	16
Stone pine/larch(late succ.)	8	10	16	6	12
Stone pine/larch(old-growth)	60	58	52	7	51
Year equilibrium is reached	2400	2470	2620	2390	2540

A – minimum stage durations

B – average stage durations

C – maximum stage durations
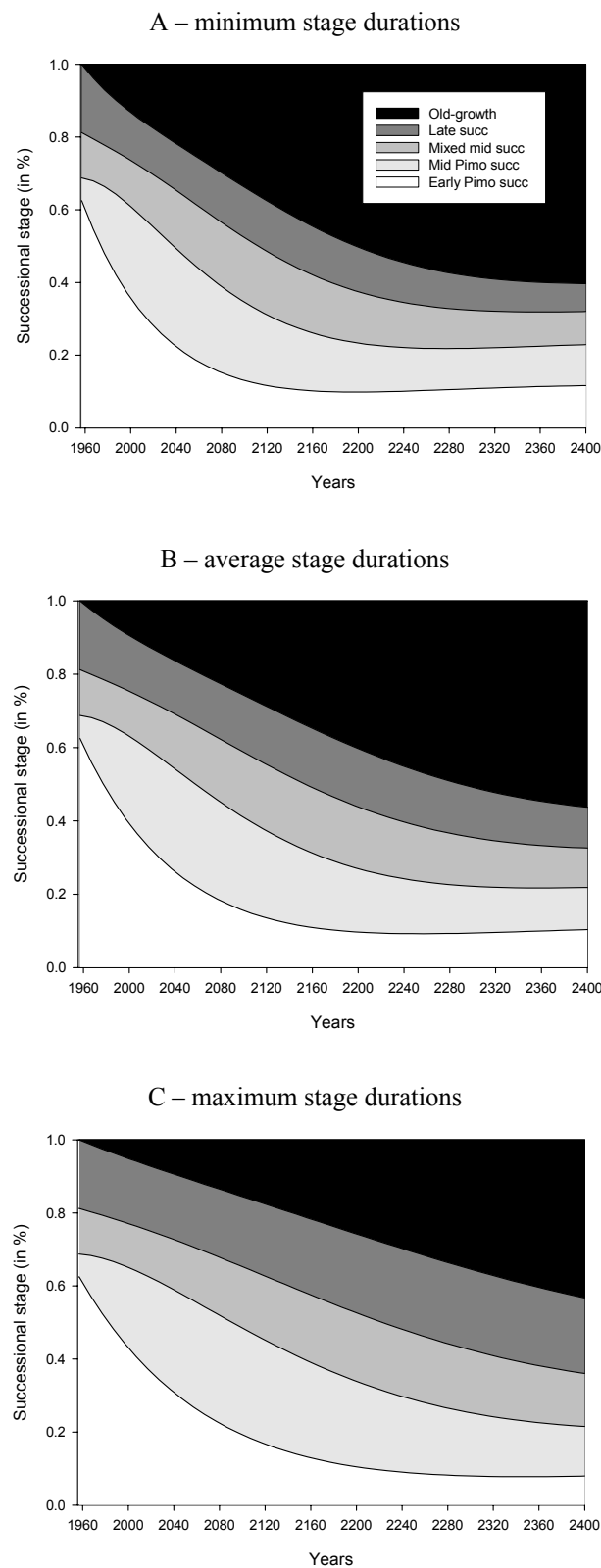
Figure 2: Successional development for the forest stands in the SNP based on the 1957 data for the 440 years from 1957 to 2397. Continued on next page.

D – formal solution of the calibration

E – heuristic solution of the calibration
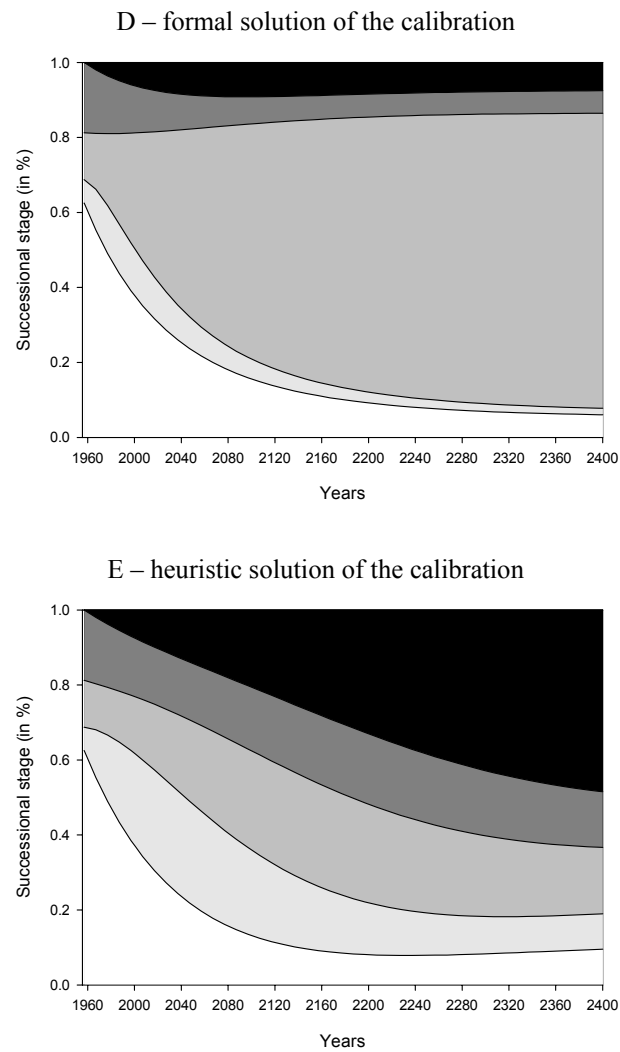
Figure 2: Continued.

