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LEHRSTUHL FÜR WALDWACHSTUMSKUNDE

**Mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies* and *Abies alba*:
productivity, management and biodiversity**

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Content

Acknowledgements	I
Abstract.....	III
Zusammenfassung.....	V
Article overview.....	VII
1 Introduction.....	1
1.1 Motivation	1
1.2 Objectives and Outline.....	7
2 Material and methods	10
2.1 Material	10
2.1.1 Study Area	10
2.1.2 Data	13
2.2 Methods.....	19
2.2.1 Statistical analyses	27
3 Results.....	30
3.1 Productivity of mixed mountain forests (Article I)	30
3.2 Transformation of pure spruce to mixed mountain forests (Article II)	32
3.3 Biodiversity along temperate forest succession (Article III).....	34
3.4 Summarising results.....	36
4 Discussion.....	37
4.1 Productivity of mixed mountain forests (Article I)	37
4.2 Transformation of pure spruce to mixed mountain forests (Article II)	40
4.3 Biodiversity along temperate forest succession (Article III).....	42
5 Conclusion	46
6 Perspectives.....	47
7 References.....	50
Appendix.....	64
A Article I	64
B Article II	76
C Article III.....	95
D Publication list.....	107

Abstract

Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst) and silver fir (*Abies alba* Mill.) at elevations between ~600 - 1,400 m above sea level cover an area of more than 10 million hectares in Europe. Connecting deciduous forests in lowlands and coniferous tree communities at high elevations, the coexistence of beech, spruce and fir has lasted for many centuries. Particularly in mountainous areas, forests are of great ecological and socio-economic importance in Central and Eastern Europe due to their provision of various ecosystem goods and services. Given that mountain forests were strongly limited by cold temperatures and short vegetation periods in the past, moderate climate change may reduce these limitations and lead to an overall increase in canopy closure and tree growth due to extended growing seasons and the effect of CO₂ fertilization. Therefore, similar to forest ecosystems in the northern latitudes, mixed-mountain forest ecosystems are expected to be strongly affected by climate warming. However, as little is known about the long-term development of the productivity and the adaptation and mitigation potential of these forest systems in Europe, reliable information on productivity is required for sustainable forest management. This thesis investigated 60 long-term experimental plots across Europe and provides information about the productivity of mixed mountain forests across a variety of European mountain areas in a standardized way for the first time. The average periodic annual volume increment (PAI) of these forests amounts to 9.3 m³ha⁻¹year⁻¹. Despite a significant increase in annual mean temperature the PAI has not changed significantly over the last 30 years. However, at the species level, significant changes in the growth dynamics were found. While beech had a PAI of 8.2 m³ha⁻¹year⁻¹ over the entire period (1980-2010), the PAI of spruce dropped significantly from 14.2 to 10.8 m³ha⁻¹y⁻¹, and the PAI of fir rose significantly from 7.2 to 11.3 m³ha⁻¹year⁻¹. Consequently, stable stand volume increments in relation to climate change were observed (Hilmers et al. 2019; see chapter 3.1 and Appendix A).

However, pure Norway spruce stands have, since medieval times, been heavily promoted as productive stand types for salt-works at sites naturally supporting mixed mountain forests. Damage to these secondary pure spruce stands has been steadily increasing in recent decades. To address these problems, alternative management concepts are being intensively discussed. A possible option to improve the stability and resilience of the stand is the transformation from pure Norway spruce stands into site-appropriate, sustainable and stable mixed mountain forests. In this thesis seven different transformation scenarios (e.g. slit, shelterwood and gap-coupes, strip clearcutting, do-nothing) and their impact on five evaluation

criteria (forest growth, economics, carbon sequestration, (stand) stability and biodiversity) were tested. As there are hardly any practical examples for some of the transformation scenarios available, the forest growth simulator SILVA was used to assess whether the tested transformation scenarios differ in transformation success and to observe trade-offs between the criteria of evaluation. It was shown that it is possible, by means of several trajectories, to return destabilised forests to sustainable and stable systems. Transformation is realistic, even if sophisticated silvicultural concepts are not strictly pursued (see chapter 3.2 and Appendix B).

Furthermore, it was the aim of this thesis to understand the inherent changes in species diversity as forests develop to provide an important baseline for assessing the effects of external drivers such as climate change in mixed mountain forests. The successional dynamics of forests—from canopy openings to regeneration, maturation and decay—influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g., late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity in mixed mountain forests, a quantitative understanding of how different trophic groups vary over the course of succession is needed. To fill this gap mixed mountain forests in the Bavarian Forest National Park were classified into nine successional stages using airborne LiDAR. α - and β -diversity of six trophic groups encompassing approximately 3,000 species from three kingdoms were analysed and the effect of successional stage on the number of species with and without controlling for species abundances was quantified. Furthermore, the similarity of assemblages along successional development was analysed. It was shown, that the number of species of producer and consumer groups generally followed a U-shaped pattern. In contrast to expectations, the number of saprotrophic species did not change along succession. The analysis of assemblages indicated a large contribution of succession-mediated β -diversity to regional γ -diversity. The results highlight the strong influence of forest succession on biodiversity and underline the importance of controlling for successional dynamics when assessing biodiversity change in response to external drivers such as climate change (Hilmers et al. 2018; see chapter 3.3 and Appendix C).

Zusammenfassung

Bergmischwälder aus Rotbuche (*Fagus sylvatica* L.), Fichte (*Picea abies* (L.) Karst) und Weißtanne (*Abies alba* Mill.) in Höhenlagen zwischen ~600 - 1.400 m über dem Meeresspiegel bedecken eine Fläche von mehr als 10 Millionen Hektar in Europa. Durch die Verbindung von Laubwäldern im Flachland und Nadelbaumgesellschaften in hohen Lagen dauert das Zusammenleben von Buche, Fichte und Tanne seit vielen Jahrhunderten an. Vor allem in Berggebieten sind Wälder in Mittel- und Osteuropa aufgrund der Bereitstellung verschiedener Ökosystemdienstleistungen von großer ökologischer und sozioökonomischer Bedeutung. Da die Bergwälder in der Vergangenheit durch kalte Temperaturen und kurze Vegetationsperioden stark eingeschränkt waren, kann ein moderater Klimawandel diese Einschränkungen verringern und zu einer allgemeinen Zunahme des Baumwachstums aufgrund längerer Vegetationszeiten und der Auswirkungen der CO₂-Düngung führen. Daher wird davon ausgegangen, dass Bergmischwaldökosysteme ähnlich wie Waldökosysteme in den nördlichen Breitengraden stark von der Klimaerwärmung betroffen sein werden. Da jedoch wenig über die langfristige Entwicklung der Produktivität und das Anpassungspotenzial dieser Waldsysteme in Europa bekannt ist, sind zuverlässige Informationen über die Produktivität für eine nachhaltige Forstwirtschaft erforderlich. Diese Arbeit untersuchte 60 langfristige Versuchsflächen in ganz Europa und liefert erstmals standardisierte Informationen über die Produktivität von Bergmischwäldern in verschiedenen europäischen Berggebieten. Der durchschnittliche periodische jährliche Volumenzuwachs (IV) dieser Wälder beträgt 9,3 m³ha⁻¹Jahr⁻¹. Trotz eines deutlichen Anstiegs der Jahresmitteltemperatur hat sich der IV in den letzten 30 Jahren nicht wesentlich verändert. Auf der Ebene der Arten wurden jedoch signifikante Veränderungen in der Wachstumsdynamik festgestellt. Während die Buche über den gesamten Zeitraum (1980-2010) einen IV von 8,2 m³ha⁻¹Jahr⁻¹ hatte, sank der IV der Fichte deutlich von 14,2 auf 10,8 m³ha⁻¹Jahr⁻¹, und der IV der Tanne stieg deutlich von 7,2 auf 11,3 m³ha⁻¹Jahr⁻¹. Auf Bestandesebene konnten stabile Bestandsvolumenzuwächse beobachtet werden (Hilmers et al. 2019; siehe Kapitel 3.1 und Appendix A).

Aufgrund der historischen Bewirtschaftung sind Wälder der Bergmischwaldstufe oft mit Fichten-dominierten, gleichförmigen Nadelholzreinbeständen bestockt. Die Schäden an diesen sekundären reinen Fichtenbeständen sind in den letzten Jahrzehnten jedoch stetig gestiegen. Um diese Probleme anzugehen, werden alternative Managementkonzepte intensiv diskutiert. Eine mögliche Option zur Verbesserung der Stabilität und Widerstandsfähigkeit des Bestandes ist die Umwandlung von reinen Fichtenbeständen in standortgerechte, nachhaltige und stabile Bergmischwälder. In dieser Arbeit wurden sieben verschiedene Transformationsszenarien und

ihre Auswirkungen auf fünf Bewertungskriterien (Waldwachstum, ökonomische Performanz, Kohlenstoffbindung, Bestandsstabilität und Biodiversität) getestet. Da es für einige der getesteten Transformationsszenarien kaum praktische Beispiele gibt, wurde der Waldwachstumssimulator SILVA eingesetzt, um zu beurteilen, ob sich die getesteten Transformationsszenarien im Transformationserfolg unterscheiden, und um Trade-offs zwischen den Bewertungskriterien zu beobachten. Es konnte gezeigt werden, dass es möglich ist, destabilisierte Wälder mit Hilfe mehrerer Trajektorien in nachhaltige und stabile Systeme zurückzuführen. Eine Transformation ist realistisch, auch wenn anspruchsvolle waldbauliche Konzepte nicht konsequent verfolgt werden (siehe Kapitel 3.2 und Appendix B).

Um eine wichtige Grundlage für die Bewertung der Auswirkungen von externen Faktoren wie dem Klimawandel oder der Waldbewirtschaftung auf die Biodiversität in Bergmischwäldern zu schaffen, war es darüber hinaus das Ziel dieser Arbeit zu verstehen, wie sich die Biodiversität entlang von Sukzessionsstadien entwickelt. Die Sukzessionsdynamik der Wälder - von der Kronenöffnung über die Verjüngung, Reifung und den Zerfall - beeinflusst die Menge und Heterogenität der für Waldorganismen verfügbaren Ressourcen. Der Naturschutz konzentrierte sich bislang im Wesentlichen auf ausgewählte Sukzessionsstadien (z. B. späte Sukzessionsstadien). Um jedoch umfassende Erhaltungsstrategien zu entwickeln und die Auswirkungen des Waldmanagements auf die Biodiversität zu verstehen, ist ein quantitatives Verständnis darüber erforderlich, wie die Artenzahlen unterschiedlicher trophischer Gruppen im Laufe der Sukzession variieren. Um diese Lücke zu schließen, wurden die Bergmischwälder im Nationalpark Bayerischer Wald anhand von luftgestütztem LiDAR in neun Sukzessionsstadien klassifiziert. Die α - und β -Diversität von sechs trophischen Gruppen mit rund 3.000 Arten aus drei Königreichen wurde analysiert und der Einfluss der Sukzessionsstadien auf die Anzahl der Arten quantifiziert. Darüber hinaus wurde die Ähnlichkeit von Artengemeinschaften entlang der Sukzessionsstadien analysiert. Es zeigte sich, dass die Anzahl der Arten von Produzenten- und Konsumentengruppen im Allgemeinen einem U-förmigen Muster folgte. Entgegen den Erwartungen zeigten die Artenzahlen der saprotrophen Arten keine Veränderung entlang der Sukzession. Die Analyse der Artengemeinschaften zeigte einen großen Beitrag der β -Diversität zwischen Flächen unterschiedlicher Sukzessionsstadien zur regionalen γ -Diversität. Die Ergebnisse unterstreichen den starken Einfluss der Sukzessionsdynamik von Wäldern auf die biologische Vielfalt. Dementsprechend sollten bei der Bewertung der Veränderung der Artenvielfalt als Reaktion auf externe Faktoren wie den Klimawandel potentielle sukzessionsdynamische Prozesse mit einbezogen werden (Hilmers et al. 2018; siehe Kapitel 3.3 und Appendix C).

Article overview

This cumulative thesis is based on three published articles in peer-reviewed journals. For each article, the original abstract, publication status and individual author contributions are provided. All articles can be found in the appendix can be accessed in full length via the respective DOI.

In addition, during the time span of this thesis, within a larger framework of forest ecology studies, seven further articles were published, four in peer-reviewed and three in non-peer-reviewed journals. All articles are listed in Appendix **D**.

Article I

The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe.

Torben Hilmers | Admir Avdagić | Leszek Bartkowicz | Kamil Bielak | Franz Binder | Andrej Bončina | Laura Dobor | David I. Forrester | Martina L. Hobi | Aida Ibrahimspahić | Andrzej Jaworski | Matija Klopčič | Bratislav Matović | Thomas A. Nagel | Rudolf Petráš | Miren del Rio | Branko Stajić | Enno Uhl | Tzvetan Zlatanov | Roberto Tognetti | Hans Pretzsch

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<https://doi.org/10.1093/forestry/cpz035>

Impact factor 2018: 2.876 (10/67 Forestry)

Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), and silver fir (*Abies alba* Mill.) cover a total area of more than 10 million hectares in Europe. Due to altitudinal zoning, these forests are particularly vulnerable to climate change. However, as little is known about the long-term development of the productivity and the adaptation and mitigation potential of these forest systems in Europe, reliable information on productivity is required for sustainable forest management. Using generalized additive mixed models this study investigated 60 long-term experimental plots across Europe and provides information about the productivity of mixed mountain forests for the first time. The average periodic annual volume increment (PAI) of these forests amounts to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. Despite a significant increase in annual mean temperature the PAI has not changed significantly over the last 30 years. However, at the species level, we found significant changes in the growth dynamics. While beech had a PAI of $8.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ over the entire period (1980-2010), the PAI of spruce dropped significantly from 14.2 to $10.8 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$, and the PAI of fir rose significantly from 7.2 to $11.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. Consequently, we observed stable stand volume increments in relation to climate change.

Individual contributions: I received the raw data of the long term experimental plots. I ordered and homogenized the data from the different sources and merged it with the environmental data of the sample sites (*data acquisition: 15%*). I conducted the data analyses independently and designed and produced the figures (*data analysis and figures 100%*). I wrote and revised the manuscript for the article (*writing and revising 90%*). The basic idea and concept of the

manuscript was developed together with Prof. Hans Pretzsch (*concept 60%*). All co-authors contributed by language editing.

Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas.

Torben Hilmers | Thomas Knoke | Peter Biber | Hans Pretzsch

Published 2020 in European Journal of Forest Research 139:567-584

<https://doi.org/10.1007/s10342-020-01270-y>

Impact factor 2018: 2.633 (14/67 Forestry)

Mixed mountain forests, primarily made up of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.), cover about 10×10^6 ha of submontane-subalpine altitudes in Europe. They provide invaluable ecosystem services, e.g. protection against avalanches, landslides, or rock-fall. However, pure Norway spruce stands have, since medieval times, been heavily promoted as productive stand types for salt-works at sites naturally supporting mixed mountain forests. Damage to these secondary pure spruce stands has been steadily increasing in recent decades. Furthermore, due to their previous limitation due to low temperatures and a short growing season, forest ecosystems in higher elevations are expected to be strongly affected by climate warming. To address these problems, alternative management concepts are being intensively discussed. A possible option to improve the stability and resilience of the stand is the transformation from pure Norway spruce stands into site-appropriate, sustainable and stable mixed mountain forests. In this study, we have tested seven different transformation scenarios (e.g. slit, shelterwood and gap-coupes, strip clearcutting, do-nothing) and their impact on five evaluation criteria (forest growth, economics, carbon sequestration, (stand) stability and biodiversity). As there are hardly any practical examples for some of the transformation scenarios available, we have used the forest growth simulator SILVA to assess whether the tested transformation scenarios differ in transformation success, and to observe trade-offs between the criteria of evaluation. Of the investigated scenarios, we consider the ones with gap or slit-coupes with the most beneficial overall utility values for the portfolio of the five evaluation criteria. However, we showed with our results that it is possible, by means of several trajectories, to return destabilised forests to sustainable and stable systems. We showed that a transformation is realistic, even if sophisticated silvicultural concepts are not strictly pursued.

Individual contributions: I have generated the initial data for the simulation runs using inventory data of forests in the Bavarian alps. I have carried out all simulation-runs with the forest growth simulator SILVA and have compared the simulation results with results from long-term experimental plots (*data acquisition: 75%*). I conducted the data analyses independently and designed and produced the figures (*data analysis and figures 100%*). I wrote and revised the manuscript for the article (*writing and revising: 80%*). The basic idea and concept of the manuscript was developed together with the co-authors of the article (*concept: 60%*)

Biodiversity along temperate forest succession

Torben Hilmers | Nicolas Frieß | Claus Bässler | Marco Heurich | Roland Brandl | Hans Pretzsch
| Rupert Seidl | Jörg Müller

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Impact factor 2018: 5.782 (5/59 Biodiversity conservation; 14/165 Ecology)

1. The successional dynamics of forests—from canopy openings to regeneration, maturation, and decay—influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g., late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity, a quantitative understanding of how different trophic groups vary over the course of succession is needed.

2. We classified mixed mountain forests in Central Europe into nine successional stages using airborne LiDAR. We analysed α - and β -diversity of six trophic groups encompassing approximately 3,000 species from three kingdoms. We quantified the effect of successional stage on the number of species with and without controlling for species abundances and tested whether the data fit the more-individuals hypothesis or the habitat heterogeneity hypothesis. Furthermore, we analysed the similarity of assemblages along successional development.

3. The abundance of producers, first-order consumers, and saprotrophic species showed a U-shaped response to forest succession. The number of species of producer and consumer groups generally followed this U-shaped pattern. In contrast to our expectation, the number of saprotrophic species did not change along succession. When we controlled for the effect of abundance, the number of producer and saproxylic beetle species increased linearly with forest succession, whereas the U-shaped response of the number of consumer species persisted. The analysis of assemblages indicated a large contribution of succession-mediated β -diversity to regional γ -diversity.

4. Synthesis and applications. Depending on the species group, our data supported both the more-individuals hypothesis and the habitat heterogeneity hypothesis. Our results highlight the strong influence of forest succession on biodiversity and underline the importance of controlling

for successional dynamics when assessing biodiversity change in response to external drivers such as climate change. The successional stages with highest diversity (early and late successional stages) are currently strongly underrepresented in the forests of Central Europe. We thus recommend that conservation strategies aim at a more balanced representation of all successional stages.

Individual contributions: I have received and processed the raw data of the number of species of the individual plots. I received the LiDAR data and processed them to assign the plots to the respective forest successional stages (*data acquisition: 35%*). I conducted the data analyses together with the co-authors and designed and produced the figures (*data analysis and figures 75%*). I wrote and revised the manuscript for the article (*writing and revising: 75%*). The basic idea and concept of the manuscript was developed together with Prof. Jörg Müller (*concept: 30%*)

1 Introduction

1.1 Motivation

Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst) and silver fir (*Abies alba* Mill.; hereinafter referred to as beech, spruce and fir, respectively) at elevations between ~600 - 1,400 m above sea level cover an area of more than 10 million hectares in Europe (Brus et al. 2012; EUFORGEN 2017). More than half of Central Europe's surface area consists of mountain areas, which is where most of the existing forests are concentrated (CIPRA 2007). Thus, beech-spruce–fir mountain forests which are managed in order to sustain their functions and services as risk prevention, promotion of biodiversity, wood supply and recreation cover a significant forest area in Europe. Connecting deciduous forests in lowlands and coniferous tree communities at high elevations, the coexistence of beech, spruce and fir has lasted for many centuries locally, depending on the distance from glacial refugia (Magin and Mayer 1959; Mosandl 1984).

Interactions between the three species according to literature seem to be balanced; i.e. the interactions are neither one-sided against or in favour of one of the three species (Pretzsch et al. 2015). For example, in spring conifers may benefit from the neighbourhood of leafless beech by already growing with improved access to water (Goisser et al. 2016; Rötzer et al. 2017). During the common growing season, however, the deeper roots of beech and fir (Lebourgeois et al. 2013) can provide better water supply at the expense of the shallow-rooted spruce. Moreover, in mixed mountain forests spruce and fir are typically higher than beech and can pre-empt the light due to their occupation of the upper canopy layer (Pretzsch et al. 2015). On the other hand, the high morphological plasticity enables beech to more quickly occupy the empty space in case of disturbances (Bayer and Pretzsch 2017). Both conifers reflect an isohydric strategy (Lyr et al. 1992) and show higher stem and root growth during prolonged time spans under drought than beech (Leuschner 2009; Nikolova et al. 2009). While the hazardous behaviour of the anisohydric beech can lead to tree mortality under the impact of extreme water shortage, the behaviour can be beneficial when water is abundant or moderate drought stress (e.g. Klein 2014). There are more structural and functional traits such as crown plasticity (Forrester and Albrecht 2014; Jucker et al. 2015), rooting depth (Rothe 1997; Schmid and Kazda 2002), litter decomposition (Rothe and Binkley 2001) and browsing pressure (Ammer 1996) that prevent any one of the three species from becoming a permanent winner or loser, and despite their effects changing with climate and growing conditions, the balance between the tree species is maintained. Furthermore, potential damages are rather equally distributed, with late frost and ozone susceptibility of fir and beech (Larsen et al. 1990;

Matyssek et al. 2010), the high sensitivity to smoke damage and acid deposition of fir (Elling et al. 2009), the high risk of bark beetle (Wermelinger 2004) and snow and storm damage (Spiecker 2000) of spruce. This temporal, spatial and functional complementarity and risk distribution may contribute to the overyielding of spruce and beech (Rothe 1997; Pretzsch et al. 2010), spruce and fir (Jensen 1983; Pretzsch et al. 2010; Vallet and Pérot 2011) and spruce, fir and beech (Pretzsch and Forrester 2017; Mina et al. 2018).

Particularly in mountainous areas, forests are of great ecological and socio-economic importance in Central and Eastern Europe due to their provision of various ecosystem goods and services (e.g. Ellenberg 1988; Bebi et al. 2001; Pretzsch et al. 2015; Mina et al. 2017). The strong topographic gradients and high relative relief strongly increase the propensity for soil loss through erosion (Panagos et al. 2015), as well as gravitational processes such as rock-fall, avalanches and snow-gliding (Rammer et al. 2015; Leitinger et al. 2018). Furthermore, mountain topography often facilitates heavy local precipitation events and thunderstorms and human infrastructure is often restricted to flood-prone river valley bottoms. As a consequence, the green infrastructure provided by forests is particularly relevant in mountainous countries. Due to their importance in buffering against the consequences of harsh mountain environments, mountain areas frequently have a substantially higher forest share than low elevation areas (EEA 2010). They constitute regional hotspots of forest C storage (Nabuurs et al. 2008) and are estimated to contain 11% of current global biomass stocks (Erb et al. 2018). In addition to providing regulating services to local communities, mountain forests are thus also relevant for the global climate system.

However, mixed mountain forests in Europe are severely exposed to warming temperatures with no significant changes in precipitation (Auer et al. 2007; Bircher et al. 2016). In addition, increasing natural disturbances such as windstorms or bark beetle outbreaks are to be expected (Seidl et al. 2017). Further changes in the climate system could fundamentally alter the composition and structure of mountain forests, e.g. due to climate-induced shifts in species' niches (Hanewinkel et al. 2013; Thom et al. 2017; Obojes et al. 2018). Given that mountain forests were strongly limited by cold temperatures and short vegetation periods in the past (Oberhuber 2004; Jolly et al. 2005), moderate climate change may reduce these limitations and lead to an overall increase in canopy closure and tree growth due to extended growing seasons and the effect of CO₂ fertilization (Norby et al. 1999; Kulakowski et al. 2011; Norby and Zak 2011). Therefore, similar to forest ecosystems in the northern latitudes, mixed-mountain forest

ecosystems are expected to be strongly affected by climate warming (Piao et al. 2011; Vayreda et al. 2012; Ruiz-Benito et al. 2014).

The species-specific optimum habitats are severely restricted in their geographical distribution in mountain areas. Particularly vulnerable are beech-spruce-fir mixed mountain forests that occur in areas with species-specific suboptimal vitality. Here, climate change induced changes of environmental conditions are likely to alter their competitiveness (McEvoy et al. 2013; Grace et al. 2014; Harvey et al. 2014). As a result, if beech benefits from higher temperatures at elevations between 600-1,000 m a.s.l., this may reduce the competitiveness of Norway spruce and silver fir. Any changes in the fitness and growth of one of the three species can be caused either *directly* by improved or reduced external growing conditions, or *indirectly* by a strengthening or weakening of the competitors. Nonetheless, if water becomes increasingly limiting, the effects of climate change might become negative (Pichler and Oberhuber 2007; Allen et al. 2015).

In addition, these forest systems may become more vulnerable in the future because of extensive bark beetle outbreaks and pathogens that profit from increased drought and higher temperatures under global change (Porta et al. 2008; Seidl et al. 2014). A number of studies report that in recent decades there have been more frequent problems with the natural regeneration of spruce and fir, ozone stress and drought in mixed mountain forests (Ashmore et al. 1985; Ammer 1996; Matyssek et al. 1997; Dell’Era et al. 1998; Ruehr et al. 2010; Hartl-Meier et al. 2014b; Pretzsch et al. 2015). Against the background of the strong vulnerability of these ecosystems, the Agenda 2010 for Sustainable Development explicitly states that there needs to be an intensification of the implementation of concrete measures, sustainable processes and strategies to strengthen the resilience of mountain areas (Mountain Partnership 2017). Due to the restricted climatic conditions, mountain forests are well suited to analyse the influence of climate change over a relatively short period of time (Cudlín et al. 2017). Large scale studies on mixed mountain forests and their productivity are rare and regionally limited (Preuhsler 1981; Prietzel and Christophel 2014; Pretzsch et al. 2015; Bosela et al. 2018), but necessary to support management decisions that take environmental conditions and their possible future change into account.

However, despite the superior stability of mixed-mountain forests, they have often suffered a reduction in species richness. In the German Alps, for instance, spruce has, since medieval times, been heavily promoted as a productive timber species for salt-works at sites naturally supporting mixed mountain forests (Seidl et al. 2007). However, damage to these

secondary pure spruce stands has been steadily increasing in recent decades (e.g. Briner et al. 2013). It is particularly these forests which are vulnerable to summer droughts (Lévesque et al. 2013; Zang et al. 2014), extensive bark-beetle outbreaks (Seidl et al. 2014) and pathogens (Porta et al. 2008) which are then further favoured by a warmer and possibly drier climate (Matulla et al. 2002; Lexer et al. 2002; Pepin et al. 2015). For example, Marini et al. (2012) found that forest disturbance in the European Alps was 7 times higher where spruce was planted in sites that were warmer than those within its historical climatic range. In addition, the repeated cultivation of pure spruce stands has a negative effect on soil fertility (Seidl et al. 2007). To address these problems, alternative management methods are being intensively discussed (Reininger 2000; Spiecker et al. 2004; Löff et al. 2010). A possible option to improve the stability and resilience of the stand against abiotic and biotic disturbing factors, as well as to increase productivity, is the transformation of pure spruce stands to site-appropriate mixed mountain forests at equilibrium (Fig. 1.1; Spiecker et al. 2004; Seidl et al. 2011; Pretzsch et al. 2017).

The state-of-the-art silvicultural approach in the Alps consists of small, irregular patch cuts for regenerating the forest and maintaining a high level of forest canopy cover in space and time (Cordonnier et al. 2008; Streit et al. 2009). It aims at the supply of regulating services and maintaining a relatively continuous forest cover, while enhancing resistance and resilience to disturbances (Dorren et al. 2004; Brang et al. 2006). However, management is complicated by steep terrain and low accessibility, which requires highly specialised harvesting technologies, (e.g. cable-line systems) and results in high management costs (Valente et al. 2014; Jandl et al. 2018). As an alternative one could adopt a more differentiated strategy, maintaining the existing mixed mountain forests, but transforming pure spruce in stable mixed mountain forests of mainly beech, spruce and fir. However, there are hardly any existing long term practical examples for both maintenance and transformation. Thus, simulations with a forest growth simulator might be a supporting tool to assess whether the maintenance and transformation scenarios are successful.

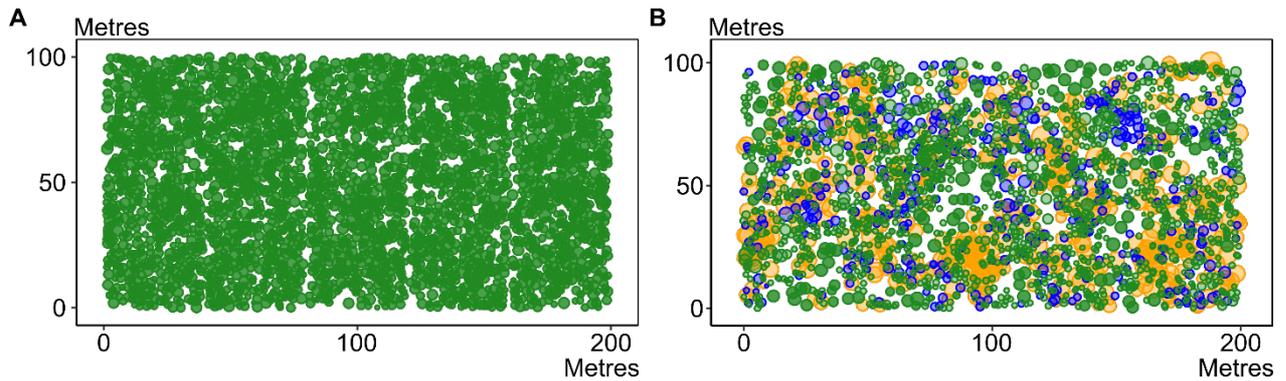


Fig. 1.1: Crown maps of a secondary pure Norway spruce stands (A) and a close-to-nature mixed mountain forest of beech, spruce and fir (B). Green, spruce; blue, fir; orange, beech; circles, crown projection.

Because mountain forests are less accessible for logging and highly relevant for protection against gravitational hazards such as avalanches, land slides, or rockfalls and other watershed services they were often managed less intensively or left in a more natural state compared with lowland forests. Because of this mixed mountain forests are furthermore well situated for studying successional dynamics and changes of biodiversity along forest succession. After a severe disturbance with high tree mortality, this forests undergo a series of successional stages. Following successful regeneration, forests canopies eventually close and subsequently diversify in both their vertical and horizontal structures. With ongoing succession, forests accumulate biomass and the initial cohort of trees gradually dies, which increases the amount of dead wood (Fig. 1.2A; Oliver and Larson 1990; Franklin et al. 2002). Despite the fundamentally dynamic nature of forests, accounting for successional dynamics remains a challenge for the development of conservation concepts (Tikkanen et al. 2007). Based on a limited number of focal species and their habitat preferences, conservation efforts often focus on one or a few successional stages (Swanson et al. 2011). For instance, it has been shown that late stages of forest succession, including plenter (mixture of trees of different ages, sizes and heights), terminal and decay stages, are the preferred habitat for species considered as typical “forest dwellers”, e.g. white-backed woodpecker in Central Europe (*Dendrocopus leucotos*; Carlson 2000). Late successional stages are often prioritized in conservation due to their high diversity in taxa, including birds, bats, saproxylic organisms (Jacobs et al. 2007; Avila-Cabadilla et al. 2009; Peña-Cuéllar et al. 2012), lichen (Kuusinen and Siitonen 1998) and fungi (Redecker et al. 2001). Variation in biodiversity along the stages of succession can also help to better understand the underlying drivers of diversity in forests. For instance, resources that are relevant for different species groups, such as light on the forest floor and dead wood, distinctly

vary with successional stage (Fig. 1.2B). Understanding the inherent changes in species diversity as forests develop provides an important baseline for assessing the effects of external drivers such as climate change (Thom et al. 2017). In the absence of such a dynamic baseline, observed changes in biodiversity that are simply the effect of forest dynamics could be easily misattributed to effects of climate change. Furthermore, understanding the variation in biodiversity over the entire course of succession could also provide a more comprehensive perspective on the effects of different management strategies on biodiversity.

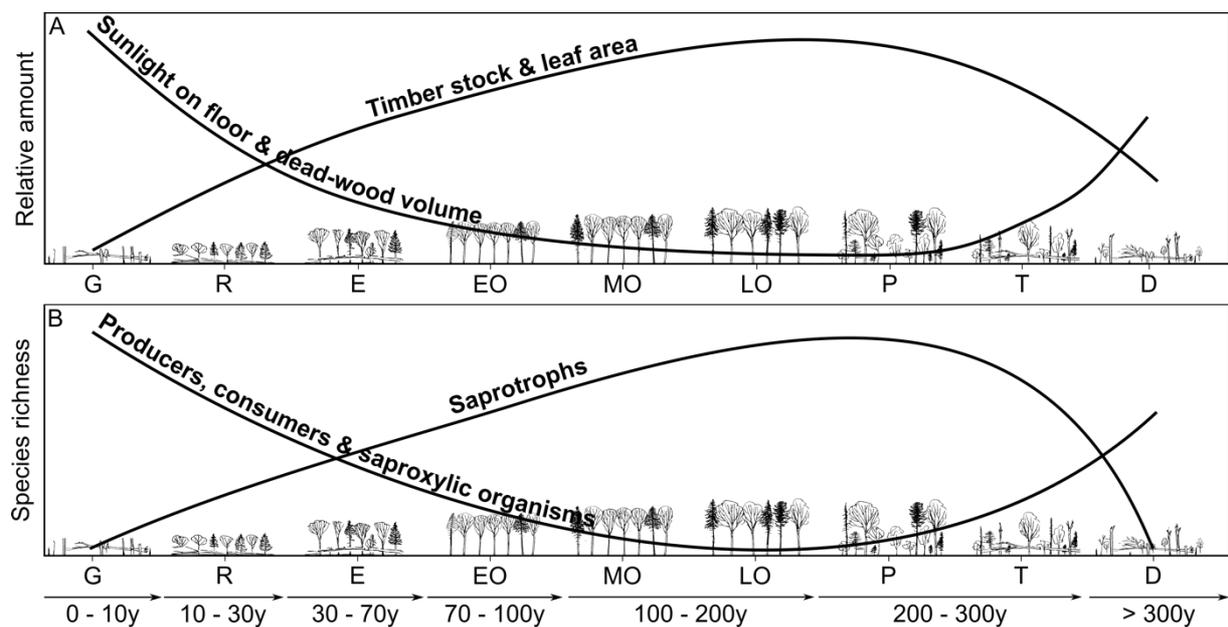


Fig. 1.2: (a) Changes in resource availability with forest succession and (b) hypothesized response of saprotrophs, saproxylic organisms, producers and consumers. The successional stages considered here follow (Tabaku 2000; Drössler and Meyer 2006; Zenner et al. 2016). Arrows represent an approximate timeline of the successional stages following Moning and Müller (2008). Note that the decay stage can occur already after 120 years due to forest disturbances, such as storms and bark beetle infestations. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid-optimum; LO, late optimum; P, plenter; T, terminal; D, decay. From Hilmers et al. (2018).