Comparing the forest development of the different scenarios over time using the percentage similarity coefficient (PS), we found that the successional changes using the average and the heuristic approach were quite similar (Figure 3). Comparing the development predicted by the average and heuristic scenario with the one derived from the formal solution, we found that similarity decreased sharply over time (Figure 3).
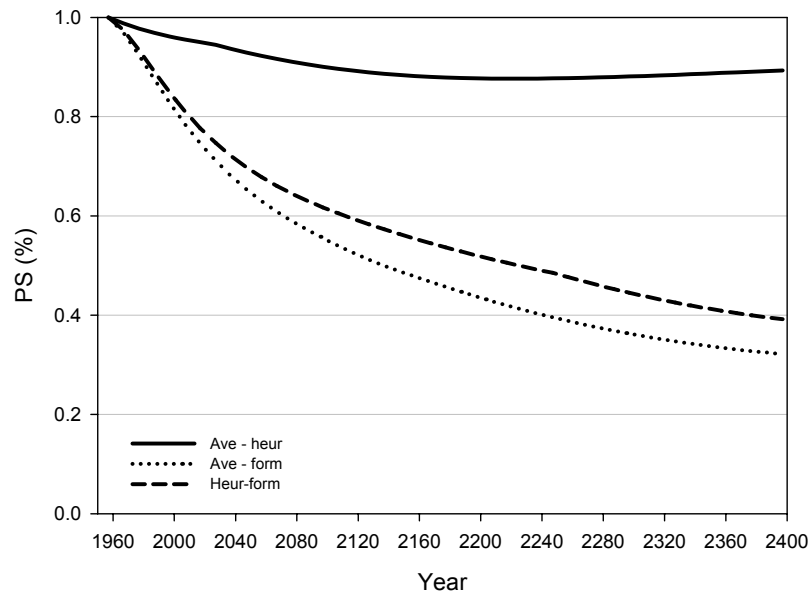
Figure 3: Percentage similarity coefficients (PS) between 1957 and 2397 between the average and heuristic solution, the average and formal solution, and the formal and heuristic solution.

Discussion

Using the minimum, average, maximum and heuristic scenarios for simulating succession in the SNP resulted in a fairly accurate fractional distribution of the different forest types for the year 2001, even though the similarity between simulated and observed data was only around 80%. Notably, the heuristic approach revealed the best results. However, none of the four scenarios succeeded in simulating the high fraction of mid-successional mixed forest stands observed in 2001. One likely reason for this anomaly could be that using only 16 stands for the comparison in 2001 is not sufficient. These 16 stands cover only a small fraction of the SNP, and they may not mirror the true distribution of the different successional stages in the study area. We believe that more empirical data, covering a much larger area, could considerably increase the comparability between simulated and empirical data. Other long-term data are not available for the study area, but the present Markov-chain model could potentially be calibrated with the spatially explicit data from the Swiss National Forest Inventory (SNFI; Brassel and Brändli 1999) conducted in the surroundings of the study area.

Another reason why the four scenarios did not succeed in simulating the high amount of mixed species stands could be that four of the five stands considered to be in the mid-successional 'mixed' stage in 2001 were located at sites with a peculiar local climate. They were found in narrow canyons and flat areas between slopes, where it is likely that

above-average soil moisture is available. Therefore, it is likely that the transition from mid-successional mountain pine stands to mid-successional mixed species stands at these sites has been considerably faster than that of the mid-successional mountain pine stands growing under the predominant dry climatic conditions of the park. However, it was not possible to sample more mixed stands located in dry sites, since these stands were usually found on very steep, hardly accessible slopes. Therefore, the model could be further improved by taking site-specific differences into account. This would mean that the complexity of the successional scheme (Figure 1) would have to be increased by introducing additional pathways or stages.

The formal solution obtained from the calibration procedure accounted for the high fraction of mid-successional mixed stands, revealing 100% similarity between the simulated and observed data. Yet, we do not think that this scenario accurately simulates the overall successional development in the study area, because i) the residence times calculated for several stages are highly unrealistic, and ii) based on expert knowledge the fraction of almost 80% mixed forests in the equilibrium cannot be considered to be realistic, since the climate in the study area is generally too dry to support the simulated widespread growth of Norway spruce and Scots pine (except at sites with untypical microclimates), as discussed above.

Overall, the simulation with the Markov-chain model predicted that forest succession in the SNP will reach an equilibrium in approximately 400 years from now. The forested area would then be comprised of large amounts of the late-successional and old-growth stages, while a smaller area would always be covered by early- to mid-successional mountain pine and mixed forest stands.

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Paper VIII

Predicting the long-term development of abandoned subalpine conifer forests in the Central European Alps

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Abstract

In the past 20 years, mathematical ecosystem models have been used intensively to predict vegetation development during primary or secondary succession, but usually, one specific model or models with the same conceptual background have been employed. Only recently, studies have been conducted where vegetation development was simulated with models of conceptually different background. Such an approach can be quite effective to more accurately predict and better understand vegetation dynamics. In order to estimate the time elapsing during succession following land abandonment in subalpine conifer forests of the Swiss National Park, we used three models of different conceptual background: i) a forest gap model, ii) a Markov chain model, and iii) a minimum spanning tree model.

Starting with a 95 to 125 year old mountain pine (*Pinus montana* Miller) forest, all three models predicted a similar successional development. Even though the forest gap model and the Markov chain model are based on totally different approaches, they both

forecasted that it would take 500 to 550 years to reach a late-successional forest stage. The minimum spanning tree, which only reveals a certain number of time steps yielding a minimum time estimate, showed a similar development of tree density (stems/ha) as the forest gap model, and therefore could potentially also forecast a time frame of approximately 550 instead of the minimum 110 years.

The simulated successional development of the forests studied was found to be slower than the ones reported from studies in the Southern Alps. However, we believe that successional processes in our study area are considerably slower due to the continental climate and the high ungulate density, and thus that our results are plausible.

Modelling forest development with three different models made it possible to obtain a fairly good estimate on how fast the successional development of these forests will take. With one particular models only, it would have been fairly difficult to gain a reliable estimate, since each of the model is constrained by different simplifying assumptions: 1) providing time steps instead of real time, thus making it difficult to estimate how long succession takes (minimum spanning tree model); 2) predicting only how the relative cover of different forest communities changes over time, but not how the single stands develop (Markov chain model); and 3) predicting the development of undisturbed stands under one single climate scenario (forest gap model).

Keywords

Forest gap model, Markov chain model, minimum spanning tree model, land use change, time estimate

Introduction

In many mountain regions of Europe, traditional agriculture and forestry have been carried out for hundreds of years. However, with recent changes in economy, these practices are no longer viable, and in many places traditional agricultural and silvicultural land uses are unlikely to be continued (Price 1995; Riederer 1996; Bätzing 1996; Broggi 1998). Therefore, the interest in understanding how pastures and forests develop after ceasing management has increased considerably over the past decades. Yet, it is difficult to assess the long-term development of abandoned or less intensively used ecosystems in

Western Europe, since most areas have been released just recently, and only few regions were not managed over longer time periods.

The Swiss National Park (SNP) is one of the few areas that was not influenced directly by humans during most of the 20th century, and it therefore provides an opportunity to study how ecosystems may develop in the absence of human intervention. While considerable knowledge on successional processes of abandoned pastures within the SNP is available (Krüsi et al. 1996, 1998, Schütz et al. 1998, 1999, 2000a,b,c, Achermann et al. 2000, Risch et al. 2001), less is known on the development of the forests. Risch et al. (2003a,b,c) investigated successional processes after ceasing management within the Park's different forest types, but to date, little is known on how long these successional processes may take in the future.

A multitude of vegetation models that can be used to assess the time required for successional changes are available today. Typically, research has been conducted using one specific model for studying ecosystem development (e.g., Buongiorno and Michie 1980, Monserud and Sterba 1996, Kienast et al. 1999, Kolbe et al. 1999, Hanewinkel and Pretzsch 2000). However, recently it has been shown that comparing different models using the same data sets may considerably increase the reliability of model predictions and facilitate model interpretation (Rykiel 1996, Bolliger et al. 2000, Guisan and Zimmermann 2000). As a result, several projects focused on comparing models of the same conceptual type (Cramer et al. 1999a,b, Mohren and Kienast 1991, van Grinsven et al. 1995, Bugmann 1996, Bugmann et al. 2001), while only a few have tried to project and compare vegetation dynamics using models of conceptually different background (e.g., Liu and Ashton 1995, Bebi 1999, Bolliger et al. 2000). The use of conceptually different models is more likely to reveal inaccuracies in our understanding of modelling vegetation dynamics, while using models based on the same modelling paradigm may be misleading because they may err in a similar way. Thus, the objective of this paper is to use three models of different conceptual background (Risch et al. 2003c, 2004a,b) to estimate how long secondary succession from an early- to a late-successional forest stage will likely take in the subalpine conifer forests of the SNP. In particular, we used i) a forest gap model (ForClim; Risch et al. 2004a), ii) a Markov chain model (Risch et al. 2004b), and iii) a minimum spanning tree model (Risch et al. 2003c).

Material and methods

Study site

The SNP is located in the southeastern part of Switzerland and covers an area of approximately 170 km², 50 km² of which are forested. The area was not influenced directly by humans during most of the 20th century. The elevation ranges from 1350 to 3170 meters above sea level (m a.s.l.), and the mean annual precipitation and mean annual temperature are 925 ± 162 mm and 0.2 ± 0.7 °C (mean ± standard deviation, measured at the weather station Buffalora located outside the Park at 1980 m a.s.l.). Stands dominated by mountain pine occupy large parts of the Park. Some other areas are covered with forests dominated by Swiss stone pine (or a mixture of Swiss stone pine and European larch) or by mixed species stands. Mountain pine forests represent the early-successional forest stages within the study area, while stone pine/larch stands are the late-successional forest types. For a more detailed description of the successional development of the Park's forests, see Risch et al. (2003a,b,c).

Long-term forest data used in models

A database of the SNP's forests exists for the year 1957 (Kurth et al. 1960). In 2001 and 2002 we re-sampled 18 stands, located within an area of approximately 80 km² in the center of the Park at elevations between 1700 to 2200 m a.s.l. The stands were randomly selected in proportion to their abundance in 1957 (Kurth et al. 1960). Trees (> 130 cm tall) were sampled on 16 points per stand using the point-centered quarter method (Greig-Smith 1983). At each of these 16 points, tree species, height (using a clinometer), and diameter at breast height (DBH, 130 cm) were determined for the four closest trees. To measure stand age, we took stem increment cores from two of the four trees per sampling point (cores taken at 30 cm above ground), resulting in a total of 32 cores per stand. For a more detailed description on stand sampling methods, see Risch et al. (2003a,b,c).

The forest gap model: ForClim

Gap models are based on the individualistic, non-equilibrium concept of vegetation dynamics developed by Gleason (1926). Central assumptions include: i) communities are ecosystem properties that emerge from tree-tree interactions on small patches, and the latter are modelled explicitly, ii) no development towards a climax state is postulated; instead, the vegetation reaches a dynamic equilibrium, i.e. the average development of all

patches reaches steady-state whereas the individual patch is in a cyclic establishment – mortality process, iii) species migration is not considered, i.e. propagule availability is unlimited, and iv) in most gap-models management is not considered.

The horizontally non-explicit model used in this study is ForClim. A detailed model description can be found in Bugmann (1994, 1996), Bugmann and Cramer (1998) and Bugmann and Solomon (2000). The model used here is version 2.9.3, as modified and validated for the SNP by Risch et al. (2004a).

The Markov-chain model

A Markov-chain model is a general modelling approach that has been used for a multitude of problems. Therefore, its underlying ecological paradigms are difficult to assess. However, translating the Markov concept into ecological theories would mean that we consider i) forest succession as a transition from one successional stage (community) to another, generally following the ideas of Clements (1936) rather than the ones of Gleason (1926), ii) communities are discrete entities of species assemblages, and iii) no change in the driving environmental forces occur. In contrast to the gap model, a Markov chain model simulates the distribution of different forest communities within the landscape and not the structural development of certain forest patches. A detailed description of the Markov chain model used in this study can be found in Risch et al. (2004b).