1.2 Objectives and Outline

The main objective of the research performed for this cumulative thesis was an improved understanding of long-term trends in productivity of mixed mountain forests comprised of beech, spruce and fir in Europe (Article I; Hilmers et al. 2019; Appendix A) and to identify possible path that can be followed to transform characteristic unstable pure spruce stands in mountain areas into semi-natural mixed forests at equilibrium (Article II; Appendix B). Furthermore, it was the aim of this thesis to understand the inherent changes in species diversity as forests develop to provide an important baseline for assessing the effects of external drivers such as climate change (Article III; Hilmers et al. 2018; Appendix C). Fig. 1.3 shows the conceptual framework of this cumulative thesis and the relationships between the three articles.

The cumulative thesis aims for three main topics:

- 1) How productive are unmanaged European mixed mountain forest stands comprised of *Fagus sylvatica*, *Picea abies* and *Abies alba* in Europe and are there any long-term trends in productivity (Article I; see Chapter 3.1 and Appendix A)?
- 2) Whether it is possible to transform characteristic secondary pure spruce stands in mountain areas to semi-natural stable forests with balanced age and tree species mixtures using different forest management scenarios, and how the different scenarios differ in terms of forest growth, economics, carbon sequestration, stand stability and biodiversity (Article II; see Chapter 3.2 and Appendix B).
- 3) How different trophic groups vary along temperate forest succession (Article III; see Chapter 3.3 and Appendix C)?

Large scale studies on mixed mountain forests and their productivity are rare and regionally limited, but necessary to support management decisions that take environmental conditions and their possible future change into account. In the first article (Hilmers et al. 2019; Appendix A) a data set of a series of long-term experimental plots across mountain regions in Europe was used. It aims to improve the knowledge about site-specific productivity and growth trends in European mixed mountain forests, and addresses the following questions: (i) how productive are mixed mountain forest systems in Europe currently and how has their productivity changed in recent decades with regard to climate change and anthropogenic influences?; and (ii) is there a shift in species-specific productivity of beech, spruce or fir over recent decades?

The reconciliation of forest growth, wood production, carbon storage and biodiversity conservation objectives has been the subject of intense debate for some time. In addition to topics in numerous studies on the economic aspects of forest transformation, the effects of forest transformation on the habitat complex of mixed mountain forests were investigated taking a holistic approach in the second article (see Appendix **B**). In this sense, the second article is devoted to the evaluation of multiple criteria of different forest transformation systems of secondary pure spruce stands, taking into account the criteria of forest growth, economics, carbon sequestration, stand stability and biodiversity. The specific objectives of the thesis are (i) to identify possible paths that can be followed to transform characteristic pure spruce stands into semi-natural mixed forests at equilibrium using different forest management scenarios; and to evaluate (ii) if the investigated management methods yield stable stands over the long run; and (iii) how the different scenarios differ in terms of forest growth, economics, carbon sequestration, stand stability and biodiversity.

The successional dynamics of forests – from canopy openings to regeneration, maturation and decay – influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g. late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity, a quantitative understanding of how different trophic groups vary over the course of succession is needed. Based on theoretical considerations and the expected changes in the amount and heterogeneity of resources along the stages of succession, the third article (Hilmers et al. 2018; Appendix **C**) hypothesized that: (i) patterns of abundance and number of species of primary producers along the course of forest succession would be U-shaped, dependent on light reaching the forest floor; patterns of consumers would be U-shaped, if they depend on the primary producers; patterns of saproxylic organisms would be U-shaped, if they are dependent on the accumulation of dead wood along succession; and patterns of saprotrophs would be hump-shaped, following the pattern of biomass accumulation; (ii) the stage of forest succession would have no effect on the number of species when abundance is accounted for, if these responses are driven by an increase in individuals, as predicted by the *more-individual hypothesis*; and (iii) species compositions in the early and late successional stages, which are characterized by open canopies, would be similar as many insects respond to the openness of the habitat.

This thesis is organized as follows. Chapter **2** presents the study areas and the utilized datasets from the long-term-experimental plots, remote sensing data, number of species and

simulation outputs. Chapter 2 highlights also the developed methods for the analyses of the productivity of mixed mountain forests, transformation efforts and the effect of forest successional stages on the number of species. Moreover, Chapter 3 summarizes the obtained results of the cumulative thesis composed of three publications. Finally, Chapter 4 discusses the applied approaches as well as the achieved results, while Chapter 5 concludes the main findings of the thesis. Finally, chapter 6 shows perspectives for future research.

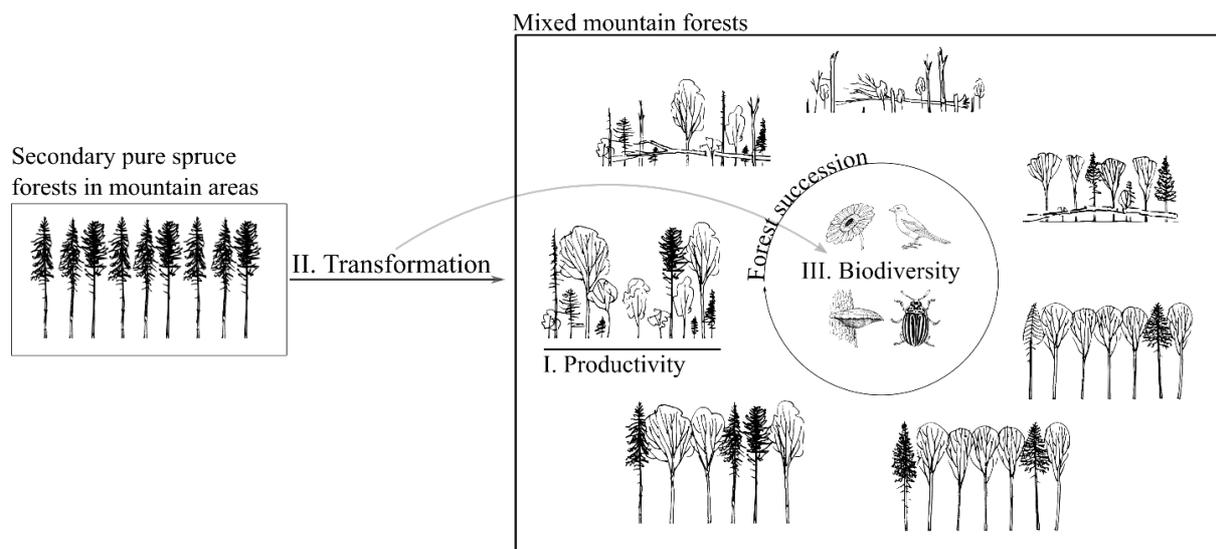


Fig. 1.3: Conceptual framework of this cumulative thesis. In a first publication, the productivity of unmanaged mixed mountain forests in Europe was examined (topic 1). In a second publication, possible transformation scenarios of destabilized pure spruce forests in mountain areas to stable mixed uneven-aged mountain forests were presented (topic 2). In a third publication the biodiversity along forest succession in mixed mountain forests was examined (topic 3). In order to evaluate the influence of the various transformation scenarios from topic 2 on forest biodiversity, the results from topic 3 were included in the study of topic 2.

2 Material and methods

2.1 Material

2.1.1 Study Area

Productivity of mixed mountain forests (Article I):

The data set for analysing the productivity of mixed mountain forests in Europe (Article I) covered most parts of the mountainous regions of Europe (Fig. 2.1) and maps a wide climatic and topographic gradient for mixed mountain forests with elevations from 733 to 1443 m, mean annual temperatures from 4.4 to 8.5 °C and annual precipitation from 813 to 2818 mm (Fig. 2.2). The dominant parental material varies between slightly consolidated (e.g. unconsolidated deposits), moderately consolidated (e.g. sedimentary rocks) and intensively consolidated (e.g. igneous and metamorphic rocks) with medium to very high available water storage capacity, low to high base saturation and very low to medium soil organic carbon contents (Panagos et al. 2012).

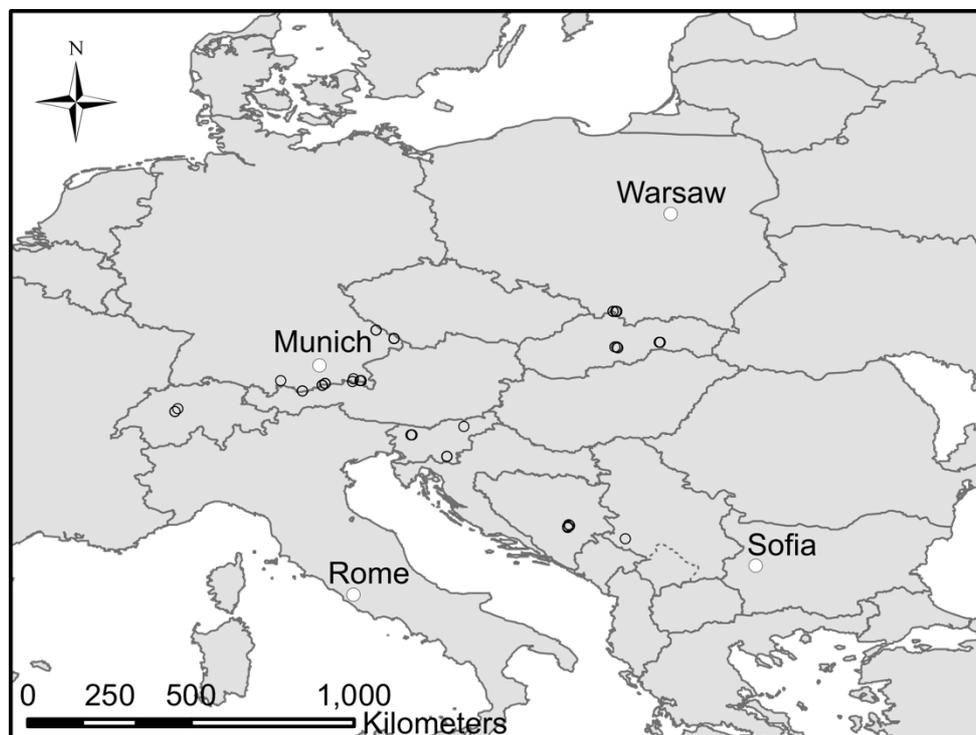


Fig. 2.1: Geographic location of the 60 long-term mixed beech-fir-spruce mountain forest experimental plots (black points). Some experimental plots are not visible (overlaid) due to scaling. From Hilmers et al. (2019).

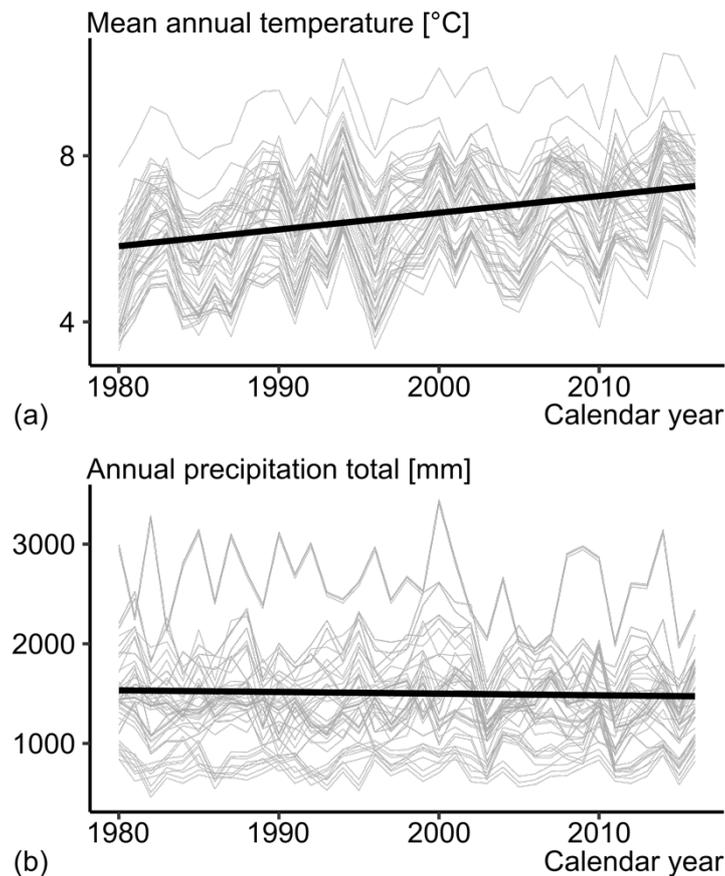


Fig. 2.2: Mean annual temperature (a) and annual precipitation totals (b) of all 60 long-term mixed mountain forest experimental plots from 1980 to 2017. Climate data from the closest available stations to the experimental plots. For 34 out of the 60 plots an elevation correction was executed based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined based on 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris et al., 2014). The black regression line is based on a linear model; the grey area depicts the 95% confidence interval (a: estimate = 0.04, $p < 0.001$; b: estimate = -1.645, $p = 0.06$). From Hilmers et al. (2019).

Transformation of pure spruce to mixed mountain forests (Article II):

Comparisons of different management scenarios to transform pure spruce stands in mountain areas to mixed uneven-aged mountain forests of beech, spruce and fir (Article II) were done using inventory data of forests in the Bavarian alps on sites of the ‘Oberbayerische Flyschvorpalpen’ (800-1200 m above sea-level, good site conditions).

Biodiversity along temperate forest succession (Article III):

To analyse changes of biodiversity along temperate forest succession (Article III) data from a survey of biodiversity and forest structure in the Bavarian Forest National Park in south-eastern Germany was used (Fig. 2.3; Bässler et al. 2008). The study area covers 24,000 ha and comprises a wide range of stages of forest succession that resulted from considerable variation in disturbance history and stand age. This variation was utilized in a space-for-time substitution approach. The total annual precipitation is between 1300 and 1900 mm and increases with elevation (Fig. 2.5), which ranges from 655 to 1420 m a.s.l. Annual mean air temperature varies between 3.5 °C at high elevations and 7.0 °C at low elevations (Bässler 2004). The national park is dominated by mixed mountain forests of spruce, fir and beech.

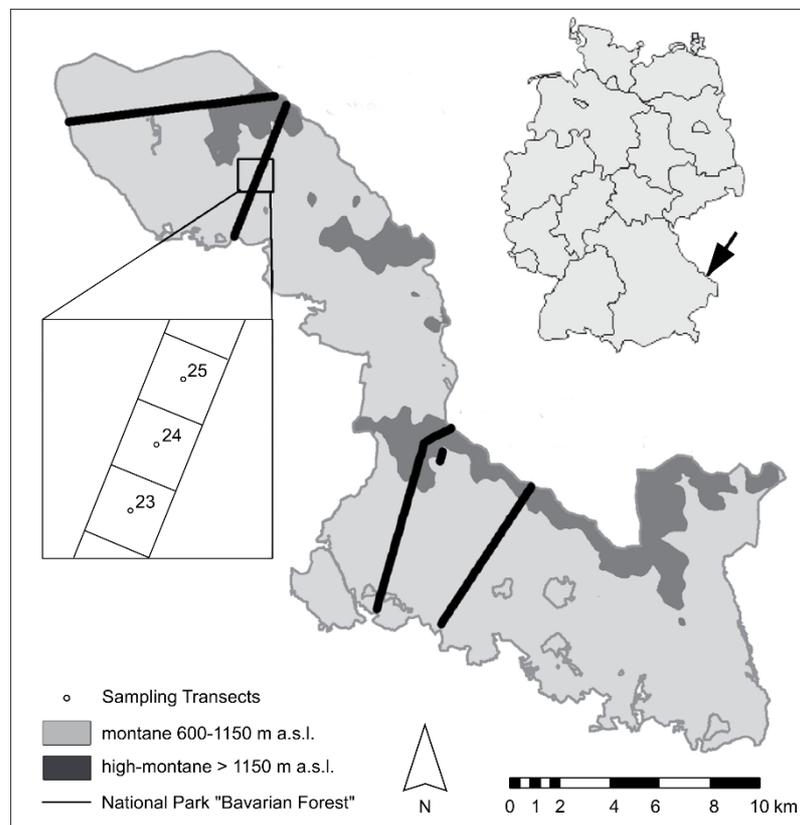


Fig. 2.3: Study area and study design of the sampling transects of Article III with indication of the boundaries of the montane and high montane zone. Based on Bässler et al. (2008).

2.1.2 Data

Productivity of mixed mountain forest in Europe (Article I):

Sixty long-term experimental plots with a total of 222 observations between 1980 and 2010, consisting of beech, spruce and fir, were investigated (Fig. 2.1; Tab. 2.1). All trees with a diameter at breast height >7cm were measured at every observation. Tree heights were measured on a subsample of trees. Thus, the volume of single trees and stands could be calculated by means of stand height curves and regionally adopted form factors. At least two of the three species (beech, spruce and fir) had to be present and each species must have had a mixture portion of at least 20 percent. On the experimental plots only low intensity thinning or no thinning was allowed. In this way, confounding growth trends with thinning effects were avoided.

This analyses focused on the periodic annual increment at the stand level (PAI). To evaluate the stand characteristics, the DESER-Norm 1993 by Johann (1993) was followed. Repeated observations at the stand level were carried out at intervals of several years and enabled the calculation of the periodic annual increment at stand level (PAI), giving the mean annual growth rates over longer time intervals. Between two observations at times t_1 and t_2 , the PAI was calculated from the difference between the wood volumes V_1 and V_2 of the remaining stand at both times plus the volume of trees which died (or were removed) between the observations.

$$PAI = (V_{2\text{ remaining}} - V_{1\text{ remaining}} + V_{\text{removed}})/(t_2 - t_1)$$

Tab. 2.1: Main characteristics of the 60 investigated long-term mixed beech-fir-spruce mountain forest experimental plots from 1980 to 2010. Standard deviations are given in brackets. The respective tree species shares were calculated using transformed SDI values according to Pretzsch and Biber (2016). From Hilmers et al. (2019).

	Country	Number of plots	Total number of observations	Number of observations per plot	Elevation	Mean annual temperature	Annual precipitation total	Volume	Basal area	Periodic annual increment	Species share		
											Beech	Spruce	Fir
		N	N	N	m a.s.l.	°C	mm	m ³ ha ⁻¹	m ² ha ⁻¹	m ³ ha ⁻¹ y ⁻¹	%	%	%
mean [sd]	Bosnia and Herzegovina	5	14	2.8 [±0.45]	1185 [±113]	7.21 [±0.7]	1269 [±84]	381.5 [±72.8]	33.4 [±4.9]	9.3 [±2.1]	21.8 [±29.9]	33.2 [±19.2]	43.5 [±18.8]
min. – max.				2 – 3	1006 – 1291	6.2 – 8.5	1095 – 1387	248.8 – 501.0	26.6 – 41.2	6.0 – 11.9	0.2 – 71.6	10.7 – 64.9	16.3 – 71.4
mean [sd]	Germany	29	116	4.14 [±0.97]	984 [±186]	6.35 [±0.7]	1605 [±366]	532.5 [±206.8]	38.0 [±12.7]	8.6 [±3.0]	18.1 [±13.9]	45.0 [±15.4]	33.1 [±14.9]
min. – max.				2 – 6	743 – 1281	4.7 – 7.6	1109 – 2191	183 – 1178.5	9.6 – 73.5	3.1 – 15.1	0 – 60.8	9.6 – 77.5	2.6 – 63.9
mean [sd]	Poland	7	21	3	983 [±57]	5.5 [±0.4]	1434 [±66]	549.8 [±77.7]	39.2 [±3.4]	6.9 [±2.7]	54.9 [±15.8]	17.8 [±18.9]	27.1 [±10.3]
min. – max.				–	902 – 1087	4.8 – 6.4	1306 – 1550	438.8 – 713.7	35.4 – 45.7	1.5 – 11.0	22.0 – 77.4	4.7 – 64.2	11.3 – 44.9
mean [sd]	Serbia	1	2	2	1270	7.1 [±0.5]	1184 [±33]	652.5 [±91.9]	51.4 [±1.4]	13.2 [±1.0]	0.5 [±0.2]	44.5 [±1.5]	55.0 [±1.7]
min. – max.				–	–	6.8 – 7.5	1161 – 1208	587.5 – 717.5	50.4 – 52.4	12.5 – 13.9	0.3 – 0.6	43.5 – 45.6	53.8 – 56.2
mean [sd]	Slovakia	6	21	4.2 [±1.3]	775 [±45]	6.1 [±0.7]	922 [±96]	710.2 [±181.8]	43.8 [±7.4]	11.2 [±3.1]	38.7 [±16.3]	17.6 [±25.7]	42.3 [±16.7]
min. – max.				3 – 6	733 – 845	4.9 – 7.3	813 – 1200	445.1 – 985.2	33.9 – 55.7	3.1 – 15.6	11.0 – 63.4	0 – 62.8	14.7 – 69.1
mean [sd]	Slovenia	8	28	3.5 [±0.53]	1171 [±264]	5.9 [±1.2]	2247 [±513]	704.4 [±158.2]	47.2 [±7.1]	10.2 [±3.0]	47.4 [±17.7]	29.3 [±29.4]	21.6 [±19.3]
min. – max.				3 – 4	910 – 1443	4.4 – 7.8	1471 – 2818	433.5 – 1030.0	35.2 – 61.9	4.6 – 17.1	20.3 – 74.1	0 – 78.2	0 – 69.8
mean [sd]	Switzerland	4	20	5	897 [±5]	7.3 [±0.3]	1426 [±26]	404.5 [±104.4]	30.9 [±6.1]	12.3 [±2.6]	12.9 [±10.7]	27.6 [±7.4]	58.8 [±13.0]
min. – max.				–	890 – 899	6.9 – 7.7	1394 – 1479	215.8 – 721.7	18.9 – 49.2	6.2 – 15.9	5.1 – 41.6	11.4 – 36.7	22.6 – 74.4
mean [sd]	All	60	222	3.8 [±1.0]	995 [±201]	6.4 [±0.9]	1563 [±461]	552.7 [±198.9]	39.0 [±11.0]	9.3 [±3.2]	26.8 [±21.3]	35.5 [±21.6]	35.1 [±18]
min. – max.				2 – 6	733 – 1443	4.4 – 8.5	813 – 2818	183 – 1178.5	9.6 – 73.5	1.5 – 17.1	0 – 77.4	0 – 78.2	0 – 74.4

Transformation of pure spruce to mixed mountain forests (Article II):

Initial data for the simulation and the assumed site productivity were deduced using inventory data of forests in the Bavarian Alps. Starting point for the simulations was formed by a total of 30 different pure spruce stands (Tab. 2.2, Fig. 2.4), which were generated by the structural generator, STRUGEN (Pretzsch 1997).

Tab. 2.2: Key forest growth data of the simulation stands. N, stem number per hectare; dg, diameter of mean basal area; hg, mean height corresponding to dg.

Species	Age	N	hg	dg	Basal area	Volume
	years	n ha ⁻¹	m	cm	m ² ha ⁻¹	m ³ ha ⁻¹
Spruce	30 - 40	2486 ± 92	10.7 ± 0.25	12.2 ± 0.25	32.8 ± 1	181.6 ± 12

All the simulated plots covered 2 ha each, at an age of 30 to 40 years, on sites of the ‘Oberbayerische Flyschvorlpen’ (800-1200 m above sea-level, good site conditions). Single layered initial stands were characterised by an average basal area of 32.8 m² ha⁻¹ with an average volume of the remaining stands of 181 m³ ha⁻¹ (Tab. 2.22).

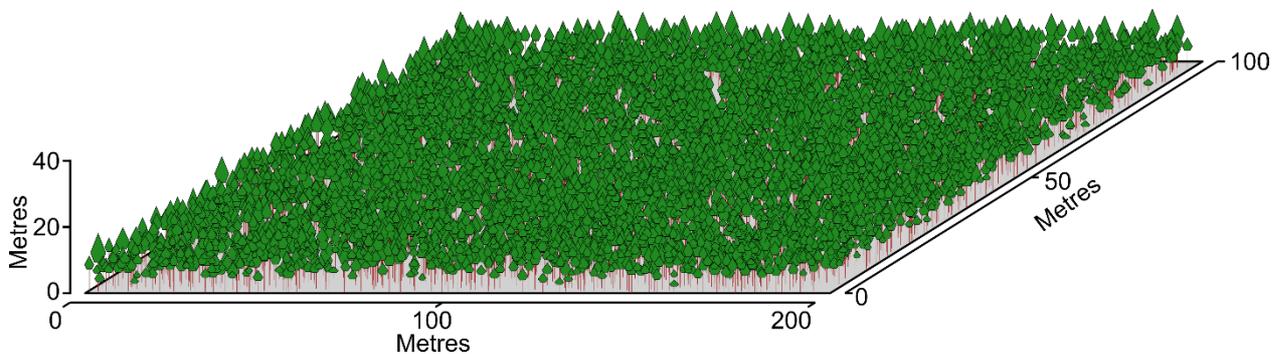


Fig. 2.4: Example of an initial stand generated with the STRUGEN structure generator (Pretzsch 1997) based on inventory data from Bayerische Staatsforsten AÖR. Location: Upper Bavarian Flyschvorlpen. Elevation 1000m above sea-level. Green, spruce.

Biodiversity along temperate forest succession (Article III):

Forest structure was characterized from field measurements and airborne light detection and ranging (LiDAR) on 287 plots (Fig. 2.3), each with a circular area of 1000 m². The plots include stands that were managed until a few decades ago and also remnants of old-growth forests. All measurements were conducted in the years 2006–2008 (Bässler et al. 2008). For each study plot, GPS coordinates were used to extract information on elevation from a digital terrain model (DTM 25) of the national park. In a space-for-time substitution approach, differences in the environmental conditions of sites often bias the analysis. Therefore, data on both soil characteristics and macro-climate were collected for each plot. Soil samples were collected as described in Peura et al. (2016). Information on soil pH, cation exchange capacity, base saturation and soil moisture were explicitly considered and a principal component analysis (PCA) based on the correlation matrix was performed. In the subsequent analyses, the first principle component to control for differences in soil conditions was used. It explained 40% of the variance in the data and describes a gradient from dry, acidic, nutrient-poor soils to moist, alkaline and nutrient-rich soils. To correct for climatic differences between the observations, elevation was used as an additional covariate, as there is a strong linear relationship between important climatic variables and elevation in the study area (Fig. 2.5).

The vegetation in the herbaceous layer (up to 1 m height), shrub layer (up to 5 m height), tree layer 1 (>5 to 15 m height) and tree layer 2 (>15 m) were estimated on 200 m² circular plots. Standing and downed woody debris were recorded in the field on each plot. Full-waveform LiDAR data were collected across the plots (Fig. 2.3) using a Riegl LMS-Q560 under leaf-on conditions in 2007 (nominal sensor altitude: 400 m, average point density: 25 points m⁻²). Single trees in an area of 1000 m² around the centre of each plot were detected using 3D segmentation. The bounding polygons of individual tree crowns were used to extract canopy variables and to distinguish deciduous from coniferous trees (Yao, Krzystek, & Heurich, 2012). Stem volume (m³) and diameter at breast height (cm; DBH) of the extracted trees were determined using multiple linear regression based on reference trees measured in the field (Heurich and Thoma 2008).

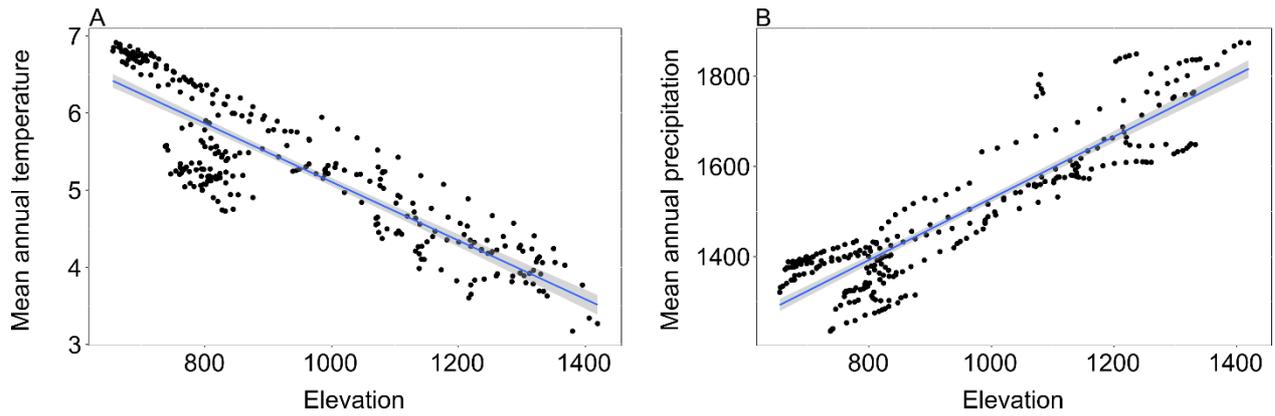


Fig. 2.5: Climate of the study region based on interpolated data from 1980 to 2006. (A) Mean annual temperature (°C) in relation to elevation (m a.s.l.) of all 287 study plots. The blue regression line is based on a linear model; the grey area depicts the 95% confidence interval ($R^2 = 0.77$, $F_{1,285} = 937.6$, $p < 0.001$). (B) Mean annual precipitation (mm) in relation to elevation (m a.s.l.) of all 287 study plots. The blue regression line is based on a linear model, with the grey area depicting the 95% confidence interval ($R^2 = 0.82$, $F_{1,285} = 1299$, $p < 0.001$). From Hilmers et al. (2018).

Variation in biodiversity with forest succession was analysed considering 2956 species from 23 taxonomic lineages. The species were group-specifically sampled in a standardized way and covered six trophic groups: producers (higher plants, lichen, mosses), consumers I (phytophagous and pollinating arthropods), consumers II (invertebrates feeding on animal tissue), consumers III (vertebrates feeding on animal tissue), saprotrophs *sensu lato* (species feeding on dead tissue) and the special case of saproxylic saprotrophs (species depending on dead wood during their life cycle). Overall, this distinction of the 23 lineages into trophic groups yielded 33 functional groups; each of these functional groups were analysed on 29–287 plots (Tab. 2.3).

Tab. 2.3: The observed 23 taxonomic groups, their association with the 6 functional groups and the number of plots (n) on which data were collected in the field. From Hilmers et al. (2018).

Producer		Consumer I		Consumer II		Consumer III		Saprotroph		Saproxilylic organism	
Taxon	n	Taxon	n	Taxon	n	Taxon	n	Taxon	n	Taxon	n
Lichens	109	Bees and wasps	36	Beetles	178	Bats	29	Beetles	178	Beetles	178
Mosses	109	Beetles	178	Dipterans	36	Birds	286	Dipterans	36	Fungi	287
Plants	287	Cicadas	36	Harvestmen	178	Shrews	178	Moths	36	Moths	36
		Dipterans	36	Lacewings	36			Snails	108		
		Grasshoppers	36	Snails	108			Springtails	178		
		Hoverflies	36	Spiders	178			Worms	87		
		Mice	178	True bugs	178						
		Moths	36								
		Sawflies	36								
		Snails	108								
		True bugs	178								

Higher plants, fungi and birds were recorded on all 287 plots for which forest structure was characterized. The other 20 taxonomic groups were sampled on subsets of the study plots due to labour-intensive collection methods. Field collections (gastropods, number of study plots surveyed, n = 108; lichen and mosses, n = 109), flight-interception traps (beetles, true bugs, cicadas, bees and wasps, lacewings, spiders and harvestmen, n = 178), pitfall traps (beetles, true bugs, cicadas, springtails, spiders and harvestmen, mice and shrews, n = 178; gastropods, n = 108), malaise traps (cicadas, grasshoppers, lacewings, sawflies, hoverflies and other dipterans, n = 36), light traps (moths, n = 36), ultrasound recordings (bats, n = 29) and hand-sorted soil samples (worms, n = 87) were used. For details of the sampling methods used for different taxa, see Bässler *et al.* (2008). Some groups were sampled using several methods. To use the full spectrum of species for the analyses, the data was aggregated by summing the abundances across the consistent sampling methods across plots. The sampling area of plants and lichens was 200 m² and for fungi 1000 m².

2.2 Methods

Productivity of mixed mountain forests (Article I):

Stand productivity was explained by using several factors. The growth of any tree and forest stand is age dependent. However, since most of the study plots under investigation are uneven-aged, it was not possible to create a useful metric regarding stand age. For this reason, the standing volume per hectare of the remaining stock as a proxy for the development stage of the forest stands was used. Furthermore, the stand density quantified by the stand density index (SDI; Reineke, 1933) was used to characterize the growing stock. To quantify the proportion of each species in the total stand with respect to the different space requirements of each individual species, the SDI values of spruce and fir were transformed into a comparable SDI referenced at beech following the model of Pretzsch and Biber (2016). Since some of the experimental plots under investigation had a long time period between two consecutive observations (> 20 years) the mean values of the stand characteristics (V, SDI) between the two observations (Assmann 1961) was used instead of their values at the beginning of the period.

In addition to the location of each plot (latitude, longitude), variables representing terrain topography were derived from digital elevation models (European Union, Copernicus Land Monitoring Service, 2019) and consisted of slope inclination (in degrees), north index (calculated from slope orientation with $\cos(2\pi \times \text{slope orientation}/360)$, where 1 indicates a north-exposed plot, -1 indicates a south-exposed plot), and east index $\sin(2\pi \times \text{slope orientation}/360)$, where 1 indicates an east-exposed plot and -1 indicates a west-exposed slope orientation). As a measure of soil productivity the dominant parental material was used (three groups: slightly, moderately and intensively consolidated) and the available water storage capacity to a depth of 1 m (AWC) from the European Soil Database v2.0 (Panagos et al. 2012).

Monthly data for mean temperature and precipitation total were collected from the closest available meteorological stations. For 34 out of the 60 plots, meteorological station based interpolated data were available. For the remaining 27 plots only station data itself were accessible and some of the stations were located further away (8.7 km on average) or at a different elevation. In order to improve the representativeness of the latter datasets, an elevation correction was used based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined using 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris et al., 2014). Temperature and precipitation were aggregated to annual mean values (mean annual temperature and annual precipitation totals) and then again averaged for the respective recording intervals. To detect possible changes in

the productivity of mixed mountain forests in Europe over the last 30 years, beyond the effect of the change in considered climate variables, also the calendar year was taken into account.

Transformation of pure spruce to mixed mountain forests (Article II)

There are hardly any existing practical examples for both maintenance of mixed mountain forests and transformation of secondary pure spruce stands to close-to-nature mixed mountain forests. Thus, simulations with the forest growth simulator SILVA 2.3 (Pretzsch and Kahn 1996; Pretzsch et al. 2002) served as a supporting tool to assess whether transformation scenarios are successful.

Assuming the help of cable yarding operations, the silvicultural goal in this thesis was to transform unstable pure spruce stands to close-to-nature mixed mountain forests of beech, spruce and fir at equilibrium. These multi-layered mixed mountain forests should have a tree species mixture of 30-40% of species other than spruce and, if at equilibrium, an exponentially decreasing stem distribution. In addition, these forests should be uneven-aged, show a high structural diversity as well as an advanced regeneration layer, containing both early- and late-successional species, on as large an area as possible. By regular moderate treatments the volume of the remaining stand is kept on an optimal level, so that the desired structural diversity and a continuous natural regeneration are obtained. While on rich sites a volume of the remaining stand of 400 - 500 m³ha⁻¹ is aimed at, on mesic sites a volume of the remaining stand of 300 - 400 m³ha⁻¹ is targeted. In order to avoid growth reduction, the respective lower value should not be undercut over a longer period of time. Very poor sites were not taken into account, as regular management often takes a back seat in these areas and aspects of forest conservation and protection forest management are in the foreground.

The state-of-the-art silvicultural approach in the Alps (e.g. Bayerische Staatsforsten AöR 2018), is intended to aim at transforming secondary pure spruce stands into close-to-nature mixed forests at equilibrium. To sustain the unique functions and services of mixed mountain forests, the natural gap dynamics of mountain forests are emulated by silviculture (e.g. Acevedo et al. 1996; McCarthy 2001; O'Hara 2001; Ciancio et al. 2006). In this context, the most common silvicultural prescription for management is the combined shelterwood and felling-coupe system, which is composed of several stages: spruce stands at the age of 40-60 years are slightly opened up homogeneously over the whole stand area to promote natural regeneration and stability (shelterwood-coupe). Above these patches of forthcoming regeneration, the

canopy is opened up continuously or removed completely in one pass (femel-coupe) and missing tree species are planted. In the areas between the regeneration slits, only very cautious interventions (target diameter harvest) take place in order to maintain the volume of the remaining stand between 400 and 500 m³ha⁻¹ depending on site conditions. With the progressing regeneration of all three species, the regeneration slits are gradually extended by harvesting trees at the edges during the femel-coupe. By removing the over-storey step by step, 40–60 years after the first harvest, the whole stand area is regenerated as the regeneration patches grow together. Except for the initial shelterwood-coupe, any remaining thinning operations always only take place on every second cable line. After two operations on the same cable lines, the cable lines are changed. Thus, only half of the area is worked at a time and the creation and expansion of the regeneration slits takes place at different times. This procedure ensures that a heterogeneous vertical structure is created and that the cable lines can also be used over long periods of time. In order to validate the state-of-the-art silvicultural scenarios, the evaluation of multiple criteria was also applied to conventional management methods, such as strip clearcut and gap-coupe (Mosandl 1984; Tab. 2.4).

All simulations for stand development and timber production were carried out with the single-tree, distance-dependent forest growth simulator, SILVA 2.3 (Pretzsch and Kahn 1996; Pretzsch et al. 2002). Due to the partly stochastic character of SILVA, every simulation run can, despite identical starting conditions and treatment programmes, produce different results. Since the regeneration phase in particular provides crucial information for forest transformation concepts, SILVA also includes a regeneration module. The 5-year simulation steps were carried out 30 times for runs of 150 years. This means that the development of an entire forest life-cycle could be simulated. In addition, the ‘silvicultural treatments’ (e.g. gap, femel and shelterwood-coupe) and ‘creation of infrastructures’, (e.g. cable crane and cable lines) modules were supplemented for the present comparison of different silvicultural scenarios. Results of the wood-sorting were calculated using the SorSim program (Lemm et al. 2013). Cable lines, femel gaps and planting were created outside the simulator with the R software (R Core Team 2018). The stored carbon quantities in wood products, and the substitution of stored carbon by the energetic use of biomass, were calculated using a Harvested Wood Products Model (HWP) from Klein et al. (2013). Comparisons of the results of the different silvicultural scenarios were made using R (R Core Team 2018), specifically employing the dplyr package (Wickham et al. 2018).

Tab. 2.4: Simulation scenarios, their short description and references for detailed information on the simulated forest transformation scenarios.

Code	Scenario	Brief description	Regeneration	Reference
DN	Do-nothing with natural regeneration	No treatment	Natural regeneration	
G	Gap-coupes with planting	Clearance of gaps with a radius of 30m. Change of cable lines every 20 years. First operation at stand age of 35 years. Afterwards, the stand is cleared in strips.	Planting of fir and beech in gaps + natural regeneration	Mosandl, 1984
SH1	Shelterwood-coupes with natural regeneration	Partial clearance of slit-like patchy gaps (width: 30, length:25). Change of cable lines every 20 years. First operation at stand age of 35 years.	Natural regeneration	Bayerische Staatsforsten AöR (2018)
SH2	Shelterwood-coupes with planting	Partial clearance of slit-like patchy gaps (width: 30, length:25). Change of cable lines every 20 years. First operation at stand age of 35 years.	Planting of fir and beech under shelter in the patchy gaps + natural regeneration	Bayerische Staatsforsten AöR (2018)
SL1	Slit-coupes with natural regeneration	Clearance of slit-like patchy gaps (width: 15m, length: 30m). Change of cable lines every 20 years. First operation at stand age of 35 years.	Natural regeneration	Streit et al. (2009); Bayerische Staatsforsten AöR (2018)
SL2	Slit-coupes with planting	Clearance of slit-like patchy gaps (width: 15m, length: 30m). Change of cable lines every 20 years. First operation at stand age of 35 years.	Planting of fir and beech in the slits + natural regeneration	Streit et al. (2009); Bayerische Staatsforsten AöR (2018)
SC	Strip clearcutting with natural regeneration	Clearance of the stand in strips. Strip width 30m. Distance between the strips 120m. First intervention at age 80. Interval between interventions 20 years.	Natural regeneration	

The simulation results were finally compared with results from long-term experimental plots. For the validation, data from two sets of long-term experimental plots were used. On the one hand, data from 22 mixed mountain forests long-term experimental plots comprising beech, spruce and fir at elevations of between 850 and 1240 m a.s.l. in the catchment area of the Northern Limestone Alps in Bavaria (Southern Germany) were used. These plots were established in order to investigate the influence of different silvicultural treatments (femel-shelterwood-coup) on the regeneration dynamics and volume increment and were established in the 1970s (Pretzsch et al. 2015). Moreover, the results were compared with data from 14

long-term experimental pure spruce plots on high-performance sites in southern Bavaria (Röhle 1995).

To engage in differentiated discussions on all transformation scenarios (Tab. 2.4) five criteria (forest growth, economics, carbon sequestration, (stand) stability and biodiversity) were defined. The results of each silvicultural scenario and criterion are displayed scaled (best: 1, worst: 0; Koschke et al. 2012; Knoke et al. 2014). Each criterion is, in turn, made up of different factors (see Tab. 2.5). The efficiency of each scenario is quantified by summing the score of each of the studied criterion. To provide a measure of stability between the categories, the standard deviation (sd) for each forest transformation scenario was also determined.

Tab. 2.5: Overview of the categories defined for the comparison of the different forest transformation scenarios and their factors. Each factor was included in the evaluation of the respective category without weighting.

Forest growth	Economics (Net present value)	Carbon sequestration	Stability	Biodiversity (Number of species)
<ul style="list-style-type: none"> • Total productivity • Mortality • Standard deviation of tree heights 	<ul style="list-style-type: none"> • 1 % • 2 % • 3 % 	<ul style="list-style-type: none"> • In-situ + ex-situ in wood products + substitutions of fossil fuels 	<ul style="list-style-type: none"> • Survival probability of spruce * potential damaged timber • Spruce proportion in the last simulation period 	<ul style="list-style-type: none"> • Flora • Fauna • Fungi

Forest growth: The criterion forest growth consists of the factor's total productivity, mortality over the entire simulation period and the standard deviation of tree heights as a proxy for a shelter in the event of a disturbance. If the overstory is lost to disturbances the understory can immediately utilize the increasingly available resources such as light, water and nutrients, and take over important forest functions. In order to include the temporal component, the time since simulation start was classified into five classes (25 ± 10 , 50 ± 10 , 75 ± 10 , 100 ± 10 and 125 ± 10 years) and averages of each class were obtained. Each of the five values was included in the evaluation without weighting.

Economics: The harvested trees were graded after each simulation period with the help of SorSim (Lemm et al. 2013) without the dead wood fraction. The revenues were calculated using averaged timber prices provided by the Bavarian State Institute of Forestry (LWF) for 2010-2015. Harvesting costs were calculated at 48 € m^{-3} , planting costs at 6400 € ha^{-1} for beech, 1600 € ha^{-1} for spruce and 2700 € ha^{-1} for fir. The net present value (NPV) is calculated using three

different discount rates: 1%, 2% and 3%. The presented results include the financial value of the standing timber at the end of the simulation period.

Carbon sequestration: In order to calculate the stored in-situ carbon quantities of the simulation results, both the above-ground biomass, using species-specific biomass formulae (Pretzsch et al. 2014), as well as the underground biomass, with a root factor (root/shoot) according to Offenthaler and Hochbichler (2006), were estimated. The ex-situ carbon content in wood products and the substitution quantities resulting from bioenergy use (wood combustion) were calculated using a Harvested Wood Products Model (HWP) from Klein et al. (2013). In presenting the C sequestration potential of forest management on a per hectare basis, the levelisation approach was used, where the periodic C flows were summed up and discounted with an assumed social interest rate of 2% (e.g. Hoen and Solberg, 1994).

Biodiversity: The number of species of (i) flora, (ii) fauna and (iii) fungi were selected as indicators for a non-wood forest function. In order to determine the number of species of flora, fauna and fungi, each of the 30 stands was divided into 1000 m² grids. According to Zenner et al. (2016), each raster was then assigned to one of nine forest successional stages (gap, regeneration, establishment, early optimum, mid-optimum, late optimum, plenter, terminal and decay). Finally, based on the results of Hilmers et al. (2018), the number of species of flora (higher plants, lichen and mosses), fauna (phytophagous and pollinating arthropods, vertebrates and invertebrates feeding on animal tissue, species feeding on dead tissue, and species depending on dead wood during their life cycle) and fungi was able to be assigned to the individual forest successional stages. The species numbers of the entire 2 ha plots consist of the average of all 1000 m² large squares. Standard deviations were also calculated again using the average of each of the five classes (see above).

Stability: The calculations of the stability of the stand against natural disturbances were calculated on the basis of a model developed by Roessiger et al. (2013). In a mixed stand, the survival probability of the spruce is calculated by means of a Weibull function (Weibull 1951) depending on the percentage of spruce and age. The probabilities of beech and fir survival were assumed to be independent of the percentage of spruce (Roessiger et al. 2013). Survival probabilities were calculated at five different simulation points in time (see above). These survival probabilities were then multiplied by the potential amount of damaged wood volume (all spruce trees higher than 66% of the mean height of the 100 thickest spruce trees). They were then included in the valuation as separate factors without weighting. Assuming that stable stands at the end of the simulation could either appear due to the young age of the spruce, or

due to a low proportion of spruce, the share of spruce of the total stand in the last simulation period was used as an additional factor. Since those stands with a high proportion of spruce and young age will become unstable again in the future, those stands with a lower proportion of spruce were rated as better.

Biodiversity along temperate forest succession (Article III)

Plots were classified to successional stages by combining the decision trees of Zenner et al. (2016) and Tabaku (2000; Fig. 2.6). These decision trees incorporate information on canopy projection area, maximum diameter at breast height (DBH), proportion of dead wood, normalized quartile of the DBH, and the cover and height of the regeneration layer. The combination of these two protocols was necessary as Zenner et al. (2016) only considered trees with DBH >7 cm, and Tabaku (2000) explicitly also included regeneration and establishment stages. The combined decision tree was used to identify nine successional stages on 287 plots, i.e., gap, regeneration, establishment, early-optimum, mid-optimum, late-optimum, plenter, terminal and decay stages (Fig. 1.2).

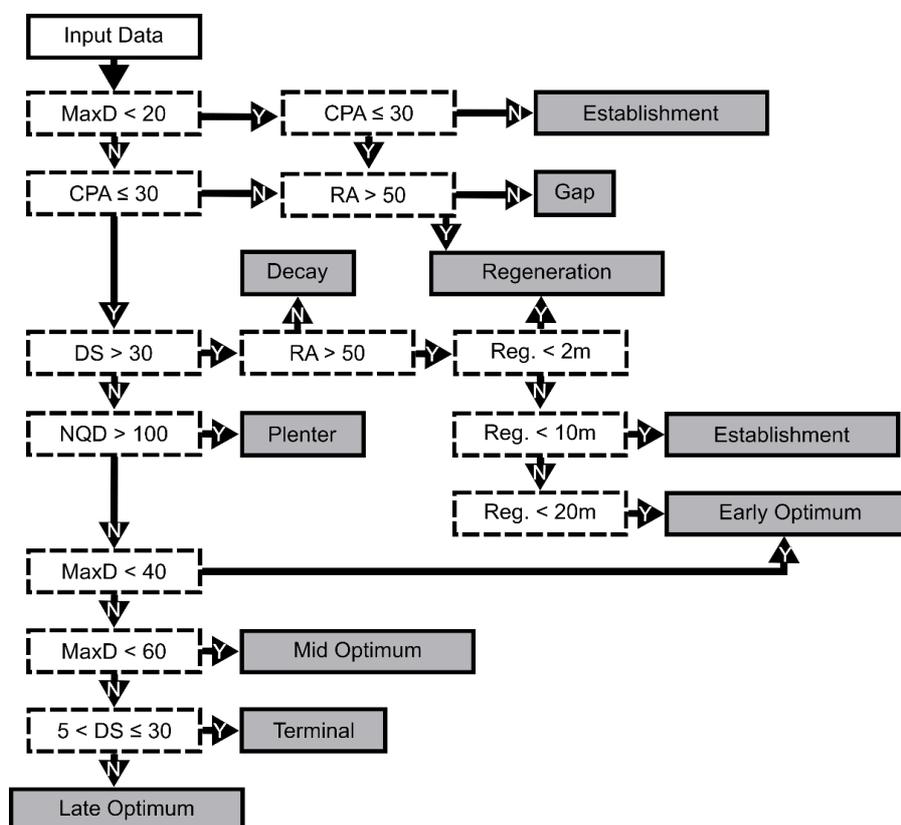


Fig. 2.6: Decision tree for assigning forest successional stages using a modified classification protocol adapted from Tabaku (2000) and Zenner et al. (2016). Each primary attribute is evaluated as a dichotomy, which assigns 1000 m² circular plots differentially if the criterion is met (Y) or not met (N). CPA, canopy projection area [%]; maxD, maximum diameter at breast height (DBH) [cm]; DS, proportion of dead wood [%]; RA, regeneration area [%]; HR, regeneration height [m]; NQD, normalized quartile of DBH. From Hilmers et al. (2018).

2.2.1 Statistical analyses

All statistical analyses in this thesis were performed in the free statistical software ‘R’ (www.r-project.org), using additional statistical add-on packages for ‘R’ as needed and as described below.

Productivity of mixed mountain forests (Article I)

To test the influence of the variables described in chapter 2.1.2 on the productivity of mixed mountain forests, a generalized additive mixed model (GAMM) with a Gaussian distribution was used using the package mgcv (Wood, 2011). The model included the periodic annual volume increment of the mixed forest plots as a dependent variable. By using a random factor (plot) as a grouping factor no pairs were taken into account twice. To account for potential autocorrelations, plot geographical location was treated as a two-dimensional non-linear smoother. Since climate change led to changes of the mean annual temperatures at same elevations (see Fig. 2.2a), the combination of elevation and mean annual temperature was also integrated into the model as a two-dimensional smoother. If the term of the calendar year nevertheless remained significant, it was assumed that other factors besides the considered climate variables, such as late frost events, nitrogen inputs etc., influenced stand growth (cf. Pretzsch et al., 2014). The determination of the degrees of freedom of the nonparametric terms is part of the fitting process (Wood, 2011; Package mgcv). In order to investigate whether the productivity of the individual species (beech, spruce and fir) has changed in recent decades, the species-specific stand values were extrapolated to one hectare. The species shares at the beginning of each period were used as a scaling factor, which were calculated from the transformed SDI values. Again, a generalized additive mixed model (GAMM) was applied by species with the scaled periodic annual volume increment as the dependent variable and a random factor (plot) was used as the grouping factor. The model selection from the extensive models was carried out with a principal component analysis (PCA) and further supported by testing all possible mathematical models using all combinations of variables by Akaike information criterion (AIC; Barton, 2018). Explanatory variables, which were used as factors in the model, were tested for significance using the R-package multcomp (Hothorn et al., 2016).

Biodiversity along temperate forest succession (Article III)

To test the influence of successional stage on the diversity of the 33 functional groups in the six trophic levels (Tab. 2.3), generalized linear mixed models with a Poisson distribution were calculated. Either the number of species sampled on each plot (Gotelli & Colwell 2001) or abundances (i.e., the number of all sampled individuals of a taxon) as response variables was modelled, with successional stage as the predictor. To test for regular trends across successional stages using linear and quadratic contrasts, the factor forest successional stage was coded as ordered. Elevation and soil characteristics were included as additional predictor to control for confounding effects of the local conditions. To account for the overdispersion frequently observed in models of count data, an observation-level random effect (i.e., the plot) was included in all models (Harrison 2014). First, the overall effect (U- or humpshaped response) of the forest successional stage modelled with linear and quadratic contrasts on the number of species or abundances of all 33 functional groups was calculated. Whether differences in the number of species are in accordance with the predictions of the *more-individuals hypothesis* or the *habitat heterogeneity hypothesis* was tested by controlling for abundances in a subsequent model using the number of species as response variable, while accounting for abundances. Second, the models were used to predict the number of species in each group while keeping elevation and soil parameters constant. Since forest successional stages do not always proceed in an orderly manner in reality (e.g., due to storms or bark beetle infestation), the successional stage was incorporated as an unordered factor in this case. Predictors were tested for significance using a general linear hypothesis testing framework as implemented in the multcomp r package version 1.4-6 (Hothorn et al. 2016).

At the community level, multiple-site dissimilarities for taxonomic groups were calculated using the Sørensen dissimilarity index and partitioned the thus derived β -diversity into its additive turnover and nestedness components as implemented in the betapart r package version 1.4-1 (Baselga et al. 2017). To quantify the contribution of β -diversity among plots and among stages of forest succession to the γ -diversity in the study system, additive diversity partitioning as implemented in the r package vegan, version 2.4-3 (Oksanen et al., 2017) was used. For a statistical test of the potential effects of forest succession on assemblages, multivariate analyses of variance using distance matrices based on presence–absence data were performed, applying the adonis function with 999 permutations as implemented in the vegan package. These analyses considered taxonomic groups with sufficiently high numbers of species not separated into trophic levels (i.e., excluding taxonomic groups with ≤ 30 species).

Changes in species composition of these taxa along forest succession were illustrated using partial correspondence analyses conditioned on the effects of elevation and soil. Furthermore, the number of unique species for early (gap, regeneration and establishment), mid (early, mid and late optimum), and late (plenter, terminal and decay) stages of forest succession were calculated to evaluate the importance of individual stages for certain species of the taxa under study. In this case, a fixed number of plots in the early, mid and late stages were resampled for each taxon in this thesis and the number of species unique to these forest successional stages was calculated. The fixed number of plots was defined as half the number of plots of the rarest stage for each taxon. The resampling procedure was randomly repeated 1,000 times, and the mean number of unique species per forest succession phase was calculated.

3 Results

3.1 Productivity of mixed mountain forests (Article I)

Investigating 60 long-term experimental plots the productivity of mixed beech-spruce-fir mountain forests was analysed across a variety of European mountain areas in a standardized way for the first time (Hilmers et al. 2019). The results show that despite a significant increase in annual mean temperature and stable precipitation, the average productivity of European mixed mountain forests has not changed significantly over the last decades (Fig. 3.1). The studied mixed mountain forests showed constant volume growth during the last 30 years, amounting to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$.

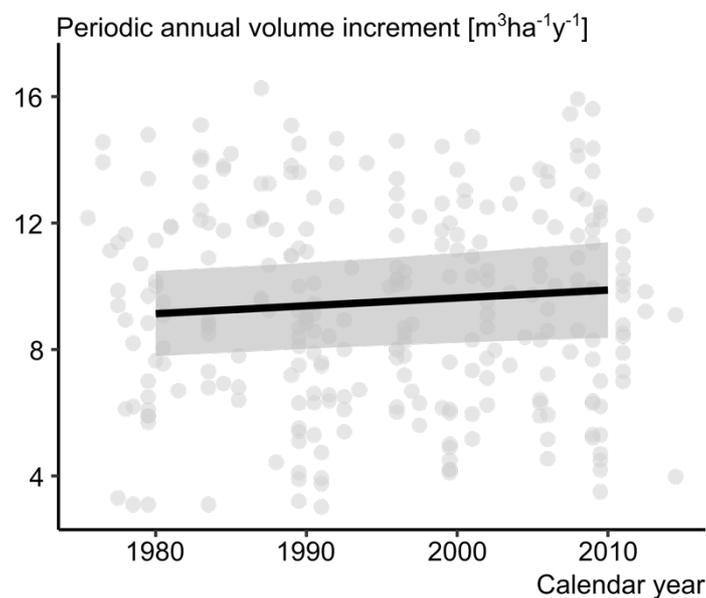


Fig. 3.1: Periodic annual volume increment of the investigated long-term experimental plots of beech, spruce and fir over the calendar year. The annual volume increment was predicted using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. Predictor variables were the volume of the remaining stand, the interaction between latitude and longitude, the interaction between elevation and mean annual temperature, the dominant parental material and the species proportions of the three tree species involved, beech, spruce and fir. For the predictions, the prediction variables were kept constant at the mean value. The grey area indicates the standard error. From Hilmers et al. (2019).

Thus, climate change seems to have no impact on the productivity of mixed mountain forests in Europe, at least within the time span of this thesis. At the tree species level, however, significant changes in the growth dynamics of the three species were found. Each species (beech, spruce and fir) reacted to climate change in a different way (Fig. 3.2). The PAI of spruce

decreased significantly while the PAI of fir increased significantly. The productivity of beech remained constant over the last 30 years.

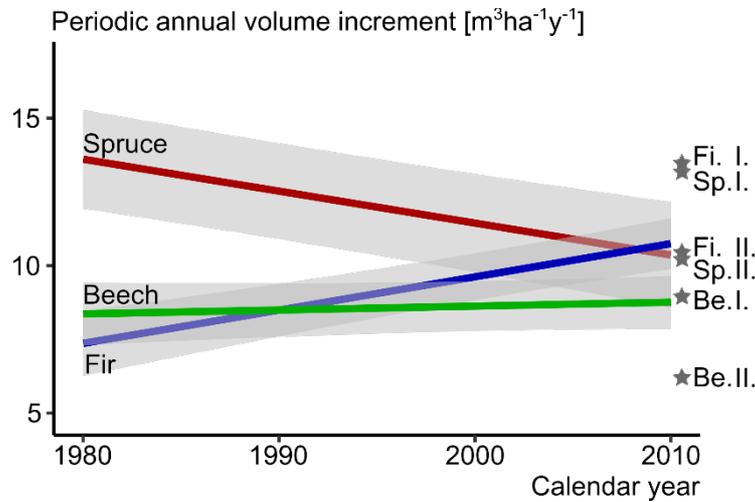


Fig. 3.2: Periodic annual volume increment over the calendar year of the tree species beech, spruce and fir in the long-term experimental forest plots. The periodic annual volume increment of the three tree species was scaled using the species share derived from SDI proportions. Estimation was done using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. For the prediction, the predictor variables were kept constant at the mean value. The grey area indicates the standard error. Stars show the mean annual volume increment of the first (I.) and second (II.) yield classes of the three tree species spruce (Sp.), fir (Fi.) and beech (Be.) at age 100 according to the yield tables of Hausser, (1956), von Guttenberg, (1915) and Wiedemann, (1949). From Hilmers et al. (2019).

Thus, climate change has led to a shift in the competitive strength of the involved tree species. Furthermore, in the case of spruce, a declining productivity with warming temperature trends at higher elevations was observed. The productivity of fir increases with warming temperature trends at high elevations. Moreover, the calendar year had a negative effect for spruce and positive for fir, suggesting that other changing factors different than mean temperature are strengthening their productivity long term trends.

3.2 Transformation of pure spruce to mixed mountain forests (Article II)

A possible option to improve the stability and resilience of stands in mountain areas is the transformation of destabilized secondary pure spruce stands. It was shown that it might be possible to transform secondary pure spruce stands to stable, uneven-aged, mixed mountain forests at equilibrium with five of the seven scenarios (Fig. 3.3).

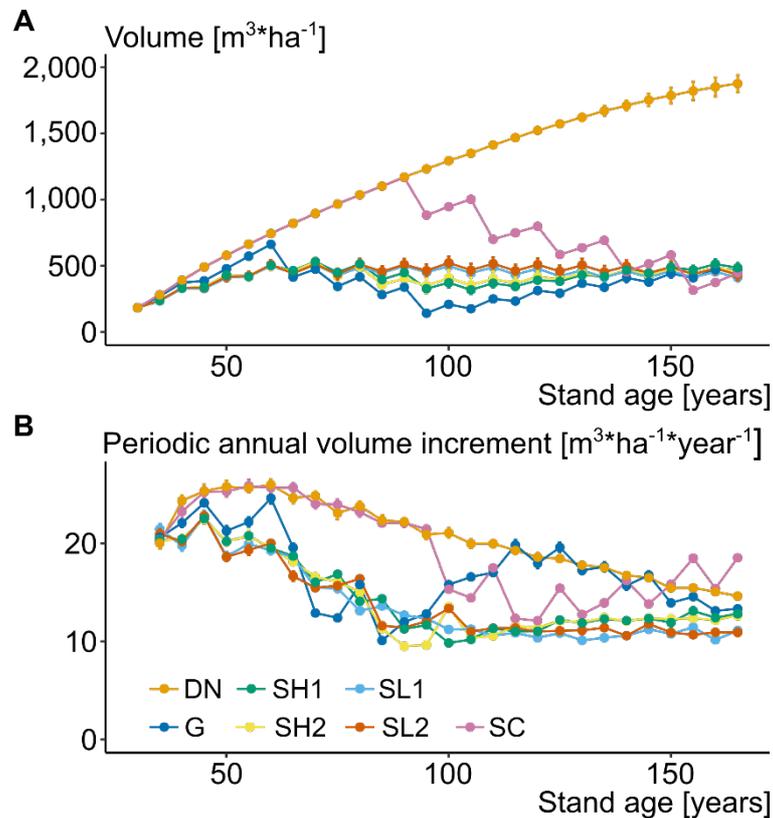


Fig. 3.3: Volume of the remaining stand in $\text{m}^3 \cdot \text{ha}^{-1}$ (A) and current annual volume increment in $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (B) with standard errors, resulting from different tree growth between 30 simulations, above stand age of all the simulated transformation scenarios. DN, do-nothing scenario; G, Gap-coupe with planting of beech and fir; SH1, shelterwood-coupe with natural regeneration; SH2, shelterwood-coupe with planting of fir and beech; SL1, slit-coupe with natural regeneration; SL2, slit-coupe with planting of fir and beech; SC, strip clearcutting with natural regeneration. See Tab. 2.4 for a detailed description of the different scenarios.

It is also these five scenarios (gap, shelterwood, slit, with planting of fir and beech and with natural regeneration) which are expected to maintain these structures of balanced age and tree species mixture in the long-term with regular forest interventions. The evaluation of multiple criteria allows the seven scenarios to be divided into three groups (Fig. 3.4). The do-nothing scenario only achieves the highest score in the category of biodiversity. The shelterwood and

strip clearcut scenarios show highly divergent scores, while the slit and gap scenarios achieved high scores in all categories.

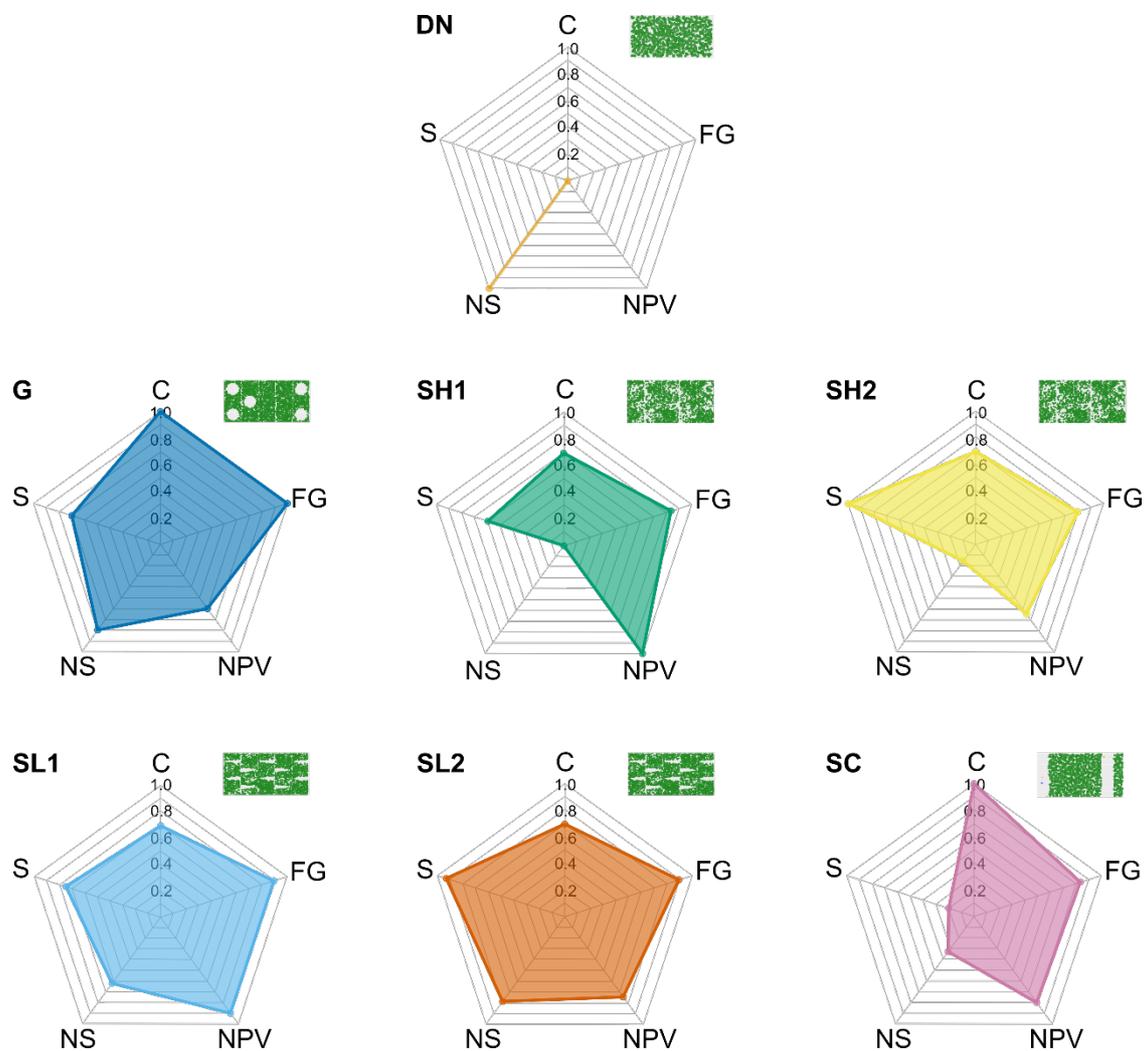


Fig. 3.4: Radarchart of the evaluation of multiple criteria. FG, forest growth; NPV, net present value; C, carbon sequestration; S, stability; NS, number of species. The scaled results of the respective factors of each criterion are shown (see Tab. 2.5 for explanation). Results were scaled between 0 and 1. Results evaluated with 1 represent the best scenario in comparison to the other scenarios. Categories rated 0 show the worst scenario. DN, do-nothing scenario; G, Gap-coupe with planting of beech and fir; SH1, shelterwood-coupe with natural regeneration; SH2, shelterwood-coupe with planting of fir and beech; SL1, slit-coupe with natural regeneration; SL2, slit-coupe with planting of fir and beech; SC, strip clearcutting with natural regeneration. See Tab. 2.4 for a detailed description of the different scenarios.