The minimum spanning tree model

A minimum spanning tree model is a statistical method that is based on linking time series of vegetation development in a space-for-time approach (Pickett 1989). This approach rather follows the ideas of Clements (1936), assuming that during secondary succession the landscape develops towards a steady state, and after a long time a self-sustaining endpoint will be reached (Pickett 1989). In contrast to the other two models, a minimum spanning tree model does not reveal a specific duration for successional processes, but it results in a certain number of time steps that function as surrogates of actual time units (Wildi and Schütz 2000, Risch et al. 2003c). However, since this type of model is based on time series of vegetation surveys, structural features can be displayed for each time step, which is a distinct difference to the Markov approach. A detailed description of the minimum spanning tree model can be found in Risch et al. (2003c).

Simulation of successional processes in the SNP

The forest gap model ForClim (V2.9.3) was run for 120 patches that were initialised with empirical data from the year 1957 (for details on initialisation see Risch et al. 2004a) for the time period 1957 to 2957. Climate data were taken from the weather station Buffalora (1980 m a.s.l.) located just outside the Park. The model parameters kSlAsp, kDeathP, kBrow, and kEstP were adapted to SNP conditions according to the descriptions in Risch et al. (2004a).

The Markov chain model was initialised with forest cover percentages from 1957, and run for the time period 1957 to 2957 in ten year time steps using the heuristic approach described in Risch et al. (2004b). The successional development predicted by the minimum spanning tree model was taken from Risch et al. (2003c).

Results

Predicted successional development using the forest gap model ForClim

Starting with a stand dominated by mountain pine, the forest gap model ForClim predicted that the forest composition continuously changes towards a stone pine dominated forest (Figure 1). Equilibrium will be reached around the year 2600, thus succession from a mountain pine stand (95 to 125 years in age in 1957) to a late-successional stone pine forest will take approximately 550 years, or around 650 years after an area was clear cut.
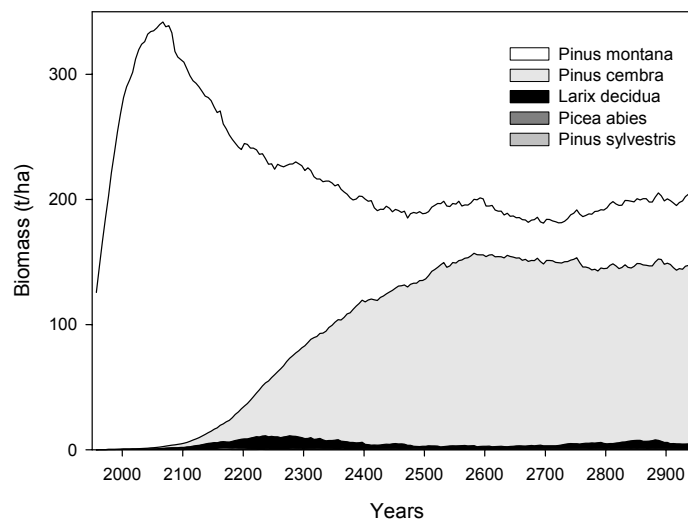
Figure 1: Successional development of mountain pine forests in the SNP as predicted by the ForClim model.

During succession, an initial decrease in the total number of stems/ha in the mountain pine dominated forests (self-thinning) is predicted, followed by an increase at the time the late-successional stone pine starts to establish (Figure 2). With aging of the established stone pine trees, horizontal and vertical stratification is predicted to lead to a decrease in the total number of stems/ha (Figure 2).
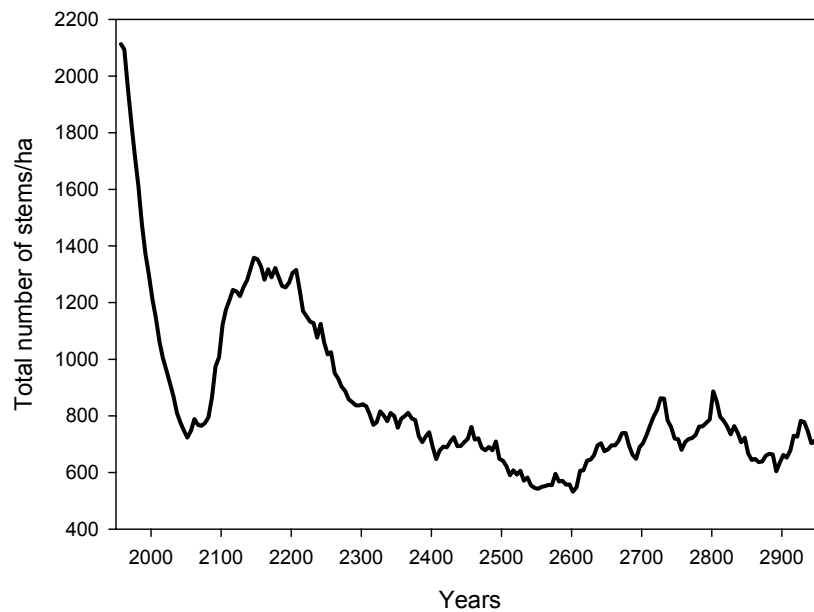
Figure 2: Simulated development of the number of stems/ha during succession using the forest gap model. Simulations were conducted with ForClim version V2.9.3.