3.3 Biodiversity along temperate forest succession (Article III)

The results showed that the number of species of most taxa largely follow a U-shaped pattern along forest succession (Fig. 3.5). However, saprotrophic organisms did not show a hump-shaped response to forest succession as expected, and saproxylic fungi showed a hump-shaped response and not a U-shaped response to forest succession.

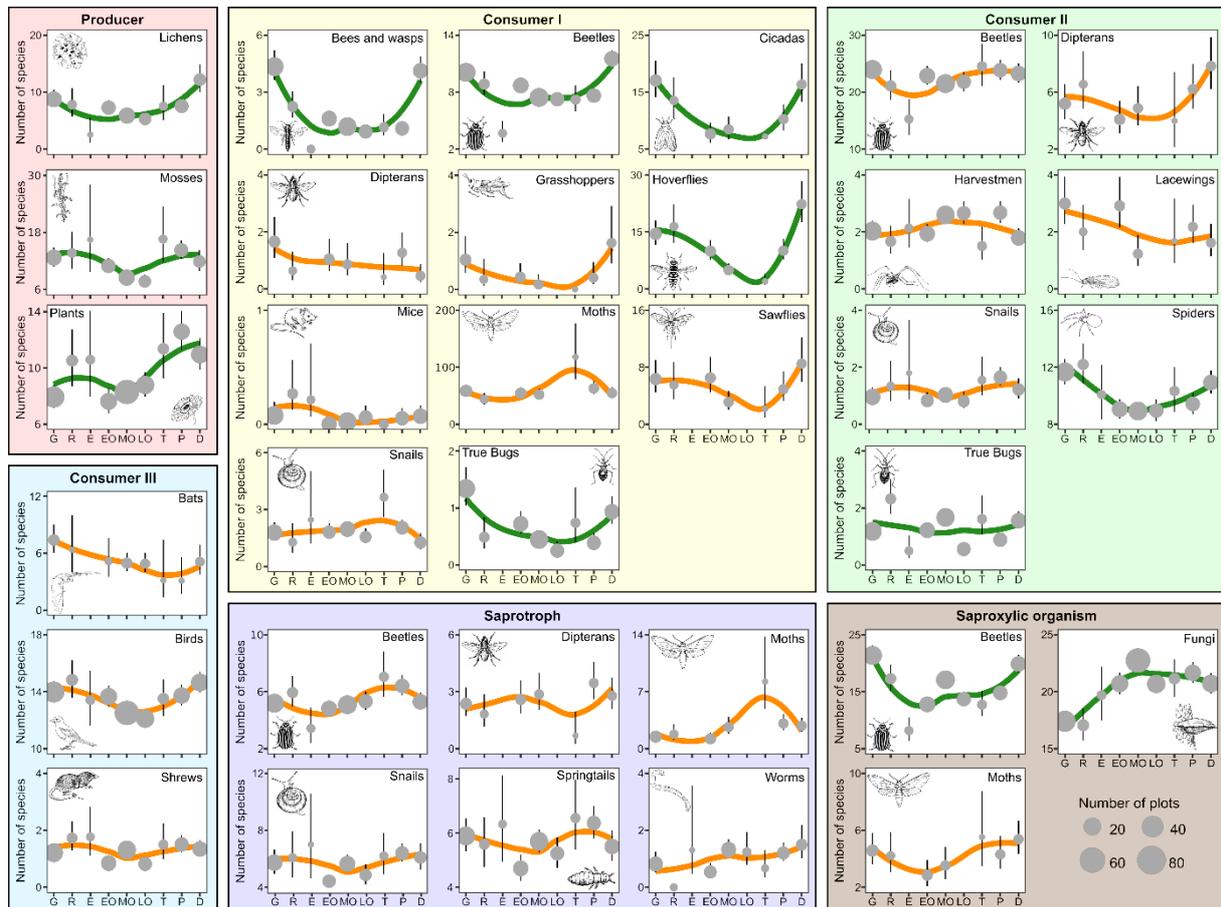


Fig. 3.5: Variation in the number of species of 33 functional groups with stages of forest succession. The number of species was predicted using a generalized linear mixed model with Poisson error and an observation-level random effect. Predictor variables were the forest successional stage as an unordered factor, elevation and soil parameters. For the predictions, elevation (800 m. a.s.l.) and soil parameters (mean value of the soil characteristics; PC1) were kept constant. Lines were generated by fitting a loess curve. Green lines indicate taxonomic groups whose number of species is significantly affected by the forest successional stage; orange lines indicate taxonomic groups whose number of species is not significantly affected by forest successional stage. Black bars indicate the SE within each successional stage. Note that data were not available for some taxonomic groups in some successional stages. Abbreviations are explained in Fig. 1.2.

For most groups, the effect of forest succession was strongly affected by the abundances of the respective groups, which provides strong support for the more-individuals hypothesis. However, a response of several taxa to forest succession was found even after controlling for the effect of abundance. Overall, the diversity of plants, animals and fungi showed diverging patterns along forest succession, with peak diversity values in early and late stages (Fig. 3.6).

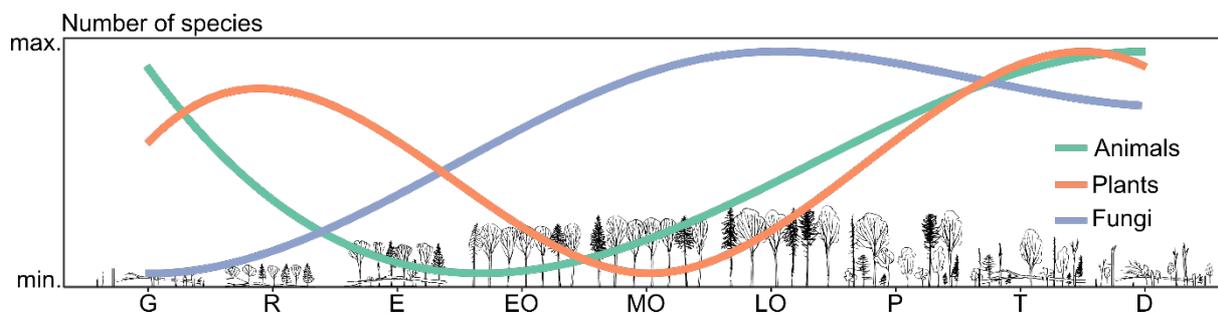


Fig. 3.6: Normalized sum of predicted number of species along forest succession for the three kingdoms animals, plants and fungi. Lines were generated by fitting a loess curve. Abbreviations are explained in Fig. 1.2. From Hilmers et al. (2018).

Highest rates of species turnover were found among successional stages and the most similar assemblages were found in early and late successional stages (open canopies; Fig. 3.7). Most unique species were found in the early and late stages of forest succession.

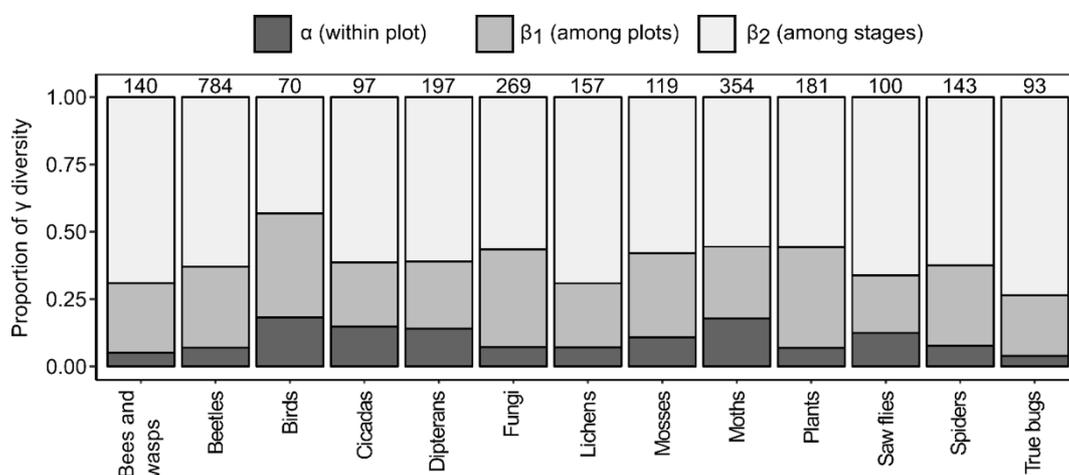


Fig. 3.7: Proportion of γ -diversity due to α -diversity and β -diversity among plots and among stages of forest succession according to additive diversity partitioning. Results are based on presence–absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 30 species). γ -Diversity for taxonomic groups is denoted above the respective bar. From Hilmers et al. (2018).

3.4 Summarising results

In terms of stand growth, the results of this thesis showed that mixed-mountain forest ecosystems are rather resilient against disturbances such as acid deposition, climate warming and ozone. As growth reductions of one of the three species were compensated by a growth increase of the others the stand productivity of mixed mountain forests of beech, spruce and fir in total has hardly changed over the last 30 years (Article I; Hilmers et al. 2019; Appendix A).

Based on these results, there is little reason not to transform destabilised secondary spruce stands in mountain areas to these mixed forests of beech, spruce and fir. The results of this thesis showed that it is possible, by means of several trajectories, to return destabilised forests to sustainable and stable systems. A transformation is realistic, even if sophisticated silvicultural concepts are not strictly pursued (Article II; Appendix B).

In addition to the increased resistance and resilience, these uneven-aged mixed forests also show high numbers of species. However, highest number of species were found in the early and very late stages of forest succession and many of the investigated species occur exclusively in these successional stages. Although it is particularly these stages of forest succession which are strongly underrepresented in the forests of Central Europe, the results showed that high biodiversity values cannot be achieved by set-aside forests alone, but also by active management if a certain amount of deadwood remains in the forest. Furthermore, it was shown that also intermediate successional stages support a wide variety of taxa and communities. and highest rates of species turnover were found between the different successional stages (Article III; Hilmers et al. 2018; Appendix C).

According to the findings of this thesis it might be an option to transform destabilised secondary spruce stands in mountain areas to uneven-aged mixed forests at equilibrium in order to suffer fewer human casualties and economic damage in the future. In order to increase biodiversity at the landscape level, however, in addition to these mixed forests at equilibrium, all other stages of forest succession should also be represented in a balanced proportion.

4 Discussion

4.1 Productivity of mixed mountain forests (Article I)

European mixed mountain forests have so far been stable in terms of volume growth in relation to climate change. The reduction of volume increment of one species was compensated by higher volume increments of another species. Although they grow under the same conditions, spruce and fir have shown remarkably different growth patterns over the last 30 years. While fir has responded positively to recent warming, spruce productivity has declined significantly, suggesting that at constant rainfall, fir is less susceptible to warmer conditions than spruce. There is some support for the use of mixed forests as a strategy for adapting to climate change. It was shown that a more diverse tree species composition can help to compensate to some extent for the effects of climatic and anthropogenic changes.

European beech

Contrary to expectations, the results show that beech productivity did not change significantly in recent decades. Due to the warming in the last century and especially the most recent decades (Luterbacher et al. 2004; Büntgen et al. 2011) and the simultaneously high amount of precipitation, especially at higher elevations, the productivity of beech is expected to increase (cf. Tegel et al. 2014; Aertsens et al. 2014). This thesis confirms that the productivity of beech in mixed mountain forests remained stable or increased slightly, albeit not significantly, throughout Europe between 1980 and 2010. This is consistent with published measurements (Pretzsch et al. 2014; Tognetti et al. 2014; Bosela et al. 2016b) and model simulations (Hlásny et al. 2011). On the other hand, the results contradict the study of Dittmar et al. (2003), who documented a decline of radial growth of beech at higher elevations at Central European scale, and Bosela et al. (2018) who, corresponding to a significant warming trend from 1990-2010, found an average decline in beech growth in Continental Europe over the last three decades. However, as trends in productivity on the stand level also depend on stand structure (e.g. density and size distribution) it is not possible to infer the stand level productivity trends from tree level trends. Nevertheless, beech faces challenging environmental changes, especially in mountainous areas. Environmental changes in the Alpine regions are mainly characterised by acid and nitrogen deposits, and O₃ pollution (Brang 1998; Flückiger and Braun 1999; Smidt and Herman 2004). Muzika et al. (2004), for example, found significant negative correlations between air pollutants (O₃, NO₂ and SO₂) and the growth of beech and spruce in the Carpathian Mountains. In addition, there are natural influences due to climate change such as late frost events and drought stress (Dittmar et al. 2003; Jump et al. 2006; Bontemps et al. 2009), as well

as biotic diseases, such as fungal infestation (Cherubini et al. 2002). Furthermore, Dittmar and Elling (2007) found increasing crown transparency and reduced vitality in recent years based on long-term crown condition surveys of beech trees in mixed mountain forests of the Bavarian Alps. Although beech was exposed to these negative effects on tree growth, its productivity on stand level has remained unchanged in recent decades.

Silver fir

Fir exhibited accelerating growth rates during the last few years. This is remarkable, as fir experienced a strong decline in growth across Europe caused by sulphur dioxide emissions in the years 1970-1990 (Diaci et al. 2011; Uhl et al. 2013; Büntgen et al. 2014; Čavlović et al. 2015) or low summer temperatures in the 1960s and 1970s (Bosela et al. 2016a, 2018). This thesis might provide additional evidence for this event, as the productivity of fir was the lowest among the analysed tree species at the beginning of the study period. Efforts to reduce emissions since the 1980s, combined with a warmer, but not drier, climate (Diaci et al. 2011; Uhl et al. 2013; Büntgen et al. 2014), have probably enabled the significant increase in fir productivity. These results are in line with studies by Bosela et al. (2018) and Büntgen et al. (2014), who also demonstrated an unprecedented increase in productivity in Central Europe's fir stands. However, a recent Europe-wide study on the growth of fir throughout the Holocene (Büntgen et al. 2014) describes increasing radial growth in the Italian Alps and the Apennines until the turn of the millennium, but not beyond. Bosela et al. (2018) showed that fir populations in the southern parts of the Alps may have recently experienced growth limitation due to drought. Seemingly, fir populations close to the Mediterranean distribution limit already show a drought-induced growth depression, which will become even more critical in a warmer and drier future. However, there are indications that the sensitivity of fir to drought stress decreases when mixed with beech (Lebourgeois et al. 2013; Metz et al. 2016; Vitali et al. 2017) or when the genetic diversity is high (Gazol and Camarero 2016).

Norway spruce

As shown in the present thesis and previous studies (e.g. Schöpfer et al. 1997; Uhl et al. 2013), the growth relation of spruce and fir in mixed mountain forests has changed significantly in recent decades. These results illustrate the importance of external factors on the competitive relationships between species and thus on their growth dynamics. With regard to resistance to emissions, spruce is mostly classified as particularly resistant, beech as less resistant, and fir as particularly sensitive (Rohmeder and von Schönborn 1965). This may explain the superior

productivity of spruce compared to fir in the 1980s. In the meantime, however, the reduction of the emission load and the recovery of fir have led to a direct improvement in fir's fitness and thus also an indirect improvement in the competitive relationship with spruce and beech (Elling et al. 2009; Uhl et al. 2013; Büntgen et al. 2014; Bosela et al. 2018). While the high PAI of spruce in the 1980s was presumably favoured by the growing depression of fir (by allocating more resources to spruce in mixed stands that were previously available to fir), the recovery of fir is highly likely to have an effect on spruce's growth behaviour. Spruce is - without human intervention - pushed back into its real niche by the resurgence of fir, which it held before the beginning of the emission load and weakening of fir (Uhl et al. 2013). A further explanation for the significant decrease in spruce productivity at the stand level is the vulnerability of spruce to increasing summer droughts (Lévesque et al. 2013; Zang et al. 2014), wind disturbances and bark beetle outbreaks.

Effects of mixing

A number of recent studies showed that species diversity has a positive effect on volume growth (Zhang et al. 2012; Toïgo et al. 2015). A higher number of species is also expected to mitigate the negative effects of extreme climatic events through higher growth resistance and resilience (Jucker et al. 2014; Metz et al. 2016; Gazol and Camarero 2016). Although this thesis cannot directly estimate the benefit of mixed stands of beech, spruce and fir in higher elevations, there are indications that the three tree species in mixed stands show no lower growth rates than monospecific pure stands. Other authors show significant increases in this mixture compared to monocultures. Pretzsch and Forrester (2017), for example, showed an average increase of 20 per cent in the productivity of mixed mountain forests compared to neighbouring pure stands. Mina et al. (2018) found that beech trees in temperate European mixed mountain forests generally benefit from the admixture of spruce and fir. Further studies on the mixing of at least two of the three species show, depending on site quality, clear increases in mixed stands of spruce and fir (Forrester et al. 2013; Forrester and Albrecht 2014) or beech and spruce (Pretzsch et al. 2010) compared to monospecific pure stands.

Nevertheless, the results clearly indicate that growth in a mixture does not shield the three species from the effects of long-term changes in environmental conditions. For example, it was shown that the PAI of spruce has declined significantly over the last three decades under a number of conditions in Europe. At the stand level, however, Europe's mixed mountain forests appear to be stable and it is possible to achieve risk diversification by mixing the three tree species. These results are in line with the results of Hartl-Meier et al. (2014a, b), who in their

study on mixed mountain forests in the Northern Limestone Alps and the Berchtesgaden Alps come to the conclusion that mixed mountain forests can adapt well to temperature increases caused by climate change and that there may be no change in tree species composition.

However, in the face of climate change and in order to fulfil the Paris climate agreement (UNFCCC 2015), there is currently a high pressure on these forests. In order to meet these challenges, it is particularly important to develop strategies to enhance the adaptation (resilience) and mitigation potential of these forests in the future.

4.2 Transformation of pure spruce to mixed mountain forests (Article II)

Forestry has been changing throughout its history in response to the changing needs of human populations and changing supplies of forest resources and values to satisfy these needs (Kimmins and Blanco 2011). Worldwide, there is a multitude of forests which have been destabilised during history. For example, the forests in Bangladesh or the temperate rainforests in Canada and the USA face similar challenges to the destabilised forests in the Alps of Europe resulting from the former salt-works supply. They are to be transformed to sustainable, stable but managed systems. The results of the thesis at hand showed that there are several equivalent trajectories to achieve these goals. Thus, the risk of failure if one does not strictly follow a sophisticated guideline is low.

Except for the do-nothing and strip clearcut scenarios, forest transformation might be possible with five of the seven scenarios. The newly introduced species (beech and fir) can be established by planting or natural regeneration after artificial disturbances such as shelterwood, slit or gap-coupes.

In their study on the transformation of even-aged to uneven-aged stands of Norway spruce, Hanewinkel and Pretzsch (2000) showed that a transformation is strongly dependent on the gap-size. They showed that regeneration can only be established from gap-sizes larger than 40 m in diameter. However, this study only includes the regeneration of spruce. This thesis demonstrates that smaller gap-sizes are sufficient if shade tolerant species are involved in the transformation process by planting or natural regeneration if potential mast trees are located nearby. The smaller interventions also have less impact on the periodical mean stem volume increment at the stand level. This is in line with Brunner et al. (2006) who demonstrated, based on silvicultural scenario modelling, a transformation of Norway spruce stands by under-planting with beech in a gradually opened stand of Norway spruce.

Regulation of the mixture could be accomplished in SILVA only by thinning crop trees at a very early age. However, in the long-run, the small-scale interventions of the slit-coupe scenarios might better support asynchronous forest dynamics than the other scenarios and thus support the forest's inherent adaptive mechanisms (Morin et al. 2014). In the do-nothing scenario, spruce remained dominant until the end of the simulation and the regeneration of fir and beech appeared only slowly. Suggestions by e.g. Drever et al. (2006) that unmanaged development might enable natural processes to restore the original species composition of the forests cannot be supported by the thesis at hand, at least not in the timespan of the simulation period. The slow rate of tree species change agrees with Schelhaas et al. (2015), who suggested that European forests are very inert and that altering their species composition requires a long time. Simulation results of Hlásny et al. (2017) in the Goat Backs mountain area of Slovakia also confirm these results. However, larger natural disturbances are to be expected in mountainous forests (Bircher et al. 2016), and the partial accumulation of the natural regeneration of non-spruce species is realistic (Buma and Wessman 2013). In all scenarios, climate change and disturbance-mediated support to tree species diversity should be considered as an opportunity for forest adaptation efforts in spruce-dominated stands. Embracing the structural and compositional diversity created by natural disturbances can make ecosystems more robust to future disturbance. Such a different perspective on natural disturbances can complement classical forest protection approaches, in that protection focuses on assets of high value in the landscape for which risks can be reduced efficiently, while resilience is fostered and natural disturbances are embraced in other parts of the landscape (Seidl 2014). In areas where the tree species composition has been strongly altered by past forest management, disturbances may facilitate the development of a more site-adapted species composition (Thom et al. 2017).

Long-term safeguarding of forest transformation

Although the slit and shelterwood scenarios reach steady-state conditions at the last 50 years of the simulation-runs, these structures can only be artificially maintained in their characteristic structures by continuous removal in the upper and middle layers. Without silvicultural interventions over a longer period of time, the upper and middle layers may become so dense that the regeneration layer no longer receives enough light, precipitates and the balanced age structure are lost (Pretzsch 2019). Anyway, as long as there are continuous silvicultural interventions, tree species compositions will remain stable due to the slit and shelterwood scenarios and will ensure the desired forest redevelopment in the long-term. The gap scenario also suggests that the transformation will be successful in the long-term. Although this scenario is, due to the higher amounts of harvested wood, less stable in terms of periodic annual increment over the entire simulation period, this scenario achieves a balanced tree species mix and age structure at the end of the simulation-runs. In terms of productivity, these stands, with a balanced age and tree species mixture, have the advantage of being more productive compared to neighbouring pure stands (Pretzsch et al. 2015) on the one hand, and, on the other hand, that a potential reduction in the volume increment of one species can be compensated for by higher volume increments of another species (Hilmers et al. 2019).

4.3 Biodiversity along temperate forest succession (Article III)

In Europe the majority of forests are currently of intermediate age, as a result of heavy exploitation during and after the first half of the 20th century (Vilén et al. 2012). Late stages of forest succession, such as the terminal and decay stages, are largely absent, as most forests are harvested before trees reach old age (Faustmann 1995). Similarly, early successional stages are kept as short as possible by planting trees (Parker et al. 2000) or employing silvicultural techniques that accelerate stand development (Dale et al. 2001).

However, disturbances can promote heterogeneity in forest landscapes especially in secondary pure spruce forests in mountain areas. They increase light availability and the amount of dead wood at the stand level, which is beneficial for many forest-dwelling species. Consequently, many species, including some important red-listed species, respond positively to disturbances (Beudert et al. 2015). In this thesis it was shown that the number of plant and animal species in disturbed forests equalled that in old-growth forests (Hilmers et al. 2018). Nonetheless, how disturbances will impact individual species strongly depends on the species'

habitat requirements and life history strategy, with both positive and negative effects being reported in the literature. It is also important to note that the largely positive effects of disturbances on biodiversity can be negated by salvage and sanitation logging activities for many species (Thorn et al. 2018).

Stages of forest succession

Although the youngest and oldest successional stages would appear to be different, they actually are almost the same because succession is cyclic. The generation of old trees decays contemporarily with the growth of a new generation. In this thesis, the difference between the youngest and oldest stages is in the 30% threshold of the canopy projection area. Nevertheless, the gap stage and the decay stage differ markedly as the canopy projection area in the gap stage is considerably lower than in the decay stage. Dead-wood volume is not included in the criteria for gaps and regeneration stages, although stands with low and high volumes of dead wood are dissimilar, especially for saproxylic species. In the study area, the forest successional stages establishment, late optimum and plenter were underrepresented due to forest history. This highlights an important limitation of a space-for-time approach as applied in this thesis, which inter alia assumes that the analysed stands have a consistent management and disturbance history (Dieler et al. 2017). Thus, particularly the results concerning these underrepresented stages should be interpreted with caution.

The LiDAR approach revealed advantages but also limitations in the classification of successional stages, namely the ability to capture canopy closure across large spatial scales but the difficulty in characterizing the understorey and downed dead wood. In this context, the results quantify the changes in biodiversity across forest succession and present a dynamic baseline for the monitoring of biodiversity change in temperate forests. Future changes (e.g. driven by changes in climate or land use), whether observed or projected, need to be considered in the light of the natural dynamics of forest succession, acknowledging that there are no static reference conditions for the diversity in temperate forests.

Ecology of taxa

Most taxa responded according to the predictions derived from the variation in critical resources across the stages of forest succession. The high number of species of producers in both the early and late successional stages is most likely driven by shifts in primary production from trees to herbs, mosses and lichens, which depends on sunlight reaching the forest floor (Zehetgruber et al. 2017). This U-shaped response increases the resource availability for phytophagous insects

(Bouget and Duelli 2004). Previous analyses in the study region have shown that the number of species of several arthropod groups increases with forest development from closed forest to open canopies (Müller et al. 2008). For arthropods, this is partly an effect of increased activity of ectotherms under the higher temperatures associated with open habitats. However, the results indicate that for consumer groups, the effect of forest succession on the number of species is not only driven by more individuals, but also reflects an increase in habitat heterogeneity. An increase in the abundance and number of species controlled for abundance of first-order consumers is frequently followed by an increase in the abundance of predators, such as spiders, beetles and birds, which results from bottom-up trophic interactions (Campbell and Donato 2014). However, it was found that although the amount of dead wood was high on the study plots in early stages of forest succession, this was not reflected in the number of species of wood-decaying (saproxylic) fungi. This is consistent with the more detailed analyses of Krah et al. (2018), which show that the mere amount of dead wood is a relatively poor predictor of the number of these fungal species. The number of fungal species might be driven more strongly by the host tree species, host size, dieback history and canopy openness than by the amount and heterogeneity of dead wood (Abrego and Salcedo 2013; Heilmann-Clausen et al. 2015; Krah et al. 2018).

High turnover rates between stands, as was shown in this thesis, can be driven by sampling effort, with higher turnover rates with lower sampling effort locally, but also can occur because of ecological differences between stands. The present thesis showed that species turnover along successional stages contributed most strongly to the overall γ -diversity. This indicates that for the promotion of forest diversity at the landscape scale, heterogeneity in forest successional stages is more important than within-stand heterogeneity, which is in accordance with the results of another recent multi-taxon analysis of forest diversity in Europe's temperate forests (Schall et al. 2017).

Implications for forest management

Based on the finding that both α -diversity and the number of unique species is highest in early and late stages of forest succession, it can be recommended that conservation efforts focus on these particular stages, which are currently underrepresented in Europe (Hilmers et al. 2018). Late successional stages cannot be produced artificially but have to develop naturally over long time periods (but see Speight, 1989 and Sebek et al., 2013 for techniques inducing premature senescence). α -diversity can be promoted in the short term by creating and maintaining early stages of succession, and this is an important option for ecosystem management (for

experimental evidence, see Sebek et al., 2015). Canopy openings are a frequent result of logging activities, but these openings often lack the dead-wood resources required by many saproxylic taxa (Heikkala et al. 2016). Based on that findings, it can be recommended that in silviculture, the canopy should be opened by, e.g. creating gaps, to increase the photosynthetically active radiation at the forest floor, and some dead wood should be retained on site. Because intermediate successional stages also support a wide variety of taxa and communities, especially plants, fungi and lichen, a comprehensive conservation strategy has to maintain all successional stages on the landscape. However, for the conservation of regional biodiversity in multifunctional forests in Europe, this would mean that the proportion of stands in early and late successional stages should be increased.

All the implications only apply to the system that was investigated, namely mixed mountain forests. However, more than half of Central Europe consists of mountain areas and most of the existing forests are concentrated there (CIPRA 2007). Moreover, other studies have shown similar results on the uniqueness of, e.g. the early successional stages (e.g. Jacobs et al. 2007; Tikkanen et al. 2007; Swanson et al. 2011), which suggests a further transferability of the results to other forests systems across Europe or temperate mountain forests of other continents.

5 Conclusion

Due to intrinsic limitation of low temperatures and short growing seasons, mountain forests, as in the Northern latitudes of Europe, are strongly affected by climate warming. According to the results of this thesis, European mixed mountain forests have so far been stable on stand level in terms of volume growth in relation to climate change. The reduction of volume increment of one species was compensated by higher volume increments of another species. Although they grow under the same conditions, spruce and fir have shown remarkably different growth patterns over the last 30 years. While fir has responded positively to recent warming, spruce productivity has declined significantly, suggesting that at constant rainfall, fir is less susceptible to warmer conditions than spruce. There is some support for the use of mixed forests as a strategy for adapting to climate change. It was shown that a more diverse tree species composition can help to compensate to some extent for the effects of climatic and anthropogenic changes. The productivity of the tree species involved in this forest system is subject to constant fluctuations. In order to maintain a stable system prepared for future changes a balanced mix of the three tree species is recommended. Even if maintaining regeneration and a good share of spruce, especially in the application of selective forestry, will be more difficult in the future. Silvicultural concepts should ensure the promotion of spruce on sites suitable for future climatic conditions while facilitating the establishment of other better adapted tree species where spruce might become at risk. In particular, the mixed mountain forests with high portions of Norway spruce, should be converted to more diverse stands by regulating the natural regeneration or by planting in favour of e.g. silver fir, beech or sycamore maple for stabilization of growth, productivity and other ecosystem services.

The results of the presented thesis show that continuous forest interventions can transform unstable secondary spruce stands in mountain areas into stable mixed mountain forests which are in a steady state in terms of stem diameter and tree species distribution. It was shown that it is possible, by means of several trajectories, to return destabilised forests to sustainable, stable but managed systems. Transformation success is realistic, even if sophisticated silvicultural concepts are not strictly pursued. In order to suffer fewer human casualties and less economic damage in the future, transformation efforts of destabilised forests should therefore be pursued worldwide.

Climate change and disturbance-mediated support to tree species diversity should be considered as an opportunity for forest adaptation efforts in spruce-dominated stands. On the example of the Bavarian Forest National Park – which has been strongly affected by bark beetle

disturbances over the past 25 years – it was shown that the number of plant and animal species in disturbed forests equalled that in old-growth forests. This thesis highlights the strong influence of forest succession on biodiversity and underline the importance of controlling for successional dynamics when assessing biodiversity change in response to external drivers such as climate change. Understanding the inherent changes in species diversity as forests develop provides an important baseline for assessing the effects of external drivers such as climate change. In the absence of such a dynamic baseline, observed changes in biodiversity that are simply the effect of forest dynamics could be easily misattributed to effects of climate change. Furthermore, understanding the variation in biodiversity over the entire course of succession could also provide a more comprehensive perspective on the effects of different management strategies on biodiversity.

6 Perspectives

Mixed mountain forests of beech, spruce and fir have existed in this composition for several centuries. In addition to the known aspects of complementarity, further research would be needed to clarify why these three tree species have existed together in this mixture for centuries without a clear winner or loser. The question of how the individual trees have reacted to stress events such as drought stress in the past and whether the reactions of the three participating tree species to these stress events have occurred synchronously or asynchronously remains unanswered.

However, the results of this thesis suggest that the tree species balance and growth stability due to tree species diversity may be compromised in future. Especially at lower elevations, where Norway spruce grew optimally in the past, drought may reduce its contribution to stand growth in the future. One additional reason for this may be the relative loss in competitiveness compared to silver fir and European beech, which are better adapted to drought. Future studies should investigate how these three species trade-off resources devoted to drought (future limiting factor) versus shade tolerance (main limiting factor over thousands of years), and how this trade-off may shift with ontogeny.

The long-term growth trajectories of Norway spruce in relation to silver fir and European beech suggest a relative advantage of fir and beech at the expense of spruce. The growth reduction of spruce in relation to fir and beech means a loss of fitness. It is expected that in the future beech will take a larger share of Europe's mixed mountain forests even at higher elevations. To date, however, it has only been analysed regionally limited how productive beech is in mixed-species stands compared to mono-specific stands in mountain

areas and how the individual tree growth of beech is in mono-specific versus mixed stands. It would also be highly relevant to analyse how beech growth in mountain areas will develop in the future under climate change. One hypothesis would be that beech growth will continue to increase under moderate climate change during the 21st century but will suffer with strong temperature increases and increasing drought frequency. Here it would be interesting to know to what extent these negative effects can be mitigated by tree species mixture.

The thesis shows possible paths that can be followed to transform secondary spruce stands in mountain areas to more stable mixed uneven-aged mountain forests at equilibrium. This steady-state condition is dependent on an exponentially decreasing stem distribution and can only be maintained by regular thinning operations. However, in order to develop long-term management plans and silvicultural guidelines for mountain forests future studies should further investigate how the three tree species involved, beech, spruce and fir, react to releases by thinning or disturbance events and how the volume increment of the three tree species is distributed among the different diameter classes at stand level. A hypothesis would be that the three tree species involved react differently to releases and grow differently in the different diameter classes, and the typical equilibrium curve is therefore also dependent on the tree species composition. If that is the case silvicultural guidelines need to account for regulating mixed species stands. However, to date it remains unanswered how interspecific interactions modify the stand dynamics of mixed and mono-specific stands. Most silvicultural guidelines apply for monocultures, ignoring interspecific interactions. They consider type, strength and frequency of thinning. For regulating mixed species stands, species interactions must be accounted for. Specifically, there is the need of spatial regulation of competition, temporal regulation of competition by temporal delay between establishment of cohorts, and density reduction beyond natural regeneration and competition resulting from overlap between generations. Models should be developed acknowledging these processes to establish guidelines on how to regulate stands continuously over the whole rotation period.