As Figure 3 shows, the forest gap model predicted that the even-aged mountain pine stands will be replaced by uneven-aged stone pine stands during succession. Even though not readily visible from Figure 3, equilibrium is reached in 2957 (reverse J-shaped tree distribution). Stone pine will be the dominating species in 2957. Note that only a few larch trees were able to establish in this simulation.
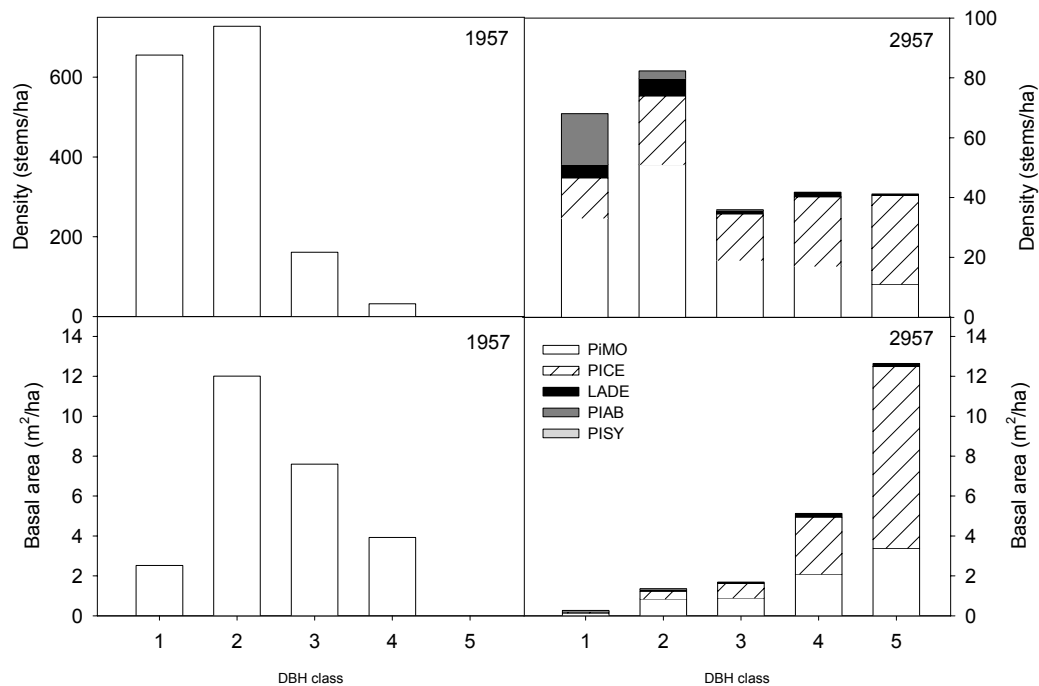
Figure 3: Structural development of the forests between 1957 and 2957 simulated with the forest gap model. Left: Total number of stems/ha and basal area of different DBH classes in the initial mountain pine stand in 1957. Right: Total number of stems/ha and basal area of different DBH classes of the late-successional stone pine stand in 2957. DBH = diameter at breast height (130 cm), DBH classes: 1 = 5 – 9 cm, 2 = 10 – 19 cm, 3 = 20 – 29 cm, 4 = 30 – 49 cm, 5 = > 50 cm. PIMO = mountain pine, PICE = Swiss stone pine, LADE = European larch, PIAB = Norway spruce, PISY = Scots pine. Simulations were made with ForClim version V2.9.3.

Predicted successional development using the Markov chain model

The predicted successional development of the forests using the Markov chain model can be found in Figure 4. In 1957, 70% of the area was covered by mountain pine forests, but according to the Markov model only 20% will be covered by this forest type in the year 2957. The amount of late-successional and old growth stone pine forests, in contrast, is predicted to increase from approximately 20% to 60% during succession. The mid-successional mixed species stands will cover about 20% of the area in 2957, after accounting for 10% of the forest cover in 1957. Using this approach, equilibrium will be reached around the year 2540 (determined as changes between two time steps < 0.5%). Therefore, the succession from a 95 to 125 year old mountain pine stand to a late-successional stone pine stand is projected to take approximately 500 years.
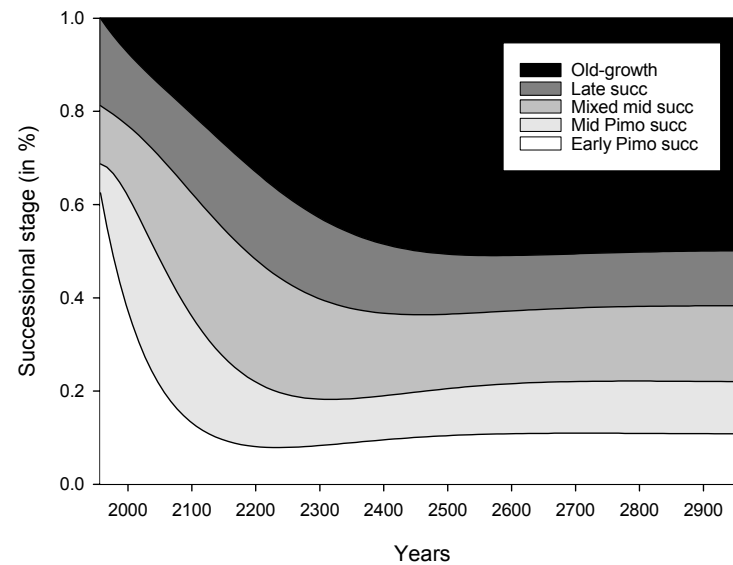
Figure 4: Successional development of the forests in the SNP between 1957 and 2957 as predicted by the Markov chain model. Early Pimo succ and Mid Pimo succ = early- and mid-successional mountain pine stands, Mixed mid succ = mid-successional mixed species stands, Late succ and Old-growth = late-successional and old-growth stone pine/larch forests.

Predicted successional development using the minimum spanning tree model

In contrast to the other two model types, the minimum spanning tree model does not mirror the successional development over a specific time span, but it gives time steps that function as surrogates of actual time. In our study, linking the time series resulted in 11 time steps (Risch et al. 2003c). The model predicted a successional development from stands dominated by mountain pine over a mixed species stage to a stone pine / larch community (Risch et al. 2003c). Based on the merged time series, one time step spans at least 10 years, thus the minimum time for succession from a 95 to 125 old mountain pine stand to a late-successional stone pine / larch stand would be 110 years (Risch et al. 2003c). The predicted development of total number of stems/ha was found to be quite similar to the predictions made with the forest gap model (Figure 5).
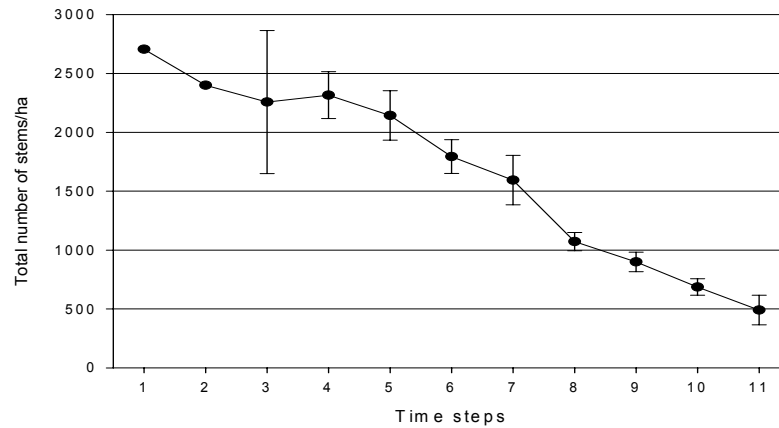
Figure 5: Successional development over 11 time steps as predicted by the minimum spanning tree model.

The structural features at time step 1 and time step 11 are shown in Figure 6. The even-aged mountain pine stands (Figure 6, left) are predicted to develop into stone pine / larch forests. The simulated fraction of larch trees at the end of the succession is quite large. At the end of succession, mostly old trees with large DBH values are dominating BA (Figure 6, right). Equilibrium is not quite reached at time step 11, since this stage represents the oldest stand sampled in 2001/02, which was approximately 300 years old. However, the distribution of the number of stems/ha is approximating a J-shape distribution when displaying the number of stems/ha on a per cm class basis (not shown).
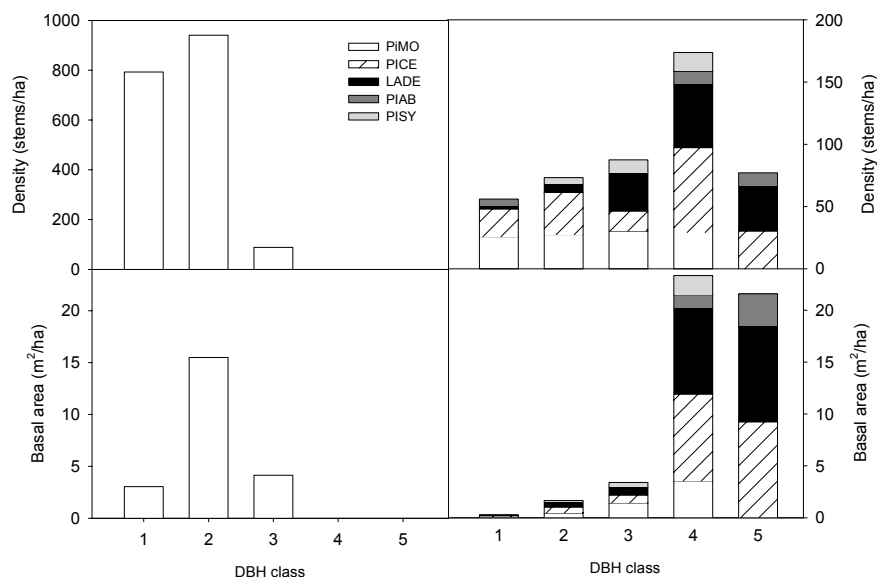
Figure 6: Structural features (number of stems/ha and basal area) at the beginning and the end of the successional development predicted by the minimum spanning tree model. Left: Structural features at time step 1. Right: Structural features at time step 11. DBH classes: 1 = 5 – 9 cm, 2 = 10 – 19 cm, 3 = 20 – 29 cm, 4 = 30 – 49 cm, 5 = > 50 cm. PIMO = mountain pine, PICE = Swiss stone pine, LADE = European larch, PIAB = Norway spruce, PISY = Scots pine.

Discussion

Predictions of general successional development using different models

Even though the three models used in this study are of different conceptual background, they all predict a very similar successional development for the forests in the SNP. Regardless of the underlying ecological concept embedded in the model, the early-successional mountain pine stand is predicted to develop into a stone pine or stone pine / larch forest. However, the forest gap model does not predict a mixed-species stage to occur at mid-succession, as the other approaches do. We believe that there are two likely reasons for this behaviour:

1)   Management has played an important role within the study area until the end of the 19th century (Parolini 1995), and thus it likely had a considerable influence on the species composition of the Park's forests. Since many forests were managed as wooded pastures, high densities of larch trees were desired to maintain low canopy closure, and therefore their establishment was promoted artificially (Parolini 1995). The minimum spanning tree model, which is based on actual stand data predicted this well. The forest gap model, in contrast, simulates succession without accounting explicitly for management (see Bugmann 1999), and therefore it does not allow shade-intolerant larch trees to establish once the canopy is closed (i.e., after initial establishment of the mountain pine forests; Oliver and Larson 1996). For this reason, the forest gap model predicts only a few larch trees in the year 2957.

2)   The forest gap model is the only of the three model types that includes climatic effects. In the mode it was used here, it only simulates succession under one given climate and does not account for the vastly different local and micro-climates that are characteristic of most mountain landscapes (e.g., different slopes, narrow canyons, ridges, flat areas between slopes). In the present study, only one site type was simulated, not the landscape-scale mixtures of site types (but see Bugmann et al. 2000). Therefore, the present ForClim simulations do not take into account that Norway spruce and Scots pine are able to establish in areas where slightly above-average soil moisture is available (Ellenberg 1996, Keller et al. 1998). Since the Markov chain and the minimum spanning tree model do not account for climate,

but are based on expert knowledge/actual forest data, they implicitly account for the differences in species composition related to micro-sites.