Furthermore, it is of high relevance to gain information about which forest structures are created by succession and forest growth processes influenced by climate change in mountain areas. A special focus should be given to the regeneration phase of forest stands, as the regeneration phase in particular provides valuable information on the later development of the stand. Forest growth simulators offer a good possibility to analyse such processes. However, forest growth simulators often lack spatially explicit, distance-dependent regeneration models. But only if the regeneration can already be reproduced spatially explicitly in the initial stage,

the long-term effect of initial structures on the later forest development can be analysed. While in the past the cause of heterogeneous forest structures was seen primarily in the differentiation phase of medium and old stands, it remains unclear to what extent the initial structures also generate variability (Homologous-precocity hypothesis, Donato et al. 2012). Questions of this kind are of great relevance for forestry practice and environmental policy, because they provide information on the extent to which the targeted complex heterogeneous forest can be achieved at all through uniform planting.

Regarding forest succession future studies could supplement chronosequence data with simulation approaches to more explicitly study long-term trajectories of forest succession. In turn, the comprehensive dataset compiled in this thesis could be linked to simulation model output in future studies, quantifying how future forest development (influenced by changing climate and disturbance regime) impacts biodiversity.

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Appendix

A Article I

Title: The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe.

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The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe

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Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), and silver fir (*Abies alba* Mill.) cover a total area of more than 10 million hectares in Europe. Due to altitudinal zoning, these forests are particularly vulnerable to climate change. However, as little is known about the long-term development of the productivity and the adaptation and mitigation potential of these forest systems in Europe, reliable information on productivity is required for sustainable forest management. Using generalized additive mixed models this study investigated 60 long-term experimental plots and provides information about the productivity of mixed mountain forests across a variety of European mountain areas in a standardized way for the first time. The average periodic annual volume increment (PAI) of these forests amounts to $9.3 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$. Despite a significant increase in annual mean temperature the PAI has not changed significantly over the last 30 years. However, at the species level, we found significant changes in the growth dynamics. While beech had a PAI of $8.2 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$ over the entire period (1980–2010), the PAI of spruce dropped significantly from 14.2 to $10.8 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$, and the PAI of fir rose significantly from 7.2 to $11.3 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$. Consequently, we observed stable stand volume increments in relation to climate change.

Introduction

Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), and silver fir (*Abies alba*

Mill.; hereinafter referred to as beech, spruce, and fir, respectively) at elevations between ~600–1 400 m above sea level cover an area of more than 10 million hectares in Europe (Brus *et al.*, 2012; EUFORGEN, 2017). More than half of Central Europe's

surface area consists of mountain areas, which is where most of the existing forests are concentrated (CIPRA, 2007). Mixed mountain forests are of high ecological and (socio-) economic importance in Central and Eastern Europe due to their provision of various ecosystem goods and services (e.g. Ellenberg, 1988; Pretzsch *et al.*, 2015; Mina *et al.*, 2017). Connecting deciduous forests in lowlands and coniferous tree communities at high elevations, the coexistence of beech, spruce, and fir has lasted for many centuries locally, depending on the distance from glacial refugia (Magin and Mayer, 1959; Mosandl, 1984). As a consequence, mixed mountain forests provide habitat for a substantial diversity of plant and animal taxa (Hilmers *et al.*, 2018).

Currently, there is a great interest in mobilizing and processing wood resources from mixed mountain forest areas (e.g. BAFU, 2015; Bayerische Staatsforsten AöR, 2018). Previous investigations on the productivity of mixed mountain forests have concentrated mainly on mixtures of two of the three species and indicate that beech generally achieves higher growth rates when grown in mixtures with conifers, because intra-specific competition is reduced (Pretzsch *et al.*, 2010; Bosela *et al.*, 2015). Under certain conditions, spruce and fir also benefit from growing in two-species mixtures (Forrester *et al.*, 2013).

Looking at three-species mixture of beech, spruce, and fir, Pretzsch *et al.* (2015) demonstrated an additional yield of about 20 per cent compared to neighbouring pure stands. But other studies show quite heterogeneous results, with complementarity effects strongly depending on climate, stand, and site conditions (Grossiord *et al.*, 2014; Mina *et al.*, 2018). Indeed, complementarity effects do not always favour beech and conifers in association (e.g. Conte *et al.*, 2018).

Due to their altitudinal zoning, however, mountain forests are particularly susceptible to the effects of climate change (Theurillat and Guisan, 2001; Beniston, 2003; Pearson and Dawson, 2003; Scherler *et al.*, 2016). The species-specific optimum habitats are severely restricted in their geographical distribution in mountain areas. Particularly vulnerable are beech-spruce-fir mixed mountain forests that occur in areas with species-specific suboptimal vitality. Here, climate change induced changes of environmental conditions

are likely to alter their competitiveness (McEvoy *et al.*, 2013; Grace *et al.*, 2014; Harvey *et al.*, 2014). In addition, these forest systems may become more vulnerable in the future because of extensive bark beetle outbreaks and pathogens that profit from increased drought and higher temperatures under global change (Porta *et al.*, 2008; Seidl *et al.*, 2014). A number of studies report that in recent decades there have been more frequent problems with the natural regeneration of spruce and fir, ozone stress, and drought in mixed mountain forests (e.g. Ashmore *et al.*, 1985; Ammer, 1996; Matyssek *et al.*, 1997; Dell'Era *et al.*, 1998; Ruehr *et al.*, 2010; Hartl-Meier *et al.*, 2014a; Pretzsch *et al.*, 2015).

Against the background of the strong vulnerability of these ecosystems, the Agenda 2010 for Sustainable Development explicitly states that there needs to be an intensification of the implementation of concrete measures, sustainable processes, and strategies to strengthen the resilience of mountain areas (Mountain Partnership, 2017). Due to the restricted climatic conditions, mountain forests are well suited to analyze the influence of climate change over a relatively short period of time (Cudlin *et al.*, 2017).

Large scale studies on mixed mountain forests and their productivity are rare and regionally limited (Preuhler, 1981; Priezel and Christophel, 2014; Bosela *et al.*, 2018, 2015; Pretzsch *et al.*, 2015), but necessary to support management decisions that take environmental conditions and their possible future change into account. This paper uses a data set of a series of long-term experimental plots across mountain regions in Europe. It aims to improve the knowledge about site-specific productivity and growth trends in European mixed mountain forests, and addresses the following questions:

(Q1) How productive are mixed mountain forest systems in Europe currently and how has their productivity changed in recent decades with regard to climate change and anthropogenic influences?

(Q2) Is there a shift in species-specific productivity of beech, spruce or fir over recent decades?

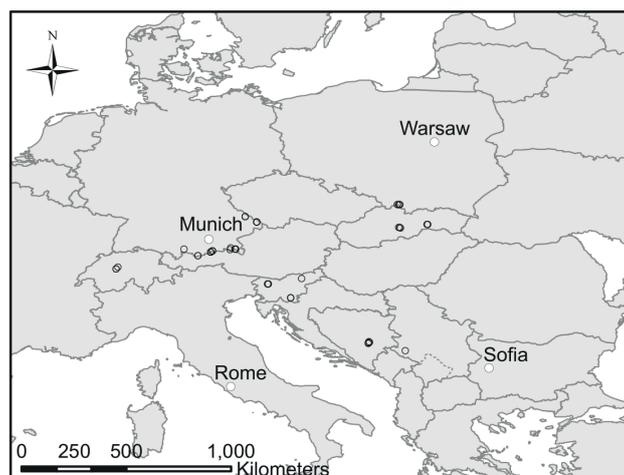


Figure 1 Geographic location of the 60 long-term mixed beech-fir-spruce mountain forest experimental plots (black points). Some experimental plots are not visible (overlaid) due to scaling.

Material and methods

Study area

Our data set covered most parts of the mountainous regions of Europe (Figure 1) and maps a wide climatic and topographic gradient for mixed mountain forests with elevations from 733 to 1443 m, mean annual temperatures from 4.4 to 8.5°C, and annual precipitation from 813 to 2818 mm (Figure 2; Table 1). The dominant parental material varies between slightly consolidated (e.g. unconsolidated deposits), moderately consolidated (e.g. sedimentary rocks), and intensively consolidated (e.g. igneous and metamorphic rocks) with medium to very high available water storage capacity, low to high base saturation, and very low to medium soil organic carbon contents (Panagos *et al.*, 2012).

Data

Sixty long-term experimental plots with a total of 222 observations between 1980 and 2010, consisting of beech, spruce, and fir, were investigated (Figure 1; Table 1). All trees with a diameter at breast height >7 cm were measured at every observation. Tree heights were measured on a subsample of trees. Thus, the volume of single trees and stands could be calculated by means of stand height curves and regionally adopted form factors. At least two of the three species (beech, spruce, and fir) had to be present and each species must have had a mixture portion of at least 20 per cent. On the experimental plots only low intensity thinning or no thinning was allowed. In this way, we avoided confounding growth trends with thinning effects.

Our study focused on the periodic annual increment at the stand level (PAI). To evaluate the stand characteristics, we followed the DESER-Norm 1993 by Johann (1993). Repeated observations at the stand level were carried out at intervals of several years, and enabled the calculation of PAI, giving the mean annual growth rates over longer time intervals. Between two observations at times t_1 and t_2 , the PAI was calculated from the difference between the wood volumes V_1 and V_2 of the remaining stand at both times plus the volume of trees which died (or were removed) between the observations.

$$PAI = (V_2_{remaining} - V_1_{remaining} + V_{removed}) / (t_2 - t_1)$$

Factors used to explain stand productivity

The growth of any tree and forest stand is age dependent. However, since most of the study plots under investigation are uneven-aged, it was not possible to create a useful metric regarding stand age. For this reason, we used the standing volume per hectare of the remaining stock (V) as a proxy for the development stage of the forest stands. Furthermore we used the stand density quantified by the stand density index (SDI; Reineke, 1933) to characterize the growing stock. To quantify the proportion of each species in the total stand with respect to the different space requirements of each individual species, the SDI values of spruce and fir were transformed into a comparable SDI referenced from beech following the model of Pretzsch and Biber (2016). Species proportions were logit transformed using the car package for R (Fox and Weisberg, 2011).

Since some of the experimental plots under investigation had a long time period between two consecutive observations (>20 years) we used the mean values of the stand characteristics (V , SDI) between the two observations (Assmann, 1961) instead of their values at the beginning of the period.

In addition to the location of each plot (latitude, longitude), variables representing terrain topography were derived from digital elevation models (European Union, Copernicus Land Monitoring Service, 2019) and

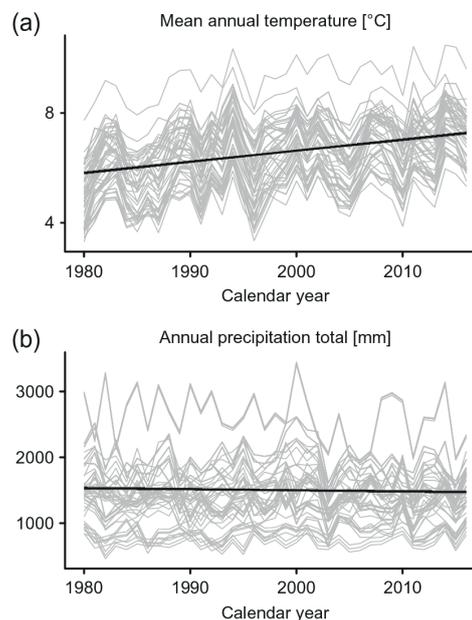


Figure 2 Mean annual temperature (a) and annual precipitation totals (b) of all 60 long-term mixed mountain forest experimental plots from 1980 to 2017. Climate data from the closest available stations to the experimental plots. For 34 out of the 60 plots an elevation correction was executed based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined based on 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris *et al.*, 2014). The black regression line is based on a linear model (a: estimate = 0.04, $P < 0.001$; b: estimate = -1.645 , $P = 0.06$).

consisted of slope inclination (in degrees), north index (calculated from slope orientation with $\cos(2\pi \times \text{slope orientation}/360)$, where 1 indicates a north-exposed plot, -1 indicates a south-exposed plot), and east index ($\sin(2\pi \times \text{slope orientation}/360)$, where 1 indicates an east-exposed plot and -1 indicates a west-exposed slope orientation). As a measure of soil productivity we used the dominant parental material (three groups: slightly, moderately and intensively consolidated) and the available water storage capacity to a depth of 1 m (AWC) from the European Soil Database v2.0 (Panagos *et al.*, 2012).

Monthly data for mean temperature and precipitation total were collected from the closest available meteorological stations. For 34 out of the 60 plots, meteorological station based interpolated data were available. For the remaining 27 plots only station data itself were accessible and some of the stations were located further away (8.7 km on average) or at a different elevation. In order to improve the representativeness of the latter datasets, an elevation correction was used based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined using 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris *et al.*, 2014). Temperature and precipitation were aggregated to annual mean values (mean annual temperature and annual precipitation totals) and then again averaged for the respective recording intervals. To detect possible changes in the productivity of mixed mountain forests in Europe over the last 30 years, beyond the effect of the change in considered climate variables, we also took the calendar year into account.

Table 1 Main characteristics of the 60 investigated long-term mixed beech-fir-spruce mountain forest experimental plots from 1980 to 2010. Standard deviations are given in brackets. The respective tree species shares were calculated using transformed SDI values according to Pretzsch and Biber (2016)

Country	Number of plots		Total number of observations		Number of observations per plot		Elevation m a.s.l.	Mean annual temperature °C	Annual precipitation total mm	Volume m ³ ha ⁻¹	Basal area m ² ha ⁻¹	Periodic annual increment m ³ ha ⁻¹ y ⁻¹	Species share							
	N		N		N								Beech %	Spruce %	Fir %					
mean [sd]	5		14		2.8	[±0.45]	1185	[±11.3]	1269	[±84]	381.5	[±72.8]	33.2	[±19.2]	43.5	[±18.8]				
min.—max.					2–3		1006–1291		1095–1387		26.6–41.2		6.0–11.9		0.2–71.6		10.7–64.9			
mean [sd]	29		116		4.14	[±0.97]	984	[±186]	1605	[±366]	532.5	[±206.8]	8.6	[±3.0]	18.1	[±13.9]	45.0	[±15.4]		
min.—max.					2–6		743–1281		1109–2191		9.6–73.5		3.1–15.1		0–60.8		9.6–77.5		2.6–63.9	
mean [sd]	7		21		3		983	[±57]	1434	[±66]	549.8	[±77.7]	6.9	[±2.7]	54.9	[±15.8]	17.8	[±18.9]	27.1	[±10.3]
min.—max.					—		902–1087		1306–1550		438.8–713.7		1.5–11.0		22.0–77.4		4.7–64.2		11.3–44.9	
mean [sd]	1		2		2		1270		1161	[±208]	587.5	[±71.5]	12.5–13.9		0.3–0.6		43.5–45.6		53.8–56.2	
min.—max.					—		—		6.8–7.5		50.4–52.4		11.2	[±3.1]	38.7	[±16.3]	17.6	[±25.7]	42.3	[±16.7]
mean [sd]	6		21		4.2	[±1.3]	775	[±45]	922	[±96]	710.2	[±181.8]	11.2	[±3.1]	38.7	[±16.3]	17.6	[±25.7]	42.3	[±16.7]
min.—max.					3–6		733–845		813–1200		445.1–985.2		3.1–15.6		11.0–63.4		0–62.8		14.7–69.1	
mean [sd]	8		28		3.5	[±0.53]	1171	[±264]	2247	[±513]	704.4	[±158.2]	10.2	[±3.0]	47.4	[±17.7]	29.3	[±29.4]	21.6	[±19.3]
min.—max.					3–4		910–1443		1471–2818		35.2–61.9		4.6–17.1		20.3–74.1		0–78.2		0–69.8	
mean [sd]	4		20		5		897	[±5]	1426	[±26]	404.5	[±104.4]	12.3	[±2.6]	12.9	[±10.7]	27.6	[±7.4]	58.8	[±13.0]
min.—max.					—		890–899		6.9–7.7		18.9–49.2		6.2–15.9		5.1–41.6		11.4–36.7		22.6–74.4	
mean [sd]	60		222		3.8	[±1.0]	995	[±201]	1563	[±461]	552.7	[±198.9]	9.3	[±3.2]	26.8	[±21.3]	35.5	[±21.6]	35.1	[±18]
min.—max.					2–6		733–1443		4.4–8.5		9.6–73.5		1.5–17.1		0–77.4		0–78.2		0–74.4	

Modelling procedures

All analyses were performed in R 3.4.0 (R Core Team, 2018). To test the influence of the variables described above on the productivity of mixed mountain forests, we used a generalized additive mixed model (GAMM) with a Gaussian distribution using the package *mgcv* (Wood, 2011). The model included the periodic annual volume increment of the mixed forest plots as a dependent variable. By using a random factor (plot) as a grouping factor no pairs were taken into account twice. To account for potential autocorrelations, we treated plot geographical location as a two-dimensional non-linear smoother. Since climate change led to changes of the mean annual temperatures at same elevations (see Figure 2a), we also integrated the combination of elevation and mean annual temperature into the model as a two-dimensional smoother. If the term of the calendar year nevertheless remained significant, it was assumed that other factors besides the considered climate variables, such as late frost events, nitrogen inputs etc., influenced stand growth (cf. Pretzsch et al., 2014). The determination of the degrees of freedom of the nonparametric terms is part of the fitting process (Wood, 2011; Package *mgcv*; Tables S2–S4).

In order to investigate whether the productivity of the individual species (beech, spruce, and fir) has changed in recent decades, we extrapolated the species-specific stand values to one hectare. We used the species shares at the beginning of each period as a scaling factor, which we calculated from the transformed SDI values. Again, a generalized additive mixed model (GAMM) was applied by species with the scaled periodic annual volume increment as the dependent variable and a random factor (plot) was used as the grouping factor.

The model selection from the extensive models was carried out with a principal component analysis (PCA) and further supported by testing all possible mathematical models using all combinations of variables by Akaike information criterion (AIC; Barton, 2018). Explanatory variables, which were used as factors in the model, were tested for significance using the R-package *multcomp* (Hothorn et al., 2016).

Results

Trends in temperature and precipitation

When pooling the climate data of all experimental plots we found a significant positive trend of mean annual temperature over the last 30 years (Figure 2a). The analysis of the temperature development of each individual plot also showed a significant positive trend (Table S1). We found no significant trend of the annual precipitation totals in the last 30 years with the pooled dataset (Figure 2b). The detailed analyses of each experimental plot showed significant increases in precipitation only in 4 out of 60 experimental plots (Table S1).

Long term trend of productivity

The average periodic annual volume increment of mixed mountain forests in Europe amounts to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. The most important factors influencing stand productivity were the location of the plot (the further south the more productive), the interaction between elevation and temperature (with higher productivity at lower elevations), the consolidation of the dominant parental material (with a higher productivity on slightly consolidated parental material), and the volume of the remaining stand (positive effect; +). The calendar year had no significant influence on the periodic volume increment, indicating neither positive nor negative growth trends (Table 2, S2; Figure 3, S1).

Long term trend of species specific productivity

Beech showed growth rates of $8.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ over the entire investigation period with a slight, albeit not significant, increase in productivity. The most important factors influencing the volume increment of beech in mixed mountain forests were the consolidation of the dominant parental material (with highest productivity on moderately consolidated parental material) and the volume of the remaining stand (+). For beech, the model showed no significant influence of the calendar year on productivity over the last 30 years (Table 2, S3; Figure 4, S1).

At $7.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$, the periodic annual volume increment of fir was the lowest among the investigated tree species in the 1980s. However, the growth of fir rose significantly to $11.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (+36 per cent) and was thus the most productive tree species in the mixed mountain forests of Europe at the end of the study period. On average, the annual volume increment of fir was $9.7 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ over the entire investigation period (1980–2010). For fir, we found the interaction between elevation and temperature (higher productivity with increasing mean annual temperature), the consolidation of the dominant parental material (the more consolidated the more productive), and the volume of remaining stand (+) as significant drivers of stand productivity. The calendar year had a significant positive influence on the productivity of the stands (Table 2, S4; Figure 4, S1).

At the beginning of the study period, the productivity of spruce was still about $14.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ and decreased to $10.8 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (–23 per cent) in 2010. The mean periodic volume increment of spruce over the entire study period (1980–2010) in the mixed mountain forests was $11.6 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. For spruce, the location of the plot (the more south, the more productive), the interaction of elevation and temperature (with decreasing productivity at higher elevations), the consolidation of the dominant parental material (with highest productivity on slightly consolidated parental material), and the volume of the remaining stand (+) were the most important factors influencing stand productivity. Spruce productivity declined significantly in recent decades (Table 2, S5; Figure 4, S1). However, although spruce showed a significant decline in productivity over the last 30 years, it was the most productive tree species in the triumvirate for almost the entire period under study. Therefore, a higher proportion of spruce in the stand also had a positive, albeit not significant, effect on the total productivity of the stand.

Discussion

For the first time, the productivity of mixed beech-spruce-fir mountain forests was analysed across a variety of European mountain areas in a standardized way. Our results show that despite a significant increase in annual mean temperature and stable precipitation, the average productivity of European mixed mountain forests has not changed significantly over the last decades. The studied mixed mountain forests showed constant volume growth during the last 30 years, amounting to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (Q1). Thus, climate change seems to have no impact on the productivity of mixed mountain forests in Europe, at least within the time span of this study. At the tree species level, however, we found significant changes in the growth dynamics of the three species. Each species (beech, spruce, and fir) reacted to climate change in a different way. The PAI of spruce

decreased significantly while the PAI of fir increased significantly. The productivity of beech remained constant over the last 30 years (Q2). Thus, climate change has led to a shift in the competitive strength of the involved tree species. As a consequence, the proportion of tree species coexisting in the forest system has shifted in favour of beech in recent decades. After declines in the 1990s and 2000s, the proportion of fir trees has stabilized again since the 2010s (Figure S2). We found a significant influence of the interaction between elevation and temperature in the models for spruce, fir and the model of the total stand. For spruce and the total stand, productivity decreased with increasing elevation. In the case of spruce, we also observed declining productivity with warming temperature trends at higher elevations. With expected further increases in temperature, it can be assumed that the productivity of spruce at higher elevations will continue to decline. The productivity of fir increases with warming temperature trends at high elevations (Figure S1). Moreover, the calendar year had a negative effect for spruce and positive for fir, suggesting that other changing factors different than mean temperature are strengthening their productivity long term trends. PAI increases with a higher volume of the remaining stand in all cases (Tables S2-S5). This finding is in line with Pretzsch *et al.* (2015) who found a linear relationship between the volume of the remaining stand and its productivity in a study of mixed mountain forests in the Bavarian Alps.

European beech

Contrary to our expectations, results show that beech productivity did not change significantly in recent decades. Due to the warming in the last century and especially the most recent decades (Luterbacher *et al.*, 2004; Büntgen *et al.*, 2011) and the simultaneously high amount of precipitation, especially at

higher elevations (cf. Figure 2), the productivity of beech is expected to increase (cf. Aertsens *et al.*, 2014; Tegel *et al.*, 2014). Our study confirms that the productivity of beech in mixed mountain forests remained stable or increased slightly, albeit not significantly, throughout Europe between 1980 and 2010. This is consistent with published measurements (Pretzsch *et al.*, 2014; Tognetti *et al.*, 2014; Bosela *et al.*, 2016b) and model simulations (Hlásny *et al.*, 2011). On the other hand, our results contradict the study of Dittmar *et al.* (2003), who documented a decline of radial growth of beech at higher elevations at Central European scale, and Bosela *et al.* (2018) who, corresponding to a significant warming trend from 1990–2010, found an average decline in beech growth in Continental Europe over the last three decades. However, as trends in productivity on the stand level also depend on stand structure (e.g. density and size distribution) it is not possible to infer the stand level productivity trends from tree level trends.

Nevertheless, beech faces challenging environmental changes, especially in mountainous areas. Environmental changes in the Alpine regions are mainly characterized by acid and nitrogen deposits, and O₃ pollution (Brang, 1998; Flückiger and Braun, 1999; Smidt and Herman, 2004). Muzika *et al.* (2004), for example, found significant negative correlations between air pollutants (O₃, NO₂ and SO₂) and the growth of beech and spruce in the Carpathian Mountains. In addition, there are natural influences due to climate change such as late frost events and drought stress (Dittmar *et al.*, 2003; Jump *et al.*, 2006; Bontemps *et al.*, 2009), as well as biotic diseases, such as fungal infestation (Cherubini *et al.*, 2002). Furthermore, Dittmar and Elling (2007) found increasing crown transparency and reduced vitality in recent years based on long-term crown condition surveys of beech trees in mixed mountain forests of the Bavarian Alps. Although beech was exposed to these negative effects on tree growth, its productivity has remained unchanged in recent decades (Figure 4; Table 2). We assume, therefore, that the positive

Table 2 Estimated coefficients with standard error and p-values for the four final models for beech, spruce, fir, and beech-spruce-fir in mixture.

Empty cells denote variables that are not included in the models because they were excluded from the model selection. Note that the proportion values of the respective tree species were logit transformed using the package car (Fox and Weisberg, 2011)

Variable	Beech		Spruce		Fir		Beech-Spruce-Fir	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
s(Latitude, Longitude)		0.446		< 0.001		0.521		0.272
s(Elevation, Temperature)		0.11		< 0.001		0.021		0.028
Precipitation								
Slope								
North exposition								
East exposition								
Available water capacity								
Dominant parental material		< 0.001		< 0.001		< 0.001		0.532
Volume	0.006 ± 0.002	0.006	0.007 ± 0.001	< 0.001	0.006 ± 0.001	< 0.001	0.006 ± 0.001	< 0.001
Calendar year	0.042 ± 0.038	0.265	-0.087 ± 0.039	0.026	0.064 ± 0.029	0.029	0.013 ± 0.023	0.574
Proportion beech							-0.445 ± 0.387	0.252
Proportion spruce							0.559 ± 0.517	0.281
Proportion fir							-0.658 ± 0.523	0.209
R ²	0.327		0.623		0.316		0.526	
RMSE	2.751		3.004		3.545		2.113	

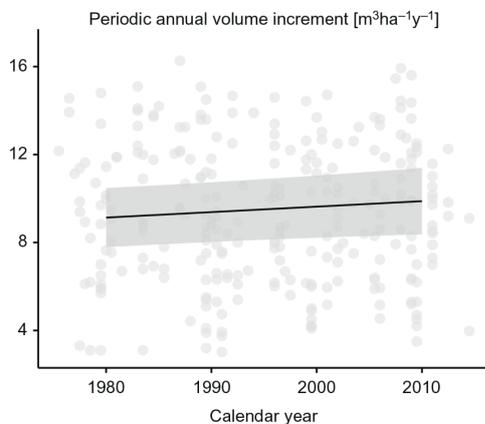


Figure 3 Periodic annual volume increment of the investigated long-term experimental plots of beech, spruce, and fir over the calendar year. The annual volume increment was predicted using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. Predictor variables were the volume of the remaining stand, the interaction between latitude and longitude, the interaction between elevation and mean annual temperature, the dominant parental material, and the species proportions of the three tree species involved, beech, spruce, and fir. For the predictions, the predictor variables were kept constant at the mean value. The grey area indicates the standard error.

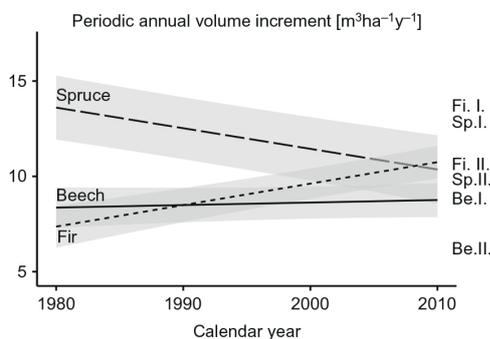


Figure 4 Periodic annual volume increment over the calendar year of the tree species beech, spruce, and fir in the long-term experimental forest plots. The periodic annual volume increment of the three tree species was scaled using the species share derived from SDI proportions. Estimation was done using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. See table 2 for the predictor variables. For the prediction, the predictor variables were kept constant at the mean value. The grey area indicates the standard error. Stars show the mean annual volume increment of the first (I.) and second (II.) yield classes of the three tree species spruce (Sp.), fir (Fi.) and beech (Be.) at age 100 according to the yield tables of Hausser (1956), von Guttenberg (1915) and Wiedemann (1949).

effect of a warmer, but not drier, climate and the negative effects of substance discharges on beech growth, have so far compensated each other. Tognetti *et al.* (2014) did not observe an influence of marked drought periods on basal area increment in beech during the twentieth century; in the absence of climatic

stress, predictions that follow increasing atmospheric CO₂ concentration effects over water use efficiency, together with rising temperature and related factors (e.g. length of growing season), would increase or stabilize productivity in healthy trees.

Silver fir

Fir exhibited accelerating growth rates during the last few years. This is remarkable, as fir experienced a strong decline in growth across Europe caused by sulphur dioxide emissions in the years 1970–1990 (Diaci *et al.*, 2011; Uhl *et al.*, 2013; Büntgen *et al.*, 2014; Čavlović *et al.*, 2015) or low summer temperatures in the 1960s and 1970s (Bosela *et al.*, 2018, 2016a). Our study might provide additional evidence for this event, as the productivity of fir was the lowest among the analysed tree species at the beginning of the study period. Efforts to reduce emissions since the 1980s, combined with a warmer, but not drier, climate (cf. Figure 2; Diaci *et al.*, 2011; Uhl *et al.*, 2013; Büntgen *et al.*, 2014), have probably enabled the significant increase in fir productivity (Figure 4). These results are in line with studies by Bosela *et al.* (2018) and Büntgen *et al.* (2014), who also demonstrated an unprecedented increase in productivity in Central Europe's fir stands. However, a recent Europe-wide study on the growth of fir throughout the Holocene (Büntgen *et al.*, 2014) describes increasing radial growth in the Italian Alps and the Apennines until the turn of the millennium, but not beyond. Bosela *et al.* (2018) showed that fir populations in the southern parts of the Alps may have recently experienced growth limitation due to drought. Seemingly, fir populations close to the Mediterranean distribution limit already show a drought-induced growth depression, which will become even more critical in a warmer and drier future. However, there are indications that the sensitivity of fir to drought stress decreases when mixed with beech (Lebourgeois *et al.*, 2013; Metz *et al.*, 2016; Vitali *et al.*, 2017) or when the genetic diversity is high (Gazol and Camarero, 2016).

Norway spruce

As shown in the present and previous studies (e.g. Schöpfer *et al.*, 1997; Uhl *et al.*, 2013), the growth relation of spruce and fir in mixed mountain forests has changed significantly in recent decades (Figure 4). These results illustrate the importance of external factors on the competitive relationships between species and thus on their growth dynamics. With regard to resistance to emissions, spruce is mostly classified as particularly resistant, beech as less resistant, and fir as particularly sensitive (Rohmeder and von Schönborn, 1965). This may explain the superior productivity of spruce compared to fir in the 1980s. In the meantime, however, the reduction of the emission load and the recovery of fir have led to a direct improvement in fir's fitness and thus also an indirect improvement in the competitive relationship with spruce and beech (Elling *et al.*, 2009; Uhl *et al.*, 2013; Büntgen *et al.*, 2014; Bosela *et al.*, 2018). While the high PAI of spruce (Figure 4) in the 1980s was presumably favoured by the growing depression of fir (by allocating more resources to spruce in mixed stands that were previously available to fir), the recovery of fir is highly likely to have an effect on spruce's growth behaviour. Spruce is—without human intervention—

pushed back into its real niche by the resurgence of fir, which it held before the beginning of the emission load and weakening of fir (Uhl *et al.*, 2013). A further explanation for the significant decrease in spruce productivity at the stand level (Figure 4, Table 2) is the vulnerability of spruce to increasing summer droughts (Lévesque *et al.*, 2013; Zang *et al.*, 2014).

Effects of mixing

A number of recent studies show that species diversity has a positive effect on volume growth (Zhang *et al.*, 2012; Toigo *et al.*, 2015). A higher number of species is also expected to mitigate the negative effects of extreme climatic events through higher growth resistance and resilience (Jucker *et al.*, 2014; Gazol and Camarero, 2016; Metz *et al.*, 2016). Although our study cannot directly estimate the benefit of mixed stands of beech, spruce, and fir in higher elevations, there are indications that the three tree species in mixed stands show no lower growth rates than monospecific pure stands. Thus, comparisons of the values from our study with the mean annual volume increment of the three tree species at age 100 from the yield tables for pure stands of Hausser (1956), von Guttenberg (1915), and Wiedemann (1949) show that beech and spruce are on average between the first and second yield class. However, due to the growth depressions at the end of the 20th century, the average PAI of fir is lower than the second yield class of the respective yield table. Other authors show significant increases in this mixture compared to monocultures. Pretzsch and Forrester (2017), for example, showed an average increase of 20 per cent in the productivity of mixed mountain forests compared to neighbouring pure stands. Mina *et al.* (2018) found that beech trees in temperate European mixed mountain forests generally benefit from the admixture of spruce and fir. Further studies on the mixing of at least two of the three species show, depending on site quality, clear increases in mixed stands of spruce and fir (Forrester *et al.*, 2013; Forrester and Albrecht, 2014) or beech and spruce (Pretzsch *et al.*, 2010) compared to monospecific pure stands.

Nevertheless, our results clearly indicate that growth in a mixture does not shield the three species from the effects of long-term changes in environmental conditions. For example, we show that the PAI of spruce has declined significantly over the last three decades under a number of conditions in Europe (Figure 4). At the stand level, however, Europe's mixed mountain forests appear to be stable (Figure 3; Table 2) and it is possible to achieve risk diversification by mixing the three tree species. These results are in line with the results of Hartl-Meier *et al.* (2014a, 2014b), who in their study on mixed mountain forests in the Northern Limestone Alps and the Berchtesgaden Alps come to the conclusion that mixed mountain forests can adapt well to temperature increases caused by climate change and that there may be no change in tree species composition.