Estimated time for succession from mountain pine to stone pine / larch forests

The gap and the Markov chain model both predicted a very similar time frame for the successional development from mountain pine to stone pine / larch forests in the SNP, even though their conceptual and ecological background is very different. They forecasted that, starting with a 95 to 125 year old mountain pine stage, a late-successional stage dominated by stone pine / larch will be reached in 500 and 550 years, respectively. The minimum spanning tree model revealed a minimum time of 110 years for succession from the same starting point (Risch et al. 2003c). This time span is considerably shorter than the one suggested by the other two model types. However, as discussed in Risch et al. (2003c), the 11 time steps covering 110 years rather represent surrogates of actual time. Since the development of the total number of stems/ha suggested by the minimum spanning tree model is fairly similar to the one predicted by the forest gap model, we believe that the successional time frame may be similar to the one predicted by the gap model; each time step of the minimum spanning tree model would therefore be about 50 instead of 10 years.

The simulated age of 600 to 650 years of stands to attain the late-successional stage is higher than the ones reported in studies conducted in the Southern Alps (150 to 450 years; De Mas and Piutti 1994, Piussi 1994, Sauermoser 1994). Looking at these results, it would be possible that both the forest gap and the Markov chain model overestimate the time required to reach a late-successional stage, and that rather the minimum time of approximately 205 to 235 years predicted by the minimum spanning tree model would be an accurate estimate. However, for the following reasons we believe that the 600 to 650 years quite accurately predict a successional development that likely is slower than in other parts of the Alps:

1) Piussi (1994) analysed the age of stone pine saplings reaching breast height (1.3 m). The saplings were between 15 to 30 years old at his study sites in the Southern Alps (Italy). Stone pines in the SNP, in contrast, were on average over 60 years old (between 20 and 120 years) when reaching the height of 1.3 m (unpublished data). This slower tree growth is likely related to the continental climate of the area, which is characterized by low precipitation, large temperature fluctuations, and high solar

radiation (Landolt 1992, Ellenberg 1996). Piussi (1994) worked in the Southern Alps, with higher amounts of rainfall and lower temperature fluctuations, and therefore it is likely that he found better tree growth (Landolt 1992, Ellenberg 1996).

2) The SNP is characterized by high densities of wild ungulates, especially red deer (Cervus elaphus L.) and chamois (Rupicarpa rupicarpa L., Haller 2002). These ungulates frequently browse on saplings (Krüsi and Moser 2000, Risch et al. 2003a,b). Even though browsing was not found to halt succession (Risch et al. 2003c), it could lead to reduced tree growth and consequently to a somewhat slower succession compared to areas with low ungulate density.

Conclusions

Simulating the successional development with three different model types revealed similar results. Using one model only, it would be fairly difficult to gain a reliable estimate for how long successional processes might take in the study area, since each of the models has drawbacks, making it difficult to come to a meaningful result: 1) The minimum spanning tree model only yields a series of time steps that do not directly predict how long succession is likely to take. 2) The Markov chain model only predicts how the entire landscape might develop, but it does not mirror the development of specific stands. 3) In the present setup, the forest gap model did not account for different micro-climates and historical management influences. However, when combining the results of all three model types, we were able to obtain a fairly good estimate of how fast the successional development of the studied forests will take.

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Synthesis

Secondary successional processes in high-elevation forest formerly hidden by management regained importance during the past decades as forestry is no longer economically viable. The fundamental aim of this study was to investigate how high-elevation forests in the Swiss National Park (SNP) develop after ceasing management, while focusing both on the changes in forest structure and composition, and on above- and belowground changes in biomass, carbon (C) and nutrient pools.

The analysis of empirical long-term stand structure data (45-year period) showed major changes in forest structure and composition between 1957 and 2001/02 (Paper I). Yet, the fact that a clear successional trend was detectable (Paper II, Figure 3) was not self-evident (see Paper II, Figure 1). Both biotic and abiotic disturbances could have had major impacts on the development of the SNP's forests between 1957 and 2001/02, therefore preventing secondary successional processes within the stands studied (Paper II). Thus, the clear successional trend observed in this study opened the possibility to not only study and simulate the forest development of selected forest types over 45-years (Paper I, III, VI, VII), but also to use a space-for-time approach to evaluate the likely shift in forest communities over time (Paper II). This methodological approach allowed me to define the different forest types likely to occur during succession (Paper II, Figure 7), which was crucial for investigating changes in total ecosystem biomass, C and nutrient pools (Paper IV and V), and for evaluating / developing ecological models to simulate the short- and long-term forest development (Paper VI, VII, and VIII).

In the following, I will discuss the major findings of this study concerning successional patterns and processes following land abandonment, as well as how changes in forest structure and composition were related to belowground biomass, C and nutrient pools. This part will be followed by a detailed description of today's distribution of mountain pine and stone pine forests to assess the applicability of the results gained from the SNP.

Successional patterns and processes following land use change in the Central European Alps

The long-term data covering 45 years of forest development in different stand types were analysed empirically and simulated with a mathematical model (Paper III, Paper VI). Both methods revealed a very similar development (Paper III, Figure 1; Paper VI, Figures 4, 5, 6). In general, I was able to observe successional changes in stand structure (shift towards larger DBH classes) and species composition (shift from shade-intolerant to shade-tolerant species). In detail, the forests in the SNP likely have developed as described below:

1) Mountain pine forests established after the last clearcuts in 1860 (stand initialisation phase). They formed even-aged, single-storied stands in 1957 (Paper III).

2) The initialisation phase is followed by a self-thinning phase. This phase is characterized by a sharp decrease in total number of mountain pines (stems/ha), no change in species composition, and high fractions of standing dead trees (Paper III, Table 1, Figure 2).

3) The self-thinning phase in turn is followed by vertical and horizontal stratification, which yields a shift from shade-intolerant to shade-tolerant species, leading to uneven-aged multi-storied forests (Paper III).

The time frame for these changes is approximately 650 years and was determined using long-term simulations with three models of different mathematical background (Paper II, VI, VII, VIII).