Contribution of mixed mountain forests to ecosystem services

Our results show how productive mixed mountain forests are in Europe and that they have not yet experienced productivity declines under the conditions of climate change. With reference

to FOREST EUROPE's six overarching criteria for sustainable forest management, we can state that mixed mountain forests in Europe make a significant contribution to the conservation of forest resources and to securing their contribution to the global carbon cycle (C sequestration), especially since large parts of European forests are located in mountain areas (CIPRA, 2007). In addition to this fact, mixed mountain forests can also make a significant contribution to maintaining the production function of European forests. In the past, parts of our investigated forests were thinned, albeit only slightly, and were able to maintain their productivity (production function) despite management.

However, in the face of climate change and in order to fulfil the Paris climate agreement (UNFCCC, 2015), there is currently a high pressure on these forests. In order to meet these challenges, it is particularly important to develop strategies to enhance the adaptation (resilience) and mitigation potential of these forests in the future. One example is the management guideline for mountain forests of the Bavarian State Forests AöR (Bayerische Staatsforsten AöR, 2018). Nevertheless, considering different stand and site conditions, and also regional and elevation dependent magnitude of climate change, management options for mixed mountain forests to fulfil future ecosystem services should be regionally adopted at the local scale (Mina *et al.*, 2017).

Conclusion

According to our results, European mixed mountain forests have so far been stable in terms of volume growth in relation to climate change. The reduction of volume increment of one species was compensated by higher volume increments of another species. Although they grow under the same conditions, spruce and fir have shown remarkably different growth patterns over the last 30 years. While fir has responded positively to recent warming, spruce productivity has declined significantly, suggesting that at constant rainfall, fir is less susceptible to warmer conditions than spruce. There is some support for the use of mixed forests as a strategy for adapting to climate change. We show that a more diverse tree species composition can help to compensate to some extent for the effects of climatic and anthropogenic changes. The productivity of the tree species involved in this forest system is subject to constant fluctuations. In order to maintain a stable system prepared for future changes a balanced mix of the three tree species is recommended. Even if maintaining regeneration and a good share of spruce, especially in the application of selective forestry, will be more difficult in the future. Our results indicate that it is possible to develop a sustainable forest management system to maintain the resilience of the forests and thus ensure the continuous provision of ecosystem goods from mixed mountain forests and at the same time minimize the effects of climate-induced changes on mixed mountain forests.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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B Article II

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Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas

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Abstract

Mixed mountain forests, primarily made up of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.), cover about 10×10^6 ha of submontane–subalpine altitudes in Europe. They provide invaluable ecosystem services, e.g. protection against avalanches, landslides or rockfall. However, pure Norway spruce stands have, since mediaeval times, been heavily promoted as productive stand types for salt works at sites naturally supporting mixed mountain forests. Damage to these secondary pure spruce stands has been steadily increasing in recent decades. Furthermore, due to their previous limitation due to low temperatures and a short growing season, forest ecosystems in higher elevations are expected to be strongly affected by climate warming. To address these problems, alternative management concepts are being intensively discussed. A possible option to improve the stability and resilience of the stand is the transformation from pure Norway spruce stands into site-appropriate, sustainable and stable mixed mountain forests. In this study, we have tested seven different transformation scenarios (e.g. slit, shelterwood and gap-coupees, strip clear-cutting, do-nothing) and their impact on five evaluation criteria (forest growth, economics, carbon sequestration, (stand) stability and biodiversity). As there are hardly any practical examples for some of the transformation scenarios available, we have used the forest growth simulator SILVA to assess whether the tested transformation scenarios differ in transformation success and to observe trade-offs between the criteria of evaluation. Of the investigated scenarios, we consider the ones with gap or slit-coupees with the most beneficial overall utility values for the portfolio of the five evaluation criteria. However, we showed with our results that it is possible, by means of several trajectories, to return destabilised forests to sustainable and stable systems. We showed that a transformation is realistic, even if sophisticated silvicultural concepts are not strictly pursued.

Keywords *Picea abies* (L.) · Pure stands · Transformation · Mixed mountain forests · Evaluation criteria

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Introduction

In addition to the often promoted Norway spruce (*Picea abies* (L.) Karst), mixed mountain forests also comprise silver fir (*Abies alba* Mill) and European beech (*Fagus sylvatica* L.). In the following, we refer to these tree species as spruce, fir and beech, respectively: They can successfully coexist in altitudes between ~600 and 1400 m above sea level and account for the largest potential share of natural forests in Southern Central Europe (Moning and Müller 2008). More than half of Central Europe's surface area consists of mountain areas, which is where most of the existing forests are concentrated (CIPRA 2007).

The presented problem and solution of transforming from artificial to close-to-nature forest is of general importance for the forest management of mountain forests worldwide (Kimmins and Blanco 2011). However, particularly

in mountainous areas, forests are of great ecological and socio-economic importance in Central and Eastern Europe due to their provision of various ecosystem goods and services (e.g. Ellenberg 1988; Forest Europe 2011; Pretzsch et al. 2015; Mina et al. 2017). The strong topographic gradients and high relative relief strongly increase the propensity for soil loss through erosion (Panagos et al. 2015), as well as gravitational processes such as rockfall, avalanches and snow gliding (Rammer et al. 2015; Leitinger et al. 2018). Furthermore, mountain topography often facilitates heavy local precipitation events and thunderstorms, and human infrastructure is often restricted to flood-prone river valley bottoms. As a consequence, the green infrastructure provided by forests is particularly relevant in mountainous countries. Due to their importance in buffering against the consequences of harsh mountain environments, mountain areas frequently have a substantially higher forest share than low-elevation areas (EEA 2010). They constitute regional hotspots of forest C storage (Nabuurs et al. 2008) and are estimated to contain 11% of current global biomass stocks (Erb et al. 2018). In addition to providing regulating services to local communities, mountain forests are thus also relevant for the global climate system.

Spruce, fir and beech have coexisted for thousands of years in mixture without active management or with close-to-nature forestry across this region (Magin 1959; Preuhler 1979). Interactions between the three species according to the literature seem to be balanced, i.e. the interactions are neither one-sided against or in favour of one of the three species (Pretzsch et al. 2015). For example, in spring conifers may benefit from the neighbourhood of leafless beech by already growing with improved access to water (Goisser et al. 2016; Rötzer et al. 2017). During the common growing season, however, the deeper roots of beech and fir (Lebourgeois et al. 2013) can provide better water supply at the expense of the shallow-rooted spruce. Moreover, in mixed mountain forests spruce and fir are typically higher than beech and can pre-empt the light due to their occupation of the upper canopy layer (Pretzsch et al. 2015). On the other hand, the high morphological plasticity enables beech to more quickly occupy the empty space in case of disturbances (Bayer and Pretzsch 2017).

Both conifers reflect an isohydric strategy (Lyr et al. 1992) and show higher stem and root growth during prolonged time spans under drought than beech (Leuschner 2009; Nikolova et al. 2009). While the hazardous behaviour of the anisohydric beech can lead to tree mortality under the impact of extreme water shortage, the behaviour can be beneficial when water is abundant or moderate drought stress (e.g. Klein 2014). There are more structural and functional traits such as crown plasticity (Jucker et al. 2015; Forrester and Albrecht 2014), rooting depth (Rothe 1997; Schmid and Kazda 2002), litter decomposition (Rothe and Binkley 2001)

and browsing pressure (Ammer 1996) that prevent any one of the three species from becoming a permanent winner or loser, and despite their effects changing with climate and growing conditions, the balance between the tree species is maintained.

In terms of stand growth, Hilmers et al. (2019) found that mixed mountain forest ecosystems are rather resilient against disturbances such as acid deposition, climate warming and ozone. As growth reductions in one of the three species were compensated by a growth increase in the others, the stand productivity of mixed mountain forests of spruce, fir and beech in total has hardly changed over the last 30 years. One possible reason for this finding is that the potential damages are rather equally distributed, with late frost and ozone susceptibility of fir and beech (Larsen et al. 1990; Matyssek et al. 2010), the high sensitivity to smoke damage and acid deposition of fir (Elling et al. 2009), the high risk of bark beetle (Wermelinger 2004) and snow and storm damage (Spiecker 2000) of spruce. This temporal, spatial and functional complementarity and risk distribution may contribute to the overyielding of spruce and beech (Pretzsch et al. 2010; Rothe 1997), spruce and fir (Jensen 1983; Pretzsch et al. 2010; Vallet and Pérot 2011; Forrester and Albrecht 2014), and spruce, fir and beech (Pretzsch and Forrester 2017; Mina et al. 2018).

However, mixed mountain forests have often suffered a reduction in species richness. In the German Alps, for instance, spruce has, since medieval times, been heavily promoted as a productive timber species for salt works at sites naturally supporting mixed mountain forests (Seidl et al. 2007). Damage to these secondary pure spruce stands, however, has been steadily increasing in recent decades (e.g. Briner et al. 2013). These forests are particularly vulnerable to summer droughts (Lévesque et al. 2013; Zang et al. 2014), extensive bark beetle outbreaks (Seidl et al. 2014) and pathogens (Porta et al. 2008). All are then further favoured by a warmer and possibly drier climate (e.g. Matulla et al. 2002; Lexer et al. 2002; Pepin et al. 2015). Marini et al. (2012) found that forest disturbance in the European Alps was seven times higher where spruce was planted in sites that were warmer than those within its historical climatic range. However, the importance of whether spruce grows within or outside its native range is decreasing as climate conditions are changing rapidly. Climate change-driven disturbances threaten spruce over virtually its entire range in Europe, and some recent disturbances have, for instance, already reached native subalpine spruce forests close to the timber line in the Alps (Hlásny et al. 2019). In addition, the repeated cultivation of pure spruce stands has a negative effect on soil fertility (Seidl et al. 2007).

To address these problems, alternative management methods are being intensively discussed (Reininger 2000; Spiecker et al. 2004; Löf et al. 2010). A possible option

to improve the stability and resilience of the stand against abiotic and biotic disturbing factors, as well as to increase productivity, is the transformation of pure spruce stands to site-appropriate mixed mountain forests (Spiecker et al. 2004; Seidl et al. 2011; Pretzsch and Forrester 2017; Hilmers et al. 2019). This transformation has two aspects: (1) a change in the species composition from pure to mixed stands and (2) a change in the stand structure from regular, even-aged stands to more complex, uneven-aged stands.

The advantages of more complex forest stands, for example their higher stability against various disturbances and their superiority regarding many ecosystem services, attract attention (Bauhus et al. 2017; Bravo-Oviedo et al. 2018). Thus, at present there is a tendency towards transformation of age-class monocultures to continuous covered forestry worldwide (Vitkova and Dhubhain 2013). An important argument for fostering more diverse forests, containing both early- and late-successional species, is the insurance hypothesis. This states that diverse ecosystems are better buffered against disturbances (have higher resistance) and recover more quickly (have higher resilience; Jactel et al. 2009). Species diversity can mean risk distribution in view of abiotic and biotic disturbances, stability of growth and permanent protection function (soil erosion, avalanches, flooding). Such mixtures recover considerably faster from disturbances than other ecosystems, due to their elevated response diversity. Moreover, higher stand diversity is positively associated with the supply of many ecosystem services.

The state-of-the-art silvicultural approach in the Alps consists of small, irregular patch cuts for regenerating the forest and maintaining a high level of forest canopy cover in space and time (Cordonnier et al. 2008; Streit et al. 2009). It aims at the supply of regulating services and maintaining a relatively continuous forest cover, while enhancing resistance and resilience to disturbances (Dorren et al. 2004; Brang et al. 2006). However, management is complicated by steep terrain and low accessibility, which requires highly specialised harvesting technologies, (e.g. cable line systems) and results in high management costs (Valente et al. 2014; Jandl et al. 2018). As an alternative, one could adopt a more differentiated strategy, maintaining the existing mixed mountain forests, but transforming pure spruce stands to mixed mountain forests of mainly spruce, fir and beech. Such a strategy is already applied by some forest enterprises (e.g. Bayerische Staatsforsten AöR 2018).

There are hardly any existing practical examples for both maintenance and transformation. Thus, simulations with the forest growth simulator SILVA 2.3 (Pretzsch and Kahn 1996; Pretzsch et al. 2002) served as a supporting tool to assess whether the tested transformation scenarios are successful. Growth models integrate the knowledge about the growth of trees and stands; they can reproduce the growth behaviour of stands with which parameters

have been set. After appropriate calibration and validation, however, they are also suitable for reproducing stand development for which there are no sample or illustrative examples yet. For example, simulation models can be used to simulate the consequences of new types of thinning, creation of infrastructures or climate change. The prerequisite for this is that the model internal growth functions reproduce the tree and stand reactions for a broad spectrum of competitive and neighbourhood situations, as well as site conditions, in a biologically plausible way. If this is the case, models can effectively contribute to the development of new management guidelines for forest management in the high mountains (Pretzsch 2019). Besides the state-of-the-art silvicultural approach in the Alps, however, other silvicultural systems (e.g. gap and strip clear-cut-coupes) were to be compared on multiple criteria.

In addition to topics in numerous studies on the economic aspects of forest transformation (Knoke et al. 2001; Hanewinkel 2001; Knoke and Plusczyk 2001; Knoke et al. 2008; Roessiger et al. 2011; Messerer et al. 2017; Beljan et al. 2018), we investigated the effects of forest transformation on the habitat complex of mixed mountain forests taking a holistic approach. In this sense, the present contribution was devoted to the evaluation of multiple criteria of different forest transformation systems of secondary pure spruce stands, taking into account the criteria of forest growth, economics, carbon sequestration, stand stability and biodiversity. Wood production (forest growth, economics) provides renewable raw materials that are in high demand and wood production jobs are maintained therewith (Sikkema et al. 2011; Hetsch 2008). Carbon sequestration contributes to the mitigation of climate change and can be fostered through both afforestation and forest management (Naudts et al. 2016). Stand stability is fundamental for providing regulating services to society (Moos et al. 2018; Altieri et al. 2018), and biodiversity is likely to play a key role in mediating the relationship between plants and ecosystem processes by influencing the physiology, activity and population dynamics of plants (Weisser and Siemann 2013). The selected criteria are strongly related to the criteria for ecological, economic and social sustainable forest management (MCPFE 1993) which include the care for (1) forest resources, (2) forest ecosystem health and vitality, (3) productive functions, (4) biological diversity, (5) protective functions and (6) socio-economic functions.

The specific objectives of the contribution were (1) to identify possible paths that can be followed to transform characteristic pure spruce stands into semi-natural mixed forests at equilibrium using different forest management scenarios and to evaluate (2) if the investigated management methods yield stable stands over the long run; and (3) how the different scenarios differ in terms of forest

growth, economics, carbon sequestration, stand stability and biodiversity.

Materials and methods

Secondary pure spruce forests

Starting point for the simulations was formed by a total of 30 different pure spruce stands (Table 1), which were generated by the structural generator, STRUGEN (Pretzsch 1997). Initial data for the simulation and the assumed site productivity were deduced using inventory data of forests in the Bavarian Alps. All the simulated plots covered 2 ha each, at an age of 30 to 40 years, on sites of the ‘Oberbayerische Flyschvorlpen’ (800–1200 m above sea level, good site conditions). Single-layered initial stands were characterised by an average basal area of 32.8 m² ha⁻¹ with an average volume of the remaining stands of 181 m³ ha⁻¹ (Table 1).

Silvicultural goals

Assuming the help of cable yarding operations, these pure spruce stands were to be transformed to semi-natural mixed mountain forests of beech, spruce and fir at equilibrium. These multi-layered mixed mountain forests should have a mixture of 30–40% of species other than spruce and, if at equilibrium, an exponentially decreasing stem distribution. In addition, this forests should be uneven-aged, show a high structural diversity as well as an advanced regeneration layer, containing both early- and late-successional species, on as large an area as possible. By regular moderate treatments, the volume of the remaining stand is kept on an optimal level, so that the desired structural diversity and a continuous natural regeneration are obtained. While on rich sites, a volume of the remaining stand of 400–500 m³ ha⁻¹ is aimed at, a volume of the remaining stand of 300–400 m³ ha⁻¹ is targeted on mesic sites. In order to avoid growth reduction, the respective lower value should not be undercut over a longer period of time. Very poor sites were not taken into account, as regular management often takes a back seat in these areas and aspects of forest conservation and protection forest management are in the foreground.

Silvicultural scenarios

The state-of-the-art silvicultural approach in the Alps (e.g. Bayerische Staatsforsten AöR 2018) is intended to aim at

transforming secondary pure spruce stands into semi-natural mixed forests at equilibrium. To sustain the unique functions and services of mixed mountain forests, the natural gap dynamics of mountain forests are emulated by silviculture (e.g. Acevedo et al. 1996; McCarthy 2001; O’Hara 2001; Ciancio et al. 2006). In this context, the most common silvicultural prescription for management is the combined shelterwood and femel-coupe system, which is composed of several stages: spruce stands at the age of 40–60 years are slightly opened up homogeneously over the whole stand area to promote natural regeneration and stability (shelterwood-coupe). Above these patches of forthcoming regeneration, the canopy is opened up continuously or removed completely in one pass (femel-coupe) and missing tree species are planted. In the areas between the regeneration slits, only very cautious interventions (target diameter harvest) take place in order to maintain the volume of the remaining stand between 400 and 500 m³ ha⁻¹ depending on site conditions. With the progressing regeneration of all three species, the regeneration slits are gradually extended by harvesting trees at the edges during the femel-coupe. By removing the overstorey step by step, 40–60 years after the first harvest, the whole stand area is regenerated as the regeneration patches grow together. Except for the initial shelterwood-coupe, any remaining thinning operations always only take place on every second cable line. After two operations on the same cable lines, the cable lines are changed. Thus, only half of the area is worked at a time, and the creation and expansion of the regeneration slits take place at different times. This procedure ensures that a heterogeneous vertical structure is created and that the cable lines can also be used over long periods of time. In order to validate the state-of-the-art silvicultural scenarios, the evaluation of multiple criteria was also applied to conventional management methods, such as strip clear-cut and gap-coupe (Mosandl 1984; Table 2).

From silvicultural guidelines to scenario simulation

All simulations for stand development and timber production were carried out with the single-tree, distance-dependent forest growth simulator, SILVA 2.3 (Pretzsch and Kahn 1996; Pretzsch et al. 2002). Due to the partly stochastic character of SILVA, every simulation run can, despite identical starting conditions and treatment programmes, produce different results. Since the regeneration phase, in particular, provides crucial information for forest transformation concepts, SILVA also includes a regeneration module. Simulations with SILVA were performed as sequences of five-year time steps. In order

Table 1 Key forest growth data of the simulation stands

Species	Age (years)	N (n ha ⁻¹)	hg (m)	dg (cm)	Basal area (m ² ha ⁻¹)	Volume (m ³ ha ⁻¹)
Spruce	30–40	2486 ± 92	10.7 ± 0.25	12.2 ± 0.25	32.8 ± 1	181.6 ± 12

N, stem number per hectare; dg, diameter of mean basal area; hg, mean height corresponding to dg

Table 2 Simulation scenarios, their short description and references for detailed information on the simulated forest transformation scenarios

Code	Scenario	Brief description	Regeneration	References
DN	Do-nothing with natural regeneration	No treatment	Natural regeneration	
G	Gap-coupes with planting	Clearance of gaps with a radius of 30 m. Change of cable lines every 20 years. First operation at stand age of 35 years. Afterwards, the stand is cleared in strips	Planting of fir and beech in gaps + natural regeneration	Mosandl (1984)
SH1	Shelterwood-coupes with natural regeneration	Partial clearance of slit-like patchy gaps (width: 30, length: 25). Change of cable lines every 20 years. First operation at stand age of 35 years	Natural regeneration	Bayerische Staatsforsten AöR (2018)
SH2	Shelterwood-coupes with planting	Partial clearance of slit-like patchy gaps (width: 30, length: 25). Change of cable lines every 20 years. First operation at stand age of 35 years	Planting of fir and beech under shelter in the patchy gaps + natural regeneration	Bayerische Staatsforsten AöR (2018)
SL1	Slit-coupes with natural regeneration	Clearance of slit-like patchy gaps (width: 15 m, length: 30 m). Change of cable lines every 20 years. First operation at stand age of 35 years	Natural regeneration	Streit et al. (2009), Bayerische Staatsforsten AöR (2018)
SL2	Slit-coupes with planting	Clearance of slit-like patchy gaps (width: 15 m, length: 30 m). Change of cable lines every 20 years. First operation at stand age of 35 years	Planting of fir and beech in the slits + natural regeneration	Streit et al. (2009), Bayerische Staatsforsten AöR (2018)
SC	Strip clear-cutting with natural regeneration	Clearance of the stand in strips. Strip width 30 m. Distance between the strips 120 m. First intervention at age 80. Interval between interventions 20 years	Natural regeneration	

to cover an overall simulation time span of 150 years, we simulated 30 such five-year periods in each run. This means that the development of an entire forest life cycle could be simulated. In addition, the ‘silvicultural treatments’ (e.g. gap, femel and shelterwood-coupe) and ‘creation of infrastructures’ (e.g. cable crane and cable lines) modules were supplemented for the present comparison of different silvicultural scenarios. The results of the wood sorting were calculated using the SorSim program (Lemm et al. 2013). Cable lines, femel gaps and planting were created outside the simulator using the data handling features of the R software (R Core Team 2018). The stored carbon quantities in wood products, and the substitution of stored carbon by the energetic use of biomass, were calculated using a harvested wood products (HWP) model from Klein et al. (2013). Comparisons of the results of the different silvicultural scenarios were made using R (R Core Team 2018), specifically employing the dplyr package (Wickham et al. 2018).

Validation of the simulation results

The simulation results were finally compared with the results from long-term experimental plots. For the validation, data from two sets of long-term experimental plots were used. On the one hand, we used data from 22 mixed mountain forests long-term experimental plots comprising beech, spruce and fir at elevations of between 850 and 1240 m a.s.l. in the catchment area of the Northern Limestone Alps in Bavaria (Southern Germany). These plots were established in order to investigate the influence of different silvicultural treatments (femel-shelterwood-coup) on the regeneration dynamics and volume increment and were established in the 1970s (Pretzsch et al. 2015). Moreover, we have compared our results with data from 14 long-term experimental pure spruce plots on high-performance sites in southern Bavaria (Röhle 1995).

Evaluation criteria

To engage in differentiated discussions on all transformation scenarios (Table 2) five criteria (forest growth, economics, carbon sequestration, stand stability and biodiversity) were defined. The results of each silvicultural scenario and

criterion were displayed scaled (best: 1, worst: 0; Koschke et al. 2012; Knoke et al. 2014). Each criterion was, in turn, made up of different factors (see Table 3). The efficiency of each scenario was quantified by summing the score of each of the studied criteria. To provide a measure of stability between the categories, the standard deviation (SD) for each forest transformation scenario was also determined.

Forest growth

The criterion forest growth consisted of the factor’s total productivity, mortality over the entire simulation period and the standard deviation of tree heights as a proxy for a shelter in the event of a disturbance. If the overstorey is lost to disturbances, the understory can immediately utilise the increasingly available resources such as light, water and nutrients and take over important forest functions. In order to include the temporal component, the time since simulation start was classified into five classes (25 ± 10 , 50 ± 10 , 75 ± 10 , 100 ± 10 and 125 ± 10 years), and averages of each class were obtained. Each of the five values was included in the evaluation without weighting.

Economics

The harvested trees were graded after each simulation period with the help of SorSim (Lemm et al. 2013) without the dead wood fraction. The revenues were calculated using averaged timber prices provided by the Bavarian State Institute of Forestry (LWF) for 2010–2015. Harvesting costs were calculated at 48 € m^{-3} , planting costs at 6400 € ha^{-1} for beech, 1600 € ha^{-1} for spruce and 2700 € ha^{-1} for fir. The net present value (NPV) was calculated using three different discount rates: 1%, 2% and 3%. The presented results included the financial value of the standing timber at the end of the simulation period.

Carbon sequestration

In order to calculate the stored in situ carbon quantities of the simulation results, both the above-ground biomass, using species-specific biomass formulae (Pretzsch et al. 2014), as

Table 3 Overview of the categories defined for the comparison of the different forest transformation scenarios and their factors

Forest growth	Economics (net present value) (%)	Carbon sequestration	Stability	Biodiversity (number of species)
Total productivity	1	In situ + ex situ in wood	Survival probability of	Flora
Mortality	2	products + substitutions of	spruce * potential dam-	Fauna
Standard deviation of tree heights	3	fossil fuels	aged timber	Fungi
			Spruce proportion in the last simulation period	

Each factor was included in the evaluation of the respective category without weighting

well as the underground biomass, with a root factor (root/shoot) according to Offenthaler and Hochbichler (2006), were estimated. The ex situ carbon content in wood products and the substitution quantities resulting from bioenergy use (wood combustion) were calculated using a harvested wood products (HWP) model from Klein et al. (2013). In presenting the C sequestration potential of forest management on a per hectare basis, we used the levelisation approach, where the periodic C flows were summed up and discounted with an assumed social interest rate of 2% (e.g. Hoen and Solberg 1994).

Biodiversity

The number of species of (1) flora, (2) fauna and (3) fungi were selected as indicators for a non-wood forest function. In order to determine the number of species of flora, fauna and fungi, each of the 30 stands was divided into 1000-m² grids. According to Zenner et al. (2016), each raster was then assigned to one of nine forest successional stages (gap, regeneration, establishment, early optimum, mid-optimum, late optimum, plenter, terminal and decay). Finally, based on the results of Hilmers et al. (2018), the number of species of flora (higher plants, lichen and mosses), fauna (phytophagous and pollinating arthropods, vertebrates and invertebrates feeding on animal tissue, species feeding on dead tissue and species depending on dead wood during their life cycle) and fungi was able to be assigned to the individual forest successional stages. The species numbers of the entire 2-ha plots consisted of the average of all 1000 m² large squares. Standard deviations were also calculated again using the average of each of the five classes since simulation start (see above).

Stability

The calculations of the stability of the stand against natural disturbances were calculated on the basis of a model developed by Roessiger et al. (2013). In a mixed stand, the survival probability of the spruce was calculated by means of a Weibull function (Weibull 1951) depending on the percentage of spruce and age. The probabilities of beech and fir survival were assumed to be independent of the percentage of spruce (Roessiger et al. 2013). Using the five classes since simulation start (see above), the survival probabilities were calculated at different simulation points in time. These survival probabilities were then multiplied by the potential amount of damaged wood volume (all spruce trees higher than 66% of the mean height of the 100 thickest spruce trees). They were then included in the valuation as separate factors without weighting. Assuming that stable stands at the end of the simulation could either appear due to the young

age of the spruce, or due to a low proportion of spruce, the share of spruce of the total stand in the last simulation period was used as an additional factor. Since those stands with a high proportion of spruce and young age will become unstable again in the future, those stands with a lower proportion of spruce were rated as better.

Results

Apart from the strip clear-cut and the do-nothing scenario, all the methods were successful for transformation into semi-natural mixed forests at equilibrium. Although natural regeneration of beech and fir was always present in the strip clear-cut scenario, spruce dominated the advanced development phases of the stands. In the do-nothing scenario, no or very little natural regeneration occurred. Differences between the shelterwood, slit and gap scenarios are shown in terms of their specific criteria.

Validation of the simulation results

Figure 1 shows the periodic annual increment versus the volume of the remaining stand in each simulation period. The results of the do-nothing scenario showed that long-term experimental plots made of pure spruce showed higher growth rates at the same volumes of the remaining stand

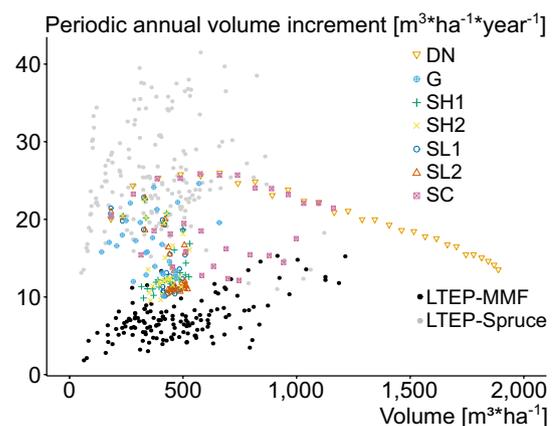


Fig. 1 Relationship between stand periodic annual volume increment and volume of the remaining stand. Black dots show the results from long-term experimental plots consisting of pure spruce (LTEP-Spruce); grey dots show the results from long-term experimental plots consisting of spruce, fir and beech (LTEP-MMF). Other symbols show the simulation results of various forest transformation scenarios. DN, do-nothing scenario; G, gap-coupe with planting of beech and fir; SH1, shelterwood-coupe with natural regeneration; SH2, shelterwood-coupe with planting of fir and beech; SL1, slit-coupe with natural regeneration; SL2, slit-coupe with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article

than experimental plots from the mixed mountain forest zone (beech, spruce and fir). The results from the simulations for all scenarios were lying between the results of the long-term experimental plots.

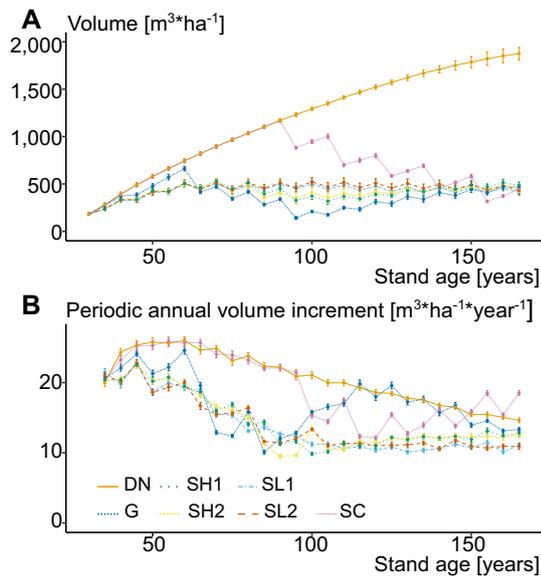
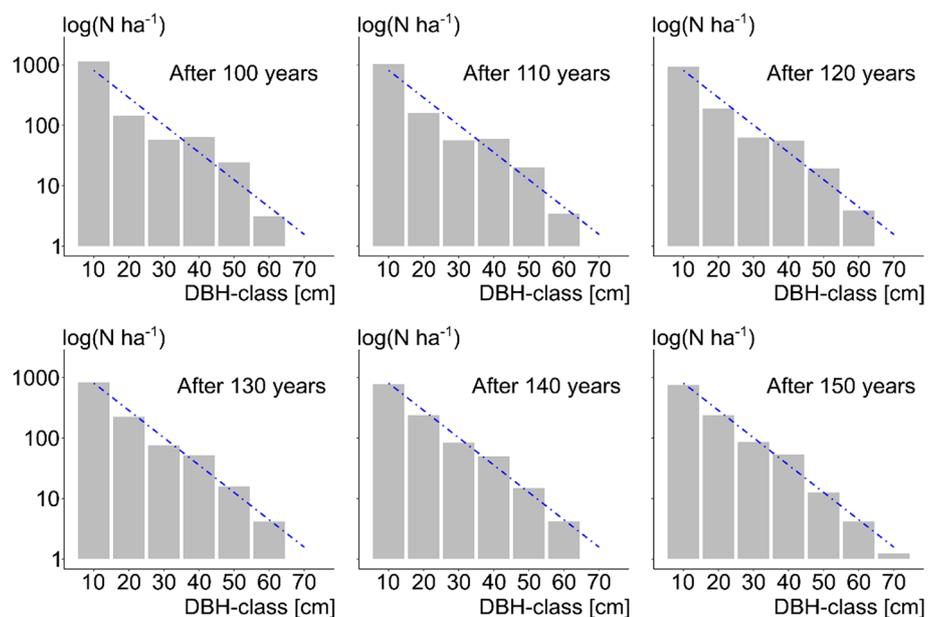


Fig. 2 Volume of the remaining stand in $\text{m}^3 \text{ha}^{-1}$ (a) and stand periodic annual volume increment in $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ (b) with standard errors, resulting from different tree growth between 30 simulations, above stand age of all the simulated transformation scenarios. DN, do-nothing scenario; G, gap-coups with planting of beech and fir; SH1, shelterwood-coups with natural regeneration; SH2, shelterwood-coups with planting of fir and beech; SL1, slit-coups with natural regeneration; SL2, slit-coups with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article

Fig. 3 Stem distribution (N/ha for DBH-classes) of the slit-coupe scenario with planting of fir and beech after 100, 110, 120, 130 and 150 years of simulation. The curve corresponds to a steady-state condition for uneven-aged stands of spruce, which could be reached in the long run (Prodan 1944). Note that the number of trees per hectare and DBH-classes was log transformed



Forest growth

The stand periodic annual volume increment (PAIV) of the slit and shelterwood scenarios stabilised from a stand age of around 80 years to a value of approx. $10 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$ and formed a steady state until the end of the simulation (Fig. 2). Volume of the remaining stand in the slit and shelterwood scenarios quickly leveled out between 400 and $500 \text{ m}^3 \text{ha}^{-1}$. Figure 3 shows how the slit scenario approaches a possible steady-state curve in the simulation run after 150 years. It is striking how the ‘gap’ in the diameter frequency distribution between 20 and 30 cm, still visible after 110 years of simulation, was filled after 130 years of simulation.

However, due to higher stand densities, the PAIV of the do-nothing scenario was higher than for all other scenarios over the entire simulation period (Fig. 2). In the case of standing volume and PAIV, the strip clear-cut scenario was similar to that of the do-nothing scenario up to the time of the first treatment. The gap scenario also showed the greatest fluctuations in terms of PAIV, similar to the standing volume.