Simultaneous with changes in stand structure and composition described above, increases in total biomass, C and nutrients pools of living trees were expected. These expectations were confirmed by our results (Paper IV, Table 2). Lowest aboveground biomass was found in the mountain pine dominated stands, whereas the highest occurred in the mid- to late-successional forests (Paper III, Table 1, 2; Paper IV, Table 4). Given this increase, decreasing pool sizes in belowground nutrients (incorporation into living biomass), and an accumulation of belowground biomass and C pools (e.g., higher amounts of living biomass leading to higher amounts of litter) would be expected. The results gained in

Paper IV showed the expected decrease in belowground nutrient pools, thus confirming the general hypothesis (Paper IV, Table 5). However, in contrast to the expected results for belowground biomass and C pools, I detected a significant decrease in mineral soil organic matter (SOM) and C (Paper IV, Table 5), while root, forest floor and woody residue, and total belowground biomass and C pools did not change significantly (Paper III, Table 4; Paper IV, Table 5).

A first approach to explain these rather unexpected results was to assess how strong frequently occurring nests of red wood ants (*Formica rufa*-group) impact belowground biomass and C pools (Paper V). These mounds (nests), reaching diameters of more than 3 m, and heights of more than 1.5 m, are built from forest floor material of the surrounding ecosystem. Yet, up to date, these conspicuous ecosystem elements have never been considered when assessing belowground C pools in a particular ecosystem, and it was not known whether collecting forest floor material for nest building purposes could significantly alter these pools. Paper V of this dissertation showed that the C pools stored in red wood ant mounds were significantly higher in late-successional than in the early-successional stands (Paper V, Table 2). Yet, the pool sizes of 0.99 t C/ha in maximum were too small to markedly influence total belowground biomass and C pools (Paper IV, V). Therefore, other factors than red wood ant mounds must be responsible for the observed decreasing trend in mineral SOM and C pools (Paper V).

Further investigations showed that changes in forest composition and structure (increase in canopy closure) led to decreasing light availability at the forests floor. This not only led to a shift from shade-intolerant to shade-tolerant species in the sapling layer (20 – 130 cm tall; Paper I - III), but it also strongly impacted understory vegetation biomass and composition (Paper III; Paper IV; Table 1). In particular the total cover of ericaceous shrubs decreased sharply (see Figure 1; Paper IV, Table 1). Ericaceous shrubs are known to provide large amounts of highly recalcitrant litter to a forest ecosystem. This litter decomposes very slowly and thus may account for the high amounts of mineral SOM and C detected in the early-successional forests stages in the study area (Paper IV).

In most studies, understory vegetation biomass is usually not considered when assessing total ecosystem biomass, C and nutrient pools, since their contribution is minor. In this study, they contributed to only 1 to 4% to the total aboveground biomass of the stands studied (Paper IV, Table 2).

Figure 1: Comparison of understory vegetation cover in an early-successional mountain pine stand and a late-successional stone pine stand. Left: Mountain pine stand (God Margunet) with a dense understory vegetation mainly dominated by ericaceous shrubs. Right: Stone pine stand (God dal Fuorn) with hardly any understory vegetation dominated by herbs and grasses (pictures Anita Risch).

Nevertheless, given the widespread occurrence of ericaceous shrubs in the understory vegetation of high-elevation forests, the results obtained in this dissertation suggest that in particular belowground C pools could behave differently in these forests than previously expected. I am aware that the information presented in Paper IV might be constrained to the study area. However, since I was not able to find any other study that assessed total ecosystem pools in high-elevation forests in Europe, the results represent new insights on how successional processes might influence total ecosystem C and nutrient pools, and could considerably help to better understand C sink and source processes in these areas.

Applicability of the results to other areas

The applicability of the results gained in this study seem to be constrained to the study area, since at first glance both early-successional mountain pine and late-successional stone pine forests do not seem to be very widespread today. However, even though many mountain pine forests were clear-cut to be used as cattle pastures or replaced by economically more valuable tree species such as larch (mountain pine can be used as fuel wood only; Gravano 2002), these forests are still found naturally in timberline ecosystems from the Pyrenees to the Carpathian Alps (Gravano 2002). The same range is still naturally occupied by stone pine forests (Busetti 2002), which also have been managed heavily in the past. Many stone pine stands were used as wooded pastures for domestic

livestock. Since these stands naturally are very dense, and thus little light penetrates to the forest floor, stone pines often were harvested and the valuable timber sold. During regeneration of the stands, larch trees with a lower canopy closure were favoured since they allow a richer vegetation to develop and thus make the forest more suitable as grazing sites for domestic livestock (Parolini 1995, Holtmeier 1990). In many cases, stone pine stands were transformed completely to stands with larch as the dominating tree species. In other cases, stone pine forests close to the timberline were removed completely in order to gain larger grazing grounds (Tranquillini 1979).

For these reasons, it can be said that the forest types studied still occur fairly wide spread today, and their importance might increase in the near future when the previously destroyed natural forest vegetation recovers after ceasing management. Thus, the information gained in this study likely is applicable to many other sites within the Alps. In addition, the knowledge gained could potentially be useful to better understand ecosystems composed of tree species with very similar ecological characteristics such as the successional transition from lodgepole pine (*Pinus contorta* Douglas ex Loudon) to whitebark pine (*Pinus albicaulis* Engelm.) in the Rocky Mountains of America (Arno and Weaver 1990, Klinka 2002a,b), or the one of Scots pine (*Pinus sylvestris* L.) to Siberian pine (*Pinus sibirica* Du Tour) in Russia (Smolonogov 1994, Walter and Breckle 1994).

Figure 2: Remaining stone pine trees of a former stone pine forest at Alp Buffalora. The area is now managed as cattle pasture (picture: Anita Risch)

Overall conclusion

The combined approach of studying successional patterns and processes with large sets of empirical data (both above- and belowground) and mathematical models applied in this study proved to be quite successful for revealing how forests dominated by mountain pine in early, and stone pine in late-succession, likely develop after ceasing management, and how long this development likely will take. Additionally, as one of the first studies assessing total ecosystem biomass, C and nutrient pools in high-elevation forests of Europe, the results of this thesis helped to increase our understanding of ecosystem C and nutrient pools. The information presented in this study likely is applicable to other areas in high-elevation regions of Europe, it may serve as baseline for what potentially could take place when natural forest types recover from heavy management, and it could help to better understand successional processes in similar ecosystems in other high-elevation areas.

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Acknowledgements

Curriculum Vitae

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