Economics

In terms of economics, the results were similar for most management scenarios. Just the results of the do-nothing and the strip clear-cut scenario differed from the others (Figs. 4, S1). The do-nothing scenario showed, due to the potential liquidation value of the portfolio at the end of the simulation period, comparable net present values only in the calculation of the net present values with a 1% discount rate. As the discount rate increased, the net present value dropped sharply and was significantly smaller than in the other scenarios.

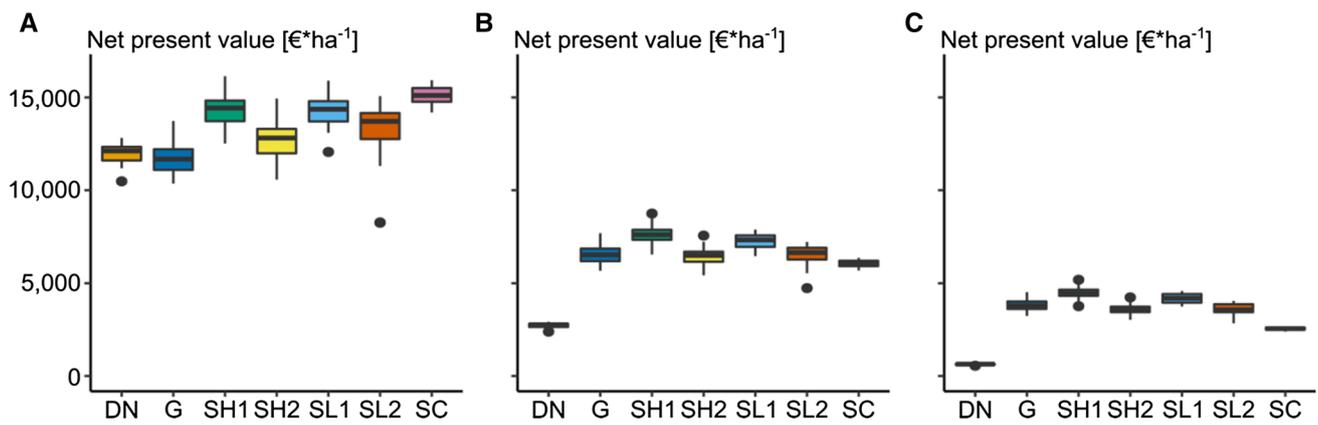


Fig. 4 Boxplots of the net present values of the different transformation scenarios. The net present value is calculated using three different interest rates: 1% (a), 2% (b) and 3% (c). The presented results include the potential liquidation value of the portfolio at the end of the simulation period. DN, do-nothing scenario; G, gap-coupees with planting of beech and fir; SH1, shelterwood-coupees with natu-

ral regeneration; SH2, shelterwood-coupees with planting of fir and beech; SL1, slit-coupees with natural regeneration; SL2, slit-coupees with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios

Table 4 Mean C sequestration (tC ha⁻¹) according to the levelisation approach in the different scenarios over 150 years

Scenario	In-situ	Wood products	Substitution	Total
DN	171.5	0.0	0.0	171.5
G	47.5	30.9	321.5	399.9
SH1	47.8	27.6	258.9	334.4
SH2	48.4	26.8	249.1	324.3
SL1	49.1	26.7	262.1	337.9
SSL2	52.4	25.3	247.7	325.4
SC	110.9	15.8	275.3	401.9

See Table 2 for abbreviations and a detailed description of the different scenarios

A very similar pattern can be observed in the strip clear-cut scenario. Even if it was still the best variant in the calculation with a discount rate of 1%, it fell behind the slit, shelterwood and gap variants in the calculation with higher discount rates. The slit, shelterwood and gap variants only differed in the planting costs of beech and fir and otherwise showed very similar results. However, the planting costs had a very strong impact on the net present values.

Carbon sequestration

Table 4 shows the mean carbon sequestration of the seven transformation scenarios, as well as the in situ storage, the carbon storage in wood products and the substitution of fossil fuels. The do-nothing scenario showed the highest in situ storage. Due to the lack of intervention, however, no carbon was stored in wood products or achieved by substituting fossil fuels. Overall, the do-nothing variant was, therefore, the

one with the lowest carbon sequestrate values. Highest values were achieved by the strip clear-cut and gap scenarios. While the strip clear-cut scenario showed high in situ carbon storage values, the gap variant had higher values in the areas of wood products and substitution of fossil fuels. The shelterwood and slit scenarios showed similar values with slightly higher values in the scenarios with natural regeneration. Overall, our results showed that the substitutions of fossil fuels were the most important factor to consider when looking at total carbon sequestration.

Stability

In terms of stability, we found the highest potential damages of spruce caused by disturbances in the do-nothing scenario (Fig. 5). Survival probabilities decreased with age. As we found the highest values of volume of the remaining stand, the potential damaged wood volume was also the highest for this scenario. For the other scenarios, the survival probabilities decreased for the first 100 years of simulations and then after increased. The proportion of spruce was 100% in the do-nothing and the strip clear-cut scenario at the end of the simulation runs. In case of slit and shelterwood, the proportions of spruce at the end of the simulations were higher in the scenarios with natural regeneration, than in the ones with plantings of beech and fir. Although beech and fir were planted in the gap scenario, the proportion of spruce at the end was still high (75%).

Biodiversity

For all three kingdoms (flora, fauna and fungi), considerable changes in the potential number of species were observed

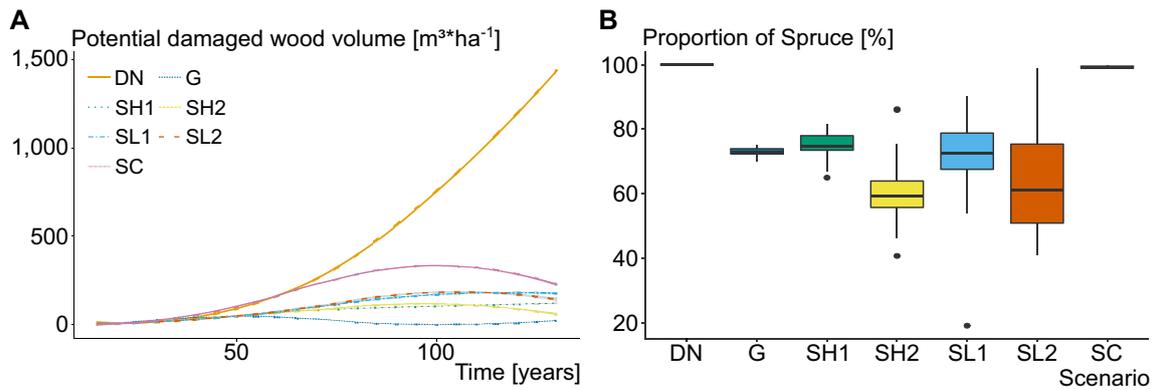


Fig. 5 Relationship between the potential damaged wood volume and the time since simulation start of all simulated scenarios (a) and the proportion of spruce in the last simulation period (b). Lines were generated by fitting a loess curve. DN, do-nothing scenario; G, gap-coups with planting of beech and fir; SH1, shelterwood-coups with natural regeneration; SH2, shelterwood-coups with planting of

fir and beech; SL1, slit-coups with natural regeneration; SL2, slit-coups with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article

over the simulation runs (Fig. 6). Vascular plants are directly dependent on sunlight reaching the forest floor. In the do-nothing scenario, little natural regeneration has occurred and mortality has opened the canopy over time. Thus, more sunlight could reach the forest floor. Therefore, we found the highest numbers of vascular plants in the do-nothing scenario after 100 years of simulation (which means a stand age of > 140 years; Fig. 6a). We observed a similar trend in the strip clear-cut scenario. However, due to the natural regeneration, the canopy closed again after the silvicultural treatments and the number of vascular plants species decreased at the end of the simulation runs. Starting with the first silvicultural treatments, we found increasing numbers of vascular plants species during the first 50 years of simulation in the slit and shelterwood scenarios. After 70 years of simulation, the number of vascular plants species decreased due to increasing canopy density and outshading and was constant during the last 50 years of simulation. We found a similar pattern in the gap-coups scenario. However, due to the strong silvicultural treatment towards the end of the simulation, the number of species increased again in this scenario.

As consumers depend on the primary producers, the number of species in the fauna kingdom showed very similar trends (Fig. 6b). The number of species rose sharply for a period in the slit, gap and shelterwood scenarios (open canopies), decreased afterwards and were constant at the end of the simulation runs. Again the number of species increased at the end of the simulation runs in the gap scenario. The do-nothing scenario showed a high number of species after 100 years of simulation.

Contrasting to the kingdoms of flora and fauna, the number of fungi species are following a bell-shaped

pattern along forest succession. We found an increasing number of species of fungi in the do-nothing and strip clear-cut scenarios peaking at 50 years of simulation (Fig. 6c). While we found just a slight decrease in the number of species in the do-nothing scenario afterwards, the number of species decreased drastically in the strip clear-cut scenario due to starting silvicultural treatments. In the slit and shelterwood scenarios, the number of species was lower during the first 70 years of simulation. However, as canopy density increased the number of fungi species was highest in these scenarios during the last 80 years of simulation. A different pattern was found in the gap-coups scenario. In this scenario, the number of species was lowest during the first 70 years of simulation, increased afterwards with a peak at 130 years of simulation and slightly decreased at the end of the simulation runs.

Evaluation with multiple criteria

Figure 7 shows the results of the overall evaluation with regard to the individual scenarios concepts. The do-nothing scenario showed the best biodiversity performance and ranked last for the other four criteria. The slit scenario with natural regeneration, slit with planting and the gap scenario showed balanced results in all categories. The results of the shelterwood scenario with natural regeneration, shelterwood with planting and the strip clear-cut scenario showed divergent results between the criteria. In order to illustrate the divergence of all the criteria within a silvicultural scenario, the standard deviation of each scenario between the categories was calculated (Fig. 8). This

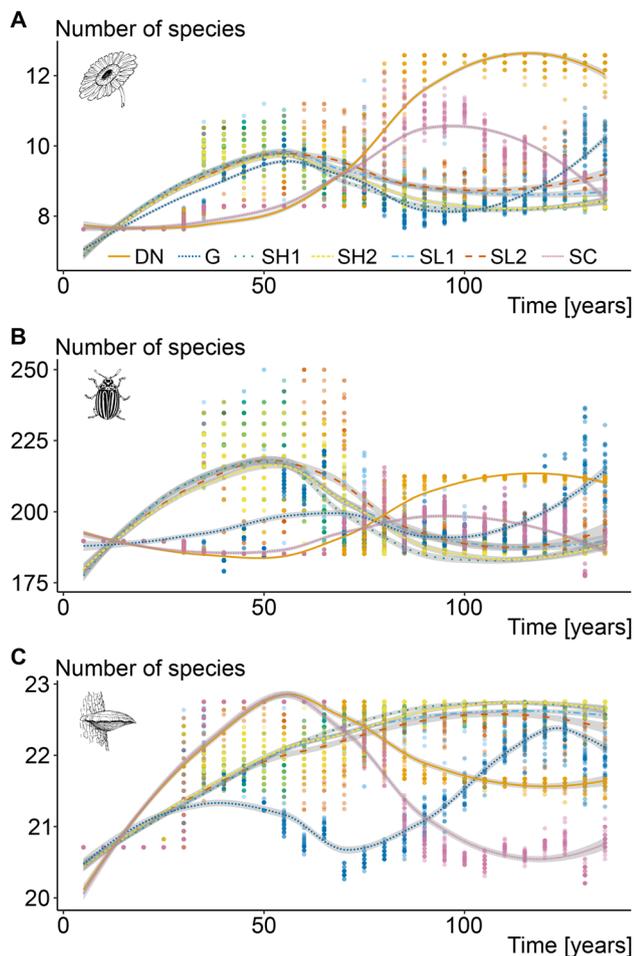


Fig. 6 Trends in the number of species of flora (a), fauna (b) and fungi (c) for time since simulation start of all the simulated scenarios. Lines were generated by fitting a loess curve. Grey areas represent the 95% confidence interval. DN, do-nothing scenario; G, gap-coupe with planting of beech and fir; SH1, shelterwood-coupe with natural regeneration; SH2, shelterwood-coupe with planting of fir and beech; SL1, slit-coupe with natural regeneration; SL2, slit-coupe with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article

approach enables a direct comparison of the individual silvicultural scenarios based on the total score. Scenarios, such as the slit scenarios with a high total score and small standard deviations between the scores, can be described as stable. The shelterwood scenarios show a relatively high total score, but at the expense of a higher standard deviation.

Discussion

It was shown that it might be possible to transform secondary pure spruce stands to stable mixed mountain forests with five of the seven scenarios (H1). It is also these five scenarios (gap, shelterwood, slit) which are expected to maintain these structures in the long term with regular forest interventions (H2). The evaluation of multiple criteria allows the seven scenarios to be divided into three groups. The do-nothing scenario only achieved the highest score in the category of biodiversity. The shelterwood and strip clear-cut scenarios showed highly divergent scores, while the slit and gap scenarios achieved high scores in all categories (H3).

While the management scenarios studied here mimic current management recommendations (Mosandl 1984; Streit et al. 2009; Bayerische Staatsforsten AöR 2018) in a highly realistic manner, it was applied uniformly across all the simulation runs. This approach disregards the potential adaptive measures of managers (Yousefpour et al. 2017), which are increasingly likely as climate change impacts worsen (Blennow et al. 2012; Seidl et al. 2016). Furthermore, it is unrealistic to presume constant site and climatic conditions for the next 150 years, as chosen in the present investigation. The simulation of a site-condition drift is, in principle, possible with the used growth model by changing the height or diameter-growth potential over time. For our simulation runs, where the central goal was the comparison of distinctly different treatment strategies, we assumed steady-state climatic and site conditions (Hanewinkel and Pretzsch 2000).

Despite these limitations, one of the backbones of this study is the reliability of the model SILVA in terms of providing the realistic quantitative results in terms of tree and stand growth. The model is used for applications in practice since the late 1990s, and the current version has been quantitatively calibrated with about 350,000 single-tree growth observations from long-term research plots (Pretzsch 2009, p. 519). Mixed mountain forests and pure spruce stands in Bavaria are particularly well represented in this data set. Thus, this study applied the model in a core area of its validity, which became also evident in the presented validation runs. The evaluation criterion *forest growth* was therefore directly covered by this validity. The other criteria (*economics, carbon sequestration, biodiversity, stability*), in contrast, were not primary simulation output variables, and they rather result from secondary calculations made on the former. However, the development of the standing stock and growth and the achievement of a long-term steady state play a crucial role, and most other criteria depend on this steady-state structure, volume and growth (Forest Europe 2011; MCPFE 1993; Dieler et al. 2017). All the methods applied and associated assumptions are documented and verified in published research works (see corresponding parts of the

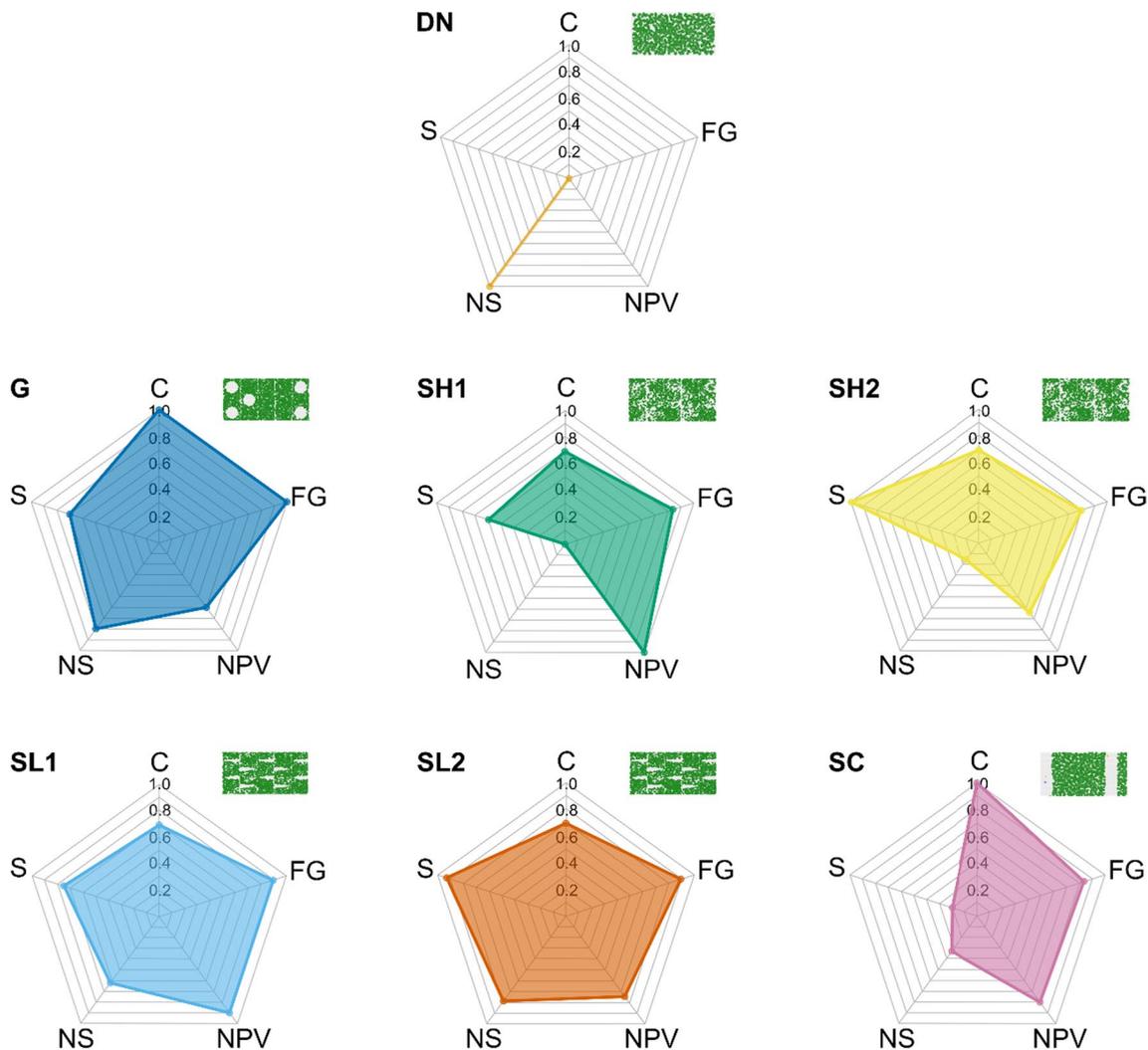


Fig. 7 Radar chart of the evaluation of multiple criteria. FG, forest growth; NPV, net present value; C, carbon sequestration; S, stability; NS, number of species. The scaled results of the respective factors of each criterion are shown (see Table 3 for explanation). The results were scaled between 0 and 1. The results evaluated with 1 represent the best scenario in comparison with the other scenarios. Categories rated 0 show the worst scenario. DN, do-nothing scenario; G,

gap-coupe with planting of beech and fir; SH1, shelterwood-coupe with natural regeneration; SH2, shelterwood-coupe with planting of fir and beech; SL1, slit-coupe with natural regeneration; SL2, slit-coupe with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios

methods section). So, we feel, our simulation and evaluation methodology—with a valid growth and yield model at its fundament—can be meaningfully applied given the goals of this study.

Forest transformation

The newly introduced species (beech and fir) can be established by planting or natural regeneration after artificial disturbances such as shelterwood, slit or gap-coupe. In their study on the transformation of even-aged to uneven-aged stands of spruce, Hanewinkel and Pretzsch (2000) showed that a transformation is strongly dependent on the gap size.

They showed that regeneration can only be established from gap sizes larger than 40 m in diameter. However, this study only includes the regeneration of spruce. Our study demonstrates that smaller gap sizes are sufficient if shade tolerant species are involved in the transformation process by planting or from natural regeneration if potential mast trees are located nearby. The smaller interventions also have less impact on the periodic annual volume increment at the stand level. This is in line with Brunner et al. (2006) who demonstrated, based on silvicultural scenario modelling, a transformation of spruce stands by under-planting with beech in a gradually opened stand of spruce.

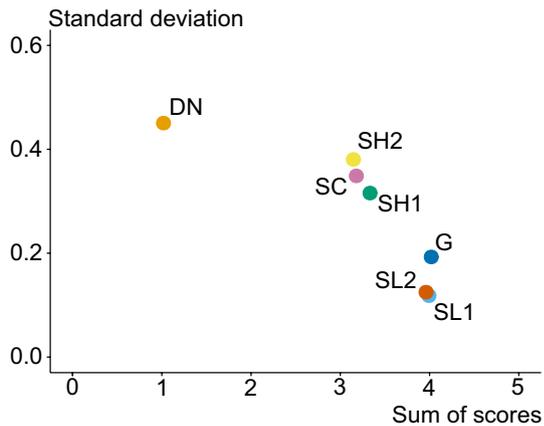


Fig. 8 Standard deviation of the scores from the five criteria (forest growth, economics, carbon sequestration, (stand) stability and biodiversity) over the sum of the scores. DN, do-nothing scenario; G, gap-coups with planting of beech and fir; SH1, shelterwood-coups with natural regeneration; SH2, shelterwood-coups with planting of fir and beech; SL1, slit-coups with natural regeneration; SL2, slit-coups with planting of fir and beech; SC, strip clear-cutting with natural regeneration. See Table 2 for a detailed description of the different scenarios and Table 3 for an overview of the five criteria

In the strip clear-cut scenario, after the removal of all the trees from the strip, natural regeneration of beech and fir started (if potential mast trees are located nearby). However, beech and fir were outcompeted by spruce later on. This may be avoided by earlier planting or groupwise separation of the three species, for example, through pre-commercial thinning (Brunner et al. 2006). Regulation of the mixture could be accomplished in SILVA only by thinning crop trees at a very early age. However, in the long run, the small-scale interventions of the slit-coupe scenarios might better support asynchronous forest dynamics than the other scenarios and thus support the forest's inherent adaptive mechanisms (Morin et al. 2014). In the do-nothing scenario, spruce remained dominant until the end of the simulation and the regeneration of fir and beech appeared only slowly. Suggestions by e.g. Drever et al. (2006) that unmanaged development might enable natural processes to restore the original species composition of the forests cannot be supported by our study, at least not in the time span of the simulation period. The slow rate of tree species change agrees with Schelhaas et al. (2015), who suggested that European forests are very inert and that altering their species composition requires a long time. The simulation results of Hlásny et al. (2017) in the Goat Backs mountain area of Slovakia also confirm these results. However, larger natural disturbances are to be expected in mountainous forests (Bircher et al. 2016), and the partial accumulation of the natural regeneration of non-spruce species is realistic (Buma and Wessman 2013). In all presented scenarios, climate change

and disturbance-mediated support to tree species diversity should be considered as an opportunity for forest adaptation efforts in spruce-dominated stands. Indeed, adverse effects, such as productivity losses or bark beetle outbreaks, must not be marginalised (Jönsson et al. 2007; Fleischer et al. 2016; Hlásny et al. 2017).

The lower stand periodic annual volume increment of long-term experimental plots has to be put into perspective to the extent that the proportion of spruce in the simulation plots was higher, and disturbing events, such as wind and bark beetle infestation, cannot be adequately represented by SILVA. As damage was not modelled in our scenarios, the standing volume of the remaining stand in the do-nothing scenario reached values of almost $2000 \text{ m}^3 \text{ ha}^{-1}$ only occasionally found on experimental plots. The comparative results from untreated long-term experimental plots with pure spruce show maximum volumes of the remaining stand of approx. $1600 \text{ m}^3 \text{ ha}^{-1}$ (Röhle 1995). We accepted this bias in the results as all the scenarios were flawed in the same way. We were interested in the relative differences and ranking of the scenarios, rather than in their absolute performance.

In order to transform the destabilised pure spruce forests into stable mixed mountain forests on a large scale, methods should be found to reduce the high harvest costs (Valente et al. 2014; Jandl et al. 2018). For example, Valente et al. (2011) demonstrate that a whole-tree system employed in alpine conditions showed lower costs and emissions and therefore offered greater economic and environmental benefits than the traditional shortwood system. Furthermore, the same authors showed that cable yarding seems to be very efficient in terms of having a minimal impact on residual stand and soil which seems particularly important against the background of already destabilised forests.

Long-term safeguarding of forest transformation

Although the slit and shelterwood scenarios reached steady-state conditions at the last 50 years of the simulation runs, these structures can only be artificially maintained in their characteristic structures by continuous removal in the upper and middle layers. Without silvicultural interventions over a longer period of time, the upper and middle layers may become so dense that the regeneration layer no longer receives enough light, precipitates and the balanced age structure is lost (Pretzsch 2019). Anyway, as long as there are continuous silvicultural interventions, tree species compositions will remain stable due to the slit and shelterwood scenarios and will ensure the desired forest redevelopment in the long term. The gap scenario also suggests that the transformation will be successful in the long term. Although this scenario is, due to the higher amounts of harvested wood, less stable in terms of stand periodic annual

volume increment over the entire simulation period, this scenario achieves a higher tree species mixture and an uneven-aged structure at the end of the simulation runs. In terms of productivity, these mixed uneven-aged stands have the advantage of being more productive compared to neighbouring pure stands (Pretzsch et al. 2015) on the one hand, and, on the other hand, that a potential reduction in the volume increment of one species can be compensated for by higher volume increments of another species (Hilmers et al. 2019).

Evaluation of multiple criteria

The evaluation of multiple criteria allowed to highlight three basic patterns: The shelterwood and strip clear-cut scenarios showed highly divergent scores, while the slit and gap scenarios achieved high scores in all categories. The do-nothing scenario only achieved the highest score in the category of biodiversity. However, as unmanaged forests are increasingly valued for their benefits in the context of biodiversity conservation (Paillet et al. 2010), an increasing share in the landscape will not necessarily lead to a reduction in important regulating ecosystem services. For example, Seidl et al. (2019) showed that, in a mountain forest landscape, the regulation of both climate and erosion was higher in unmanaged systems, compared to systems implementing current management recommendations (see also Irauschek et al. 2017; Mina et al. 2017; Langner et al. 2017). It is important to note, however, that many rural mountain communities not only depend on regulating ecosystem services, but also generate a substantial part of their income and livelihood from managing natural resources (Häyhä et al. 2015). Not managing forests might thus negatively affect rural communities and result in the loss of other important ecosystem services, such as the supply of timber and biomass for bioenergy.

Although the evaluation of multiple criteria presented here is innovative for a holistic view of silvicultural concepts, the entire forest complex should not be reduced to the criteria described here. Furthermore, the considered indicators are only proxies for the respective services and differ with regard to how closely they resemble the relevant underlying processes. However, based on the available results, the determinant effects of the different silvicultural concepts could be made visible, even for those who have not yet been able to draw on empirical studies or practical experience because of the new concepts. It was the aim of this study to develop and evaluate a set of technically feasible management options for the transformation to semi-natural mountain forests; the choice of the optimum or best scenario also depends on economic, social, legal and eco-political factors not covered by this study.

Significance for forest transformation worldwide

Forestry has been changing throughout its history in response to the changing needs of human populations and changing supplies of forest resources and values to satisfy these needs (Kimmins and Blanco 2011). Worldwide, there is a multitude of forests which have been destabilised during history. For example, the forests in Bangladesh or the temperate rainforests in Canada and the USA face similar challenges to the destabilised forests in the Alps of Europe resulting from the former salt works supply. They are to be transformed to sustainable, stable but managed systems. Our results show that there are several equivalent trajectories to achieve these goals. Thus, the risk of failure if one does not strictly follow a sophisticated guideline is low. There is little reason, therefore, why transformation of destabilised forest should not be attempted in order to suffer fewer human casualties and economic damage in the future, in many regions of the world.

Conclusion

Silvicultural scenario comparisons quantify the long-lasting impact of management decisions on the stand and landscape (Niedertscheider et al. 2017; Thom et al. 2018); they can reveal how current decisions influence the future management options and flexibility to react to environmental changes. The results of the presented study showed that continuous forest interventions can transform secondary spruce stands into mixed mountain forests which are in a steady state in terms of stem diameter and tree species distribution. Of the investigated scenarios, we consider the ones with gaps or slit cuts to have the most beneficial overall utility values for the portfolio of five evaluation criteria. If timber production is not a management goal, and the focus is on nature conservation, the do-nothing regimes turned out to be a possible solution. However, it was not the aim of this study to present the ‘best’ management regime in mountain forests, but to exemplify and demonstrate the evaluation of management options with regard to related trade-offs between evaluation criteria.

Given that mountain forest management is highly cost and labour intensive (Valente et al. 2014; Jandl et al. 2018), spatially explicit simulation models can help to evaluate silvicultural practices which have not yet been sufficiently tested in practice, even if they may not be able to reproduce future developments in detail. However, with our results, we have showed that it is possible, by means of several trajectories, to return destabilised forests to sustainable, stable but managed systems. They showed that a transformation is realistic, even if sophisticated silvicultural concepts are

not strictly pursued. In order to suffer fewer human casualties and less economic damage in the future, transformation efforts of destabilised forests should therefore be pursued worldwide.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no conflict of interest.

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C Article III

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Biodiversity along temperate forest succession

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Abstract

1. The successional dynamics of forests—from canopy openings to regeneration, maturation, and decay—influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g., late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity, a quantitative understanding of how different trophic groups vary over the course of succession is needed.
2. We classified mixed mountain forests in Central Europe into nine successional stages using airborne LiDAR. We analysed α - and β -diversity of six trophic groups encompassing approximately 3,000 species from three kingdoms. We quantified the effect of successional stage on the number of species with and without controlling for species abundances and tested whether the data fit the *more-individuals* hypothesis or the *habitat heterogeneity* hypothesis. Furthermore, we analysed the similarity of assemblages along successional development.
3. The abundance of producers, first-order consumers, and saprotrophic species showed a U-shaped response to forest succession. The number of species of producer and consumer groups generally followed this U-shaped pattern. In contrast to our expectation, the number of saprotrophic species did not change along succession. When we controlled for the effect of abundance, the number of producer and saproxylic beetle species increased linearly with forest succession, whereas the U-shaped response of the number of consumer species persisted. The analysis of assemblages indicated a large contribution of succession-mediated β -diversity to regional γ -diversity.
4. *Synthesis and applications.* Depending on the species group, our data supported both the *more-individuals* hypothesis and the *habitat heterogeneity* hypothesis. Our results highlight the strong influence of forest succession on biodiversity and underline the importance of controlling for successional dynamics when assessing biodiversity change in response to external drivers such as climate change. The successional stages with highest diversity (early and late successional stages) are currently strongly underrepresented in the forests of Central Europe. We thus recommend that conservation strategies aim at a more balanced representation of all successional stages.

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KEYWORDS

biodiversity, forest dynamics, forest succession, habitat heterogeneity, LiDAR, species density, temperate forests, β -diversity

1 | INTRODUCTION

After a severe disturbance with high tree mortality, forests undergo a series of successional stages. Following successful regeneration, forests canopies eventually close and subsequently diversify in both their vertical and horizontal structures. With ongoing succession, forests accumulate biomass, and the initial cohort of trees gradually dies, which increases the amount of dead wood (Franklin et al., 2002; Oliver & Larson, 1990). Recent studies have revealed a dynamic and increasingly complex picture of forest succession that suggests the possibility of multiple successional pathways and nonlinear effects of varying disturbance severities (Donato, Campbell, & Franklin, 2012; Tepley, Swanson, & Spies, 2013). Nevertheless, key attributes of forests, such as carbon storage and biodiversity, are inherently linked to their successional stages (Seidl, Donato, Raffa, & Turner, 2016).

Despite the fundamentally dynamic nature of forests, accounting for successional dynamics remains a challenge for the development of conservation concepts (Tikkanen, Heinonen, Kouki, & Matero, 2007). Based on a limited number of focal species and their habitat preferences, conservation efforts often focus on one or a few successional stages (Swanson et al., 2011). For instance, it has been shown that late stages of forest succession, including plenter (mixture of trees of different ages, sizes, and heights), terminal, and decay stages, are the preferred habitat for species considered as typical “forest dwellers”, e.g., white-backed woodpecker in Central Europe (*Dendrocopos leucotos*; Carlson, 2000). Late successional stages are often prioritized in conservation due to their high diversity in taxa, including birds, bats, saproxylic organisms (Avila-Cabadilla, Stoner, Henry, & Añorve, 2009; de la Peña-Cuellar, Stoner, Avila-Cabadilla, Martínez-Ramos, & Estrada, 2012; Jacobs, Spence, & Langor, 2007), lichen (Kuusinen & Siitonen, 1998), and fungi (Redecker, Szaro, Bowman, & Bruns, 2001).

Understanding the inherent changes in species diversity as forests develop provides an important baseline for assessing the effects of external drivers such as climate change (Thom et al., 2017). In the absence of such a dynamic baseline, observed changes in biodiversity that are simply the effect of forest dynamics could be easily misattributed to effects of climate change. Furthermore, understanding the variation in biodiversity over the entire course of succession could also provide a more comprehensive perspective on the effects of different management strategies on biodiversity. In Europe, for instance, the majority of forests are currently of intermediate age, as a result of heavy exploitation during and after the first half of the 20th century (Vilén et al., 2012). Late stages of forest succession, such as the terminal and decay stages, are largely absent, as most forests are harvested before trees reach old age (Faustmann, 1995). Similarly, early successional stages are kept as short as possible by planting

trees (Parker et al., 2000) or employing silvicultural techniques that accelerate stand development (Dale et al., 2001).

Variation in biodiversity along the stages of succession can also help to better understand the underlying drivers of diversity in forests. For instance, resources that are relevant for different species groups, such as light on the forest floor and dead wood, distinctly vary with successional stage. The *more-individuals hypothesis*—a variant of the *species-energy hypothesis* (Wright, 1983)—suggests that an increase in resource availability leads to more individuals (Hurlbert, 2004). In individual-rich communities, more species reach viable population sizes, which increases the observed number of species. Another factor is the diversity of resources (Cramer & Willig, 2005). If particular stages of forest succession offer more resource types than others, these stages could harbour a larger number of species. This variant of the *habitat heterogeneity hypothesis* predicts an increase in the number of species independent of abundance (MacArthur & MacArthur, 1961).

To assess changes in α - and β -diversity over forest succession, we quantified the abundance and diversity of 23 taxonomic lineages representing six trophic groups across nine successional stages of forest succession (Figure 1a). Based on theoretical considerations and the expected changes in the amount and heterogeneity of resources along the stages of succession (Figure 1a), we hypothesized that:

- (H1) patterns of abundance and number of species of primary producers along the course of forest succession would be U-shaped, dependent on light reaching the forest floor; patterns of consumers would be U-shaped, if they depend on the primary producers; patterns of saproxylic organisms would be U-shaped, if they are dependent on the accumulation of dead wood along succession; and patterns of saprotrophs would be hump-shaped, following the pattern of biomass accumulation;
- (H2) the stage of forest succession would have no effect on the number of species when abundance is accounted for, if these responses are driven by an increase in individuals, as predicted by the *more-individual hypothesis*; and
- (H3) species compositions in the early and late successional stages, which are characterized by open canopies, would be similar as many insects respond to the openness of the habitat.

2 | MATERIALS AND METHODS

2.1 | Study area

We used data from a survey of biodiversity and forest structure in the Bavarian Forest National Park in south-eastern Germany

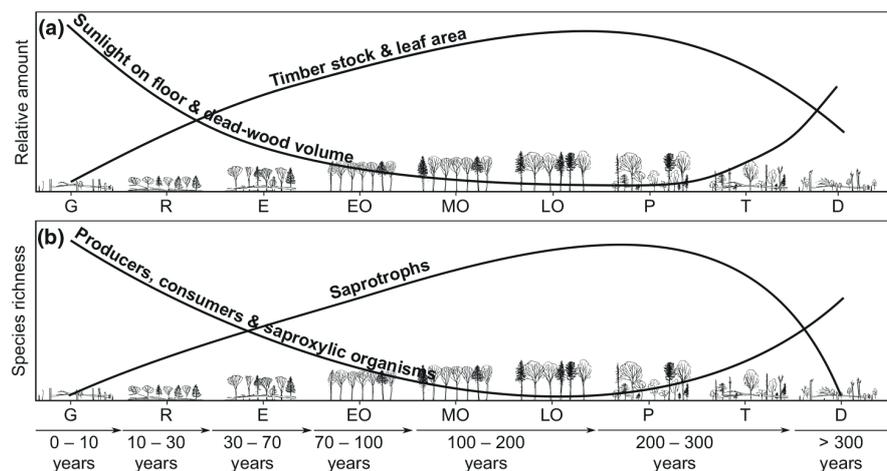


FIGURE 1 (a) Changes in resource availability with forest succession and (b) hypothesized response of saprotrophs, saproxylic organisms, producers, and consumers. The successional stages considered here follow Tabaku (2000), Drössler and Meyer (2006), and Zenner et al. (2016). Arrows represent an approximate timeline of the successional stages following Moning and Müller (2009). Note that the decay stage can occur already after 120 years due to forest disturbances, such as storms and bark beetle infestations. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid-optimum; LO, late optimum; P, plenter; T, terminal; D, decay

(Bässler, Förster, Moning, & Müller, 2008). The study area covers 24,000 ha and comprises a wide range of stages of forest succession that resulted from considerable variation in disturbance history and stand age. We utilize this variation in a space-for-time substitution approach in our analysis. The total annual precipitation is between 1,300 and 1,900 mm and increases with elevation (Supporting Information Figure S1a), which ranges from 655 to 1,420 m a.s.l. Annual mean air temperature varies between 3.5°C at high elevations and 7.0°C at low elevations (Bässler, 2004). The national park is dominated by mixed mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.).

2.2 | Data

Forest structure was characterized from field measurements and airborne light detection and ranging (LiDAR) on 287 plots, each with a circular area of 1,000 m². The plots include stands that were managed until a few decades ago and also remnants of old-growth forests. All measurements were conducted in the years 2006–2008 (Bässler et al., 2008). For each study plot, GPS coordinates were used to extract information on elevation from a digital terrain model (DTM 25) of the national park.

In a space-for-time substitution approach, differences in the environmental conditions of sites often bias the analysis. Therefore, we collected data on both soil characteristics and macro-climate for each plot (for details, see Supporting Information Appendix S1). By using elevation and the first PCA axis of soil parameter, we were able to control for potential differences.

The vegetation in the herbaceous layer (up to 1 m height), shrub layer (up to 5 m height), tree layer 1 (>5 to 15 m height), and tree layer 2 (>15 m) were estimated on 200 m² circular plots. Standing and downed woody debris were recorded in the field on each plot.

Full-waveform LiDAR data were collected across our plots using a Riegl LMS-Q560 under leaf-on conditions in 2007 (nominal sensor altitude: 400 m, average point density: 25 points m⁻²). Single trees in an area of 1,000 m² around the centre of each plot were detected using 3D segmentation (for details, see Supporting Information Appendix S1).

2.3 | Stages of forest succession

In our study, plots were classified to successional stages by combining the decision trees of Zenner, Peck, Hobi, and Commarmot (2016) and Tabaku (2000) (Supporting Information Figure S2). These decision trees incorporate information on canopy projection area, maximum diameter at breast height (DBH), proportion of dead wood, normalized quartile of the DBH, and the cover and height of the regeneration layer (Supporting Information Figure S2). The combination of these two protocols was necessary as Zenner et al. (2016) only considered trees with DBH >7 cm, and Tabaku (2000) explicitly also included regeneration and establishment stages. The combined decision tree was used to identify nine successional stages on 287 plots, i.e., gap, regeneration, establishment, early-optimum, mid-optimum, late-optimum, plenter, terminal, and decay stages (Figure 1).

2.4 | Taxonomic groups

We analysed the variation in biodiversity with forest succession considering 2,956 species from 23 taxonomic lineages. The species were group-specifically sampled in a standardized way and covered six trophic groups: producers (higher plants, lichen, mosses), consumers I (phytophagous and pollinating arthropods), consumers II (invertebrates feeding on animal tissue), consumers III (vertebrates feeding on animal tissue), saprotrophs *sensu lato* (species feeding on

dead tissue), and the special case of saproxylic saprotrophs (species depending on dead wood during their life cycle). Overall, this distinction of the 23 lineages into trophic groups yielded 33 functional groups; each of these functional groups were analysed on 29–287 plots (for details, see Supporting Information Appendix S1 and Table S1).

2.5 | Statistical analysis

All analyses were conducted in R (version 3.3.2; R Core Team, 2016). To test the influence of successional stage on the diversity of the 33 functional groups in the six trophic levels (Supporting Information Table S1), we calculated generalized linear mixed models with a Poisson distribution. We modelled either the number of species sampled on each plot (Gotelli & Colwell, 2001) or abundances (i.e., the number of all sampled individuals of a taxon) as response variables, with successional stage as the predictor. To test for regular trends across successional stages using linear and quadratic contrasts, we coded the factor forest successional stage as ordered. Elevation and soil characteristics were included as additional predictor to control for confounding effects of the local conditions. To account for the overdispersion frequently observed in models of count data, we included an observation-level random effect (i.e., the plot) in all models (Harrison, 2014). First, we calculated the overall effect (U- or hump-shaped response) of the forest successional stage modelled with linear and quadratic contrasts on the number of species or abundances of all 33 functional groups. We tested whether differences in the number of species are in accordance with the predictions of the *more-individuals hypothesis* or the *habitat heterogeneity hypothesis* by controlling for abundances in a subsequent model using the number of species as response variable, while accounting for abundances (note that with the exception of plants, all abundance values were square-root transformed). Second, we used the models to predict the number of species in each group while keeping elevation and soil parameters constant. Since forest successional stages do not always proceed in an orderly manner in reality (e.g., due to storms or bark beetle infestation), the successional stage was incorporated as an unordered factor in this case. Predictors were tested for significance using a general linear hypothesis testing framework as implemented in the `multcomp` R package version 1.4-6 (Hothorn et al., 2016).

At the community level, we calculated multiple-site dissimilarities for taxonomic groups using the Sørensen dissimilarity index and partitioned the thus derived β -diversity into its additive turnover and nestedness components as implemented in the `betapart` R package version 1.4-1 (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). To quantify the contribution of β -diversity among plots and among stages of forest succession to the γ -diversity in our study system, we used additive diversity partitioning as implemented in the R package `vegan`, version 2.4-3 (Oksanen et al., 2017). For a statistical test of the potential effects of forest succession on assemblages, we performed multivariate analyses of variance using distance matrices based on presence–absence data, applying the `adonis` function with 999 permutations as implemented in the `vegan` package.

These analyses considered taxonomic groups with sufficiently high numbers of species not separated into trophic levels (i.e., excluding taxonomic groups with ≤ 30 species). Changes in species composition of these taxa along forest succession were illustrated using partial correspondence analyses conditioned on the effects of elevation and soil. Furthermore, we calculated the number of unique species for early (gap, regeneration, and establishment), mid (early, mid, and late optimum), and late (plenter, terminal, and decay) stages of forest succession to evaluate the importance of individual stages for certain species of the taxa under study. In this case, we resampled a fixed number of plots in the early, mid, and late stages, respectively, for each taxon in our study and calculated the number of species unique to these forest successional stages. The fixed number of plots was defined as half the number of plots of the rarest stage for each taxon. The resampling procedure was randomly repeated 1,000 times, and the mean number of unique species per forest succession phase was calculated.

3 | RESULTS

3.1 | Stages of forest succession

Plots were not equally distributed across successional stages (Supporting Information Figure S3). The most prevalent stage (29% of 287 plots) was the mid-optimum stage, and the least prevalent stages (3%) were regeneration and plenter stages. Nevertheless, the distribution of plots across stages was representative for the Bavarian Forest National Park (Supporting Information Figure S3; Spearman's $\rho = 0.67$, $p < 0.05$). The successional stages differed in both elevation and soil characteristics (Supporting Information Figures S4 and S5; ANOVA: elevation $F_{8,278} = 19.8$, $p < 0.001$; soil $F_{8,278} = 5.06$, $p < 0.001$). Therefore, we used elevation and soil characteristics as control variables in the models of the number of species and abundance.

3.2 | Abundance and number of species

The response of the abundance of several taxa of producers, first-order consumers, saprotrophs, and saproxylic saprotrophs to forest succession yielded a U-shaped pattern. However, especially for taxa with low abundances or sample sizes, this response was not significant. We found no consistent response of higher order consumers to forest succession (Supporting Information Table S2). Nevertheless, the effect of the quadratic term of stages of forest succession was predominantly positive, which indicated a U-shaped response of most taxa (27 of 33 functional groups).

We found a positive quadratic term for forest successional stage for the number of species of producers and the majority of consumer taxa, which indicated a U-shaped response to forest succession. However, the number of species of most of the saprotrophic taxa did not strongly change along forest succession. Furthermore, the response patterns of saproxylic beetles and fungi were equally strong but opposing, with a U-shaped response of beetles to

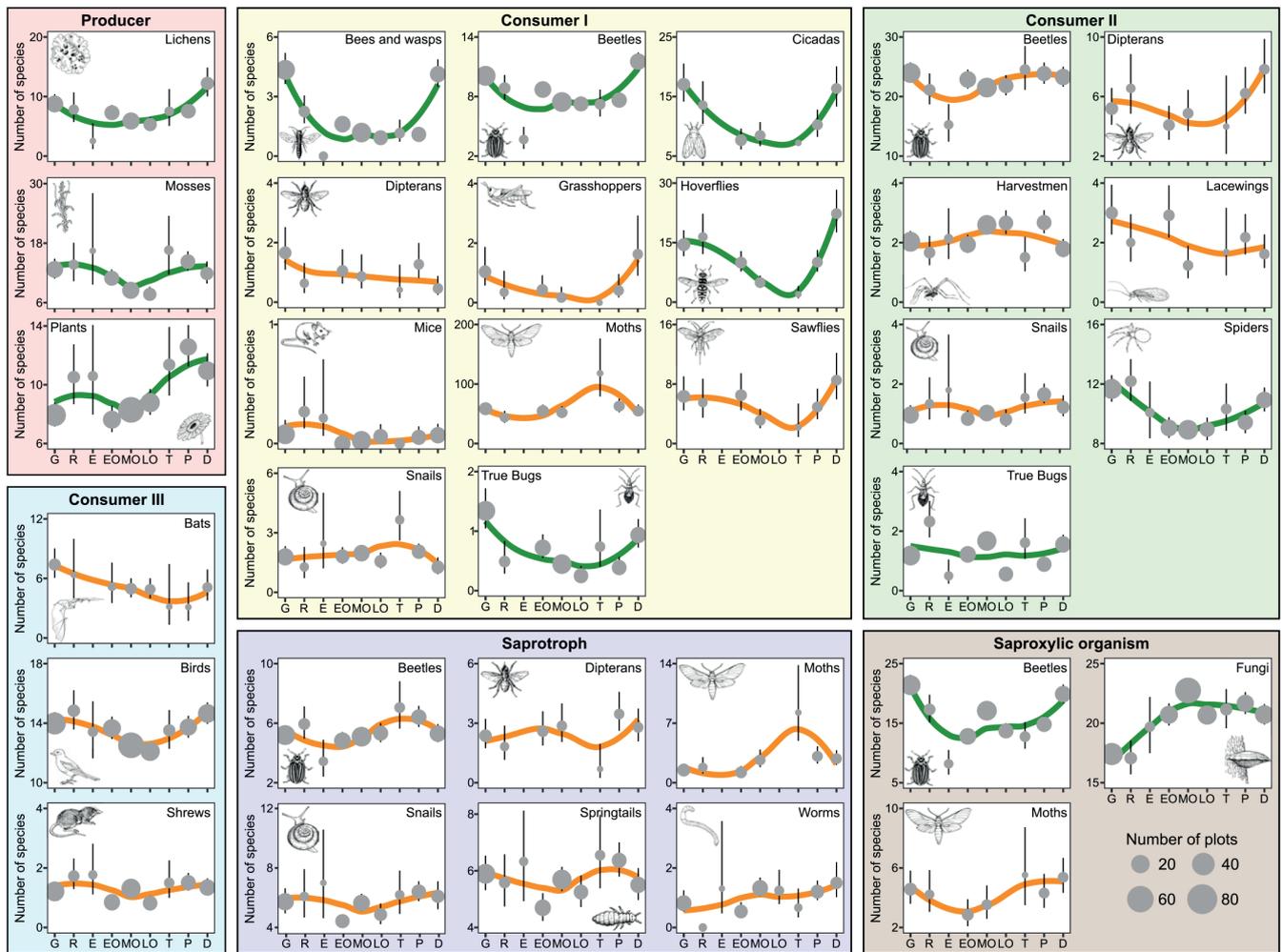


FIGURE 2 Variation in the number of species of 33 functional groups with stages of forest succession. The number of species was predicted using a generalized linear mixed model with Poisson error and an observation-level random effect. Predictor variables were the forest successional stage as an unordered factor, elevation, and soil parameters. For the predictions, elevation (800 m. a.s.l.) and soil parameters (mean value of the soil characteristics; PC1) were kept constant. Lines were generated by fitting a loess curve. Green lines indicate taxonomic groups whose number of species is significantly affected by the forest successional stage; orange lines indicate taxonomic groups whose number of species is not significantly affected by forest successional stage. Black bars indicate the SE within each successional stage. Note that data were not available for some taxonomic groups in some successional stages. Abbreviations are explained in Figure 1

forest succession and a hump-shaped response of fungi (Supporting Information Table S3, Figure 2).

When we controlled for abundances of each group in the models of the number of species, we found that abundances were the strongest predictor for every taxon analysed (Supporting Information Tables S3 and S4). However, a few taxa showed significant responses to forest succession even after we controlled for effects of abundance. Here, forest succession had a positive linear effect on plants and saproxylic beetles, i.e., over the course of forest succession, the number of species increased. The positive quadratic term in the model indicated a U-shaped response of the number of species of phytophagous beetles, true bugs, cicadas, predatory spiders, and dipterans to forest succession. By contrast, we found a negative quadratic relationship of the number of species of saprotrophic beetles and saproxylic fungi with forest succession, i.e., a hump-shaped response.

At the kingdom level, the number of plant species in the regeneration and establishment stages was particularly high, with a minimum in the optimum stages, and a secondary maximum in the terminal and decay stages of succession. Animals benefited from canopy openness, and the number of animal species in the gap stage was high, followed by a decrease in the number of species until the mid- to late-optimum stages, and a subsequent increase towards the maximum number in the decay stage. The number of species of wood-inhabiting fungi and lichens steadily increased over the course of forest succession, saturating during the plenter stage (Figure 3).

3.3 | Species composition

Overall, we found high levels of species dissimilarity among plots for all taxa (Supporting Information Figure S6). The Sørensen index

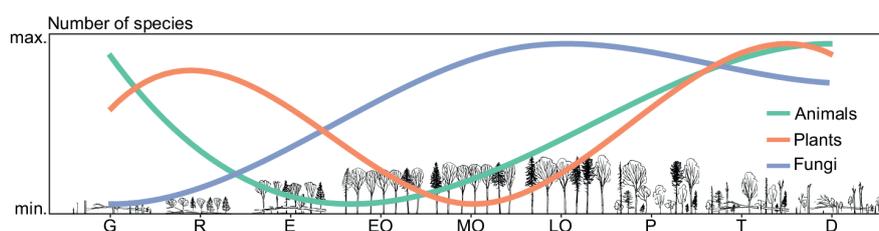


FIGURE 3 Normalized sum of predicted number of species along forest succession for the three kingdom animals, plants, and fungi. Lines were generated by fitting a loess curve. See Supporting Information Figure S9 for absolute values. Note that this figure is based on all plots, while Supporting Information Figure S9 is based on those plots that all taxa within the kingdom have in common. Abbreviations are explained in Figure 1

of dissimilarity exceeded 90% as a result of high spatial turnover; nestedness never accounted for more than 6% of the overall dissimilarity (Supporting Information Figure S6). Additive partitioning of the number of species showed that β -diversity among successional stages contributes most strongly to γ -diversity (Figure 4). Multivariate analysis of variance on distance matrices of taxonomic groups showed significant differences in species composition between successional stages for all taxa (Table 1). When we visualized the change in species composition along the course of forest succession by using partial correspondence analysis, a “circular” pattern emerged, i.e., early and late stages of succession had similar species compositions (Figure 5). Most unique species were found in the early and late stages of forest succession (Supporting Information Figure S7).

4 | DISCUSSION

Following our initial hypothesis (H1), our results showed that abundances and number of species of most taxa largely follow a U-shaped pattern along forest succession (Figure 2, Supporting Information Tables S2 and S3). However, counter to our expectations, saprotrophic organisms did not show a hump-shaped response to forest succession, and saproxylic fungi showed a hump-shaped response and not a U-shaped response to forest succession, which indicates that this latter species group does not closely track the accumulation of dead wood along forest succession. For most groups, the effect of forest succession was strongly affected by the abundances of the

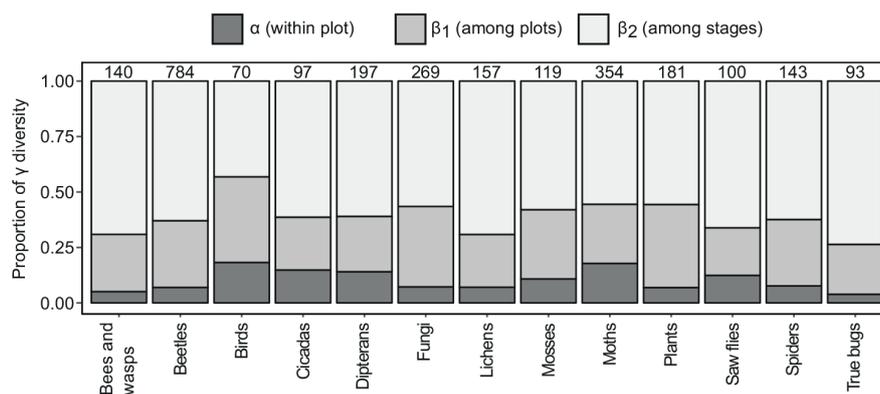
respective groups, which provides strong support for the *more-individuals hypothesis* (H2; Supporting Information Table S4). However, we found a response of several taxa to forest succession even after we controlled for the effect of abundance (Supporting Information Table S4). Overall, the diversity of plants, animals, and fungi showed diverging patterns along forest succession, with peak diversity values in early and late stages (Figure 3). We found the highest rates of species turnover among successional stages (Figure 4 and Supporting Information Figure S7) and the most similar assemblages in early and late successional stages (open canopies; H3; Figure 5).

4.1 | Stages of forest succession

Although the youngest and oldest successional stages of our study would appear to be different, they actually are almost the same because succession is cyclic. The generation of old trees decays contemporarily with the growth of a new generation. According to Supporting Information Figure S2, the difference between the youngest and oldest stages in our study is in the 30% threshold of the canopy projection area. Nevertheless, the gap stage and the decay stage in our study differ markedly as the canopy projection area in the gap stage is considerably lower than in the decay stage (Supporting Information Figure S11). Dead wood volume is not included in our criteria for gaps and regeneration stages, although stands with low and high volumes of dead wood are dissimilar, especially for saproxylic species.

In our study, the forest successional stages establishment, late optimum, and plenter were underrepresented due to forest history

FIGURE 4 Proportion of γ -diversity due to α -diversity and β -diversity among plots and among stages of forest succession according to additive diversity partitioning. Results are based on presence-absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 0 species). γ -Diversity for taxonomic groups is denoted above the respective bar



Taxon	Plots (n)	Species (n)	R ²	p-value		
				Forest successional stage	Elevation	Soil
Lichen	109	157	0.25	<0.001	0.004	0.755
Mosses	109	119	0.20	<0.001	<0.001	<0.001
Plants	282	181	0.24	<0.001	<0.001	<0.001
Cicadas	36	95	0.36	0.009	0.003	0.120
Beetles	178	783	0.21	<0.001	<0.001	0.066
Birds	283	72	0.19	<0.001	<0.001	0.003
Moths	35	354	0.33	0.009	<0.001	0.524
Sawflies	35	100	0.33	0.003	0.066	0.084
Spiders	173	143	0.29	<0.001	<0.001	0.016
True bugs	150	93	0.14	<0.001	0.002	0.142
Dipterans	36	197	0.33	<0.001	0.005	0.059
Bees and wasps	142	140	0.14	<0.001	<0.001	0.638
Fungi	286	269	0.20	<0.001	<0.001	0.015

TABLE 1 Effects of forest successional stages on species composition. Results from a multivariate analyses of variance using distance matrices (Adonis) based on presence–absence data. Significance was tested using 999 permutations. Those taxonomic groups not separated into trophic levels and with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 30 species) were analysed. R², coefficient of determination; soil, soil parameters of the plots. Significant effects are given in bold

(Supporting Information Figure S5). This highlights an important limitation of a space-for-time approach as applied here, which *inter alia* assumes that the analysed stands have a consistent management and disturbance history (Dieler et al., 2017). Thus, particularly our results concerning these underrepresented stages should be interpreted with caution. Future analyses could supplement chronosequence data with simulation approaches to more explicitly study long-term trajectories of forest succession. In turn, the comprehensive dataset compiled here (Supporting Information Table S3) could be linked to simulation model output in future studies, quantifying how future forest development (influenced by changing climate and disturbance regime) impacts biodiversity (Thom et al., 2017). Our LiDAR approach revealed advantages and also limitations in the classification of successional stages, namely the ability to capture canopy closure across large spatial scales but the difficulty in characterizing the understorey and downed dead wood. In this context, our results quantify the changes in biodiversity across forest succession and present a dynamic baseline for the monitoring of biodiversity change in temperate forests. Future changes (e.g., driven by changes in climate or land use), whether observed or projected, need to be considered in the light of the natural dynamics of forest succession, acknowledging that there are no static reference conditions for the diversity in temperate forests.

4.2 | Ecology of taxa

Most taxa responded according to our predictions derived from the variation in critical resources across the stages of forest succession (cf. Figures 1 and 2). The high number of species of producers in both the early and late successional stages is most likely driven by shifts in primary production from trees to herbs, mosses, and lichens, which depends on sunlight reaching the forest floor (Zehetgruber et al., 2017). This U-shaped response increases the

resource availability for phytophagous insects (Bouget & Duelli, 2004). Previous analyses in our study region have shown that the number of species of several arthropod groups increases with forest development from closed forest to open canopies (Müller, Bußler, Goßner, Rettelbach, & Duelli, 2008). For arthropods, this is partly an effect of increased activity of ectotherms under the higher temperatures associated with open habitats. However, our results indicate that for consumer groups, the effect of forest succession on the number of species is not only driven by more individuals but also reflects an increase in habitat heterogeneity (Supporting Information Tables S2 and S4). An increase in the abundance and number of species controlled for abundance of first-order consumers is frequently followed by an increase in the abundance of predators, such as spiders, beetles, and birds, which results from bottom-up trophic interactions (Campbell & Donato, 2014). However, we found that although the amount of dead wood was high on our study plots in early stages of forest succession (Supporting Information Figure S11), this was not reflected in the number of species of wood-decaying (saprophytic) fungi. This is consistent with the more detailed analyses of Krah et al. (2018), which show that the mere amount of dead wood is a relatively poor predictor of the number of these fungal species. The number of fungal species might be driven more strongly by the host tree species, host size, dieback history, and canopy openness than by the amount and heterogeneity of dead wood (Abrego & Salcedo, 2013; Heilmann-Clausen et al., 2015; Krah et al., 2018).

4.3 | Ecological mechanism: more-individual hypothesis and habitat heterogeneity hypothesis

With regard to the mechanisms driving biodiversity in temperate forests, our results suggest that the increase in the number

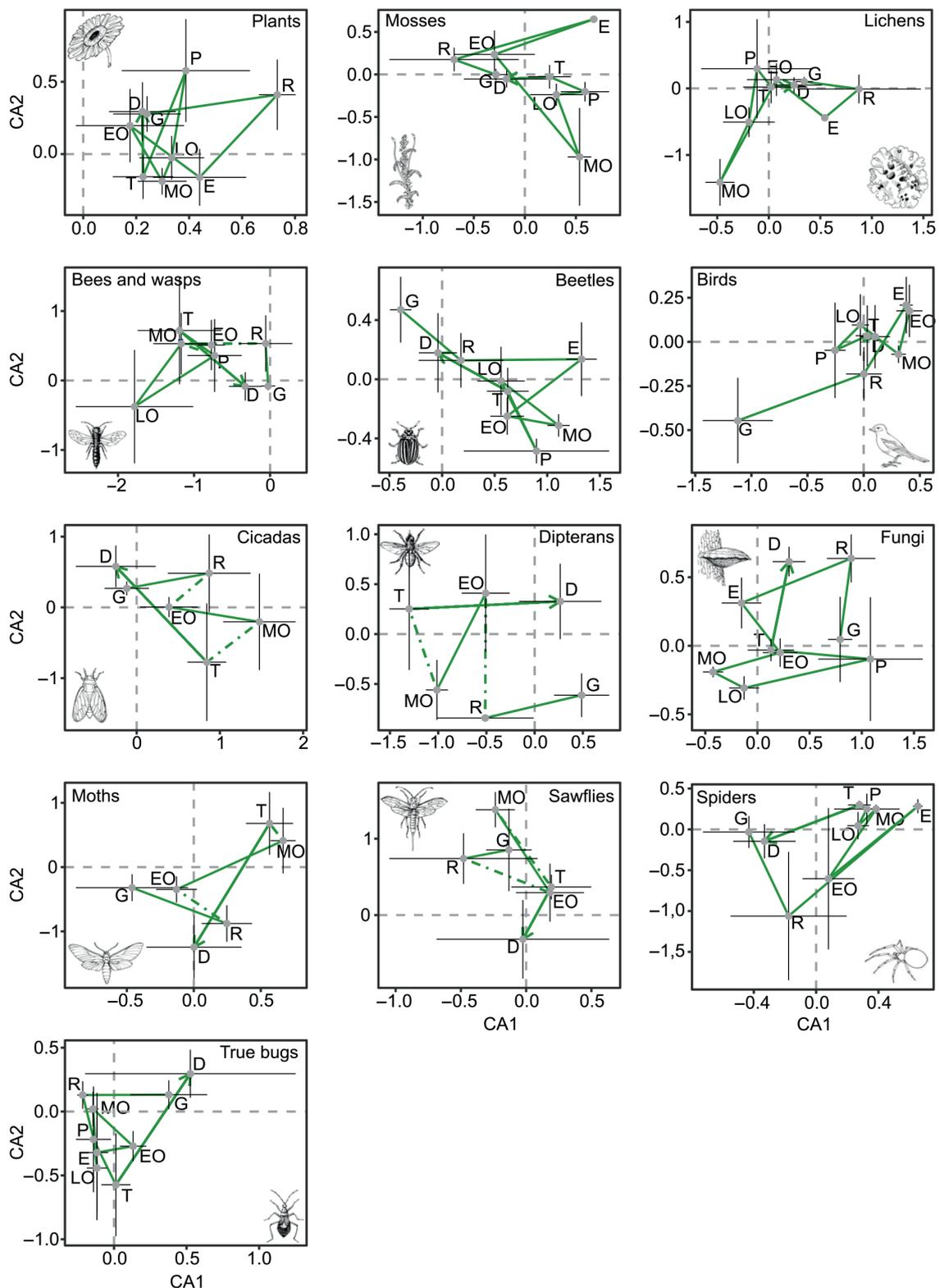


FIGURE 5 Partial correspondence analyses visualizing the response of species composition to forest succession. Results are based on presence–absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 30 species). Multivariate analysis of variance on distance matrices for the taxonomic groups showed significant differences in species composition between forest successional stages for all taxa (Table 1). Arrows indicate pathways along successional stages, black bars indicate the SE within each stage and green lines represent a significant influence of forest successional stage on species assemblages. Missing or underrepresented stages are marked with a green dashed line. CA1, first axis of correspondence analysis; CA2, second axis of correspondence analysis. Abbreviations explained in Figure 1

of species is largely based on higher abundances, as predicted by the *more-individuals hypothesis*. However, after controlling for abundances, the number of species of species-rich groups, such as beetles, true bugs, cicadas, spiders, and fungi, were still affected by the forest successional stages, which indicates variation in habitat heterogeneity in the form of host plants, microstructures or microclimates by facilitating coexistence, increasing niche space, and reducing local extinction risks (Stein & Kreft, 2015). Increased canopy openness in early and late successional stages (Supporting Information Figure S11) results in an increase in the number of species of vascular plants and mosses (Figure 3) owing to the occurrence of pioneer species with low shade tolerance. However, when we controlled for the effect of abundances, vascular plants showed a linear response to forest succession, which indicated that in early stages, the increase in the number of species is mainly driven by denser understorey vegetation and thus more individuals, rather than by habitat heterogeneity. The positive effect of forest succession on the abundance of vascular plants (Supporting Information Table S2) subsequently increases the diversity of herbivorous insects following the resource availability hypotheses. This increase in prey species might also support more predatory species. This interpretation is supported by the observed increase in the number of species of higher order consumers after we controlled for abundances.

High turnover rates between stands, as in our study (Supporting Information Figure S6), can be driven by sampling effort, with higher turnover rates with lower sampling effort locally, but also can occur because of ecological differences between stands. Our present study showed that species turnover along successional stages contributed most strongly to the overall γ -diversity (Figure 4). This indicates that for the promotion of forest diversity at the landscape scale, heterogeneity in forest successional stages is more important than within-stand heterogeneity, which is in accordance with the results of another recent multitaxon analysis of forest diversity in Europe's temperate forests (Schall et al., 2017).

4.4 | Implications for forest management

Based on our finding that both α -diversity and the number of unique species is highest in early and late stages of forest succession (Figures 2 and 3, Supporting Information Figures S7 and S10), we recommend that conservation efforts focus on these particular stages, which are currently underrepresented in Europe (Supporting Information Figure S8). Late successional stages cannot be produced artificially but have to develop naturally over long time periods (but see Speight, 1989 and Sebek, Altman, Platek, & Cizek, 2013 for techniques inducing premature senescence). α -diversity can be promoted in the short term by creating and maintaining early stages of succession, and this is an important option for ecosystem management (for experimental evidence, see Sebek et al., 2015). Canopy openings are a frequent result of logging activities, but these openings often lack the dead wood resources required by many saproxylic taxa (Heikkala,

Martikainen, & Kouki, 2016). Based on our findings, we recommend that in silviculture, the canopy should be opened by, e.g., creating gaps, to increase the photosynthetically active radiation at the forest floor, and some dead wood should be retained on site.

Because intermediate successional stages also support a wide variety of taxa and communities, especially plants, fungi, and lichen, a comprehensive conservation strategy has to maintain all successional stages on the landscape. However, for the conservation of regional biodiversity in multifunctional forests in Europe, this would mean that the proportion of stands in early and late successional stages should be increased.

All our implications only apply to the system we investigated, namely mixed mountain forests. However, more than half of Central Europe consists of mountain areas and most of the existing forests are concentrated there (CIPRA, 2007). Moreover, other studies have shown similar results on the uniqueness of, e.g., the early successional stages (e.g., Jacobs et al., 2007; Swanson et al., 2011; Tikkanen et al., 2007), which suggests a further transferability of our results to other forests systems across Europe or temperate mountain forests of other continents.

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AUTHORS' CONTRIBUTIONS

T.H., J.M., M.H., N.F., R.B. and H.P. conceived the idea and designed the methodology. T.H., C.B., and J.M. collected the data. T.H., N.F., R.B. and J.M. analysed and interpreted the data and led the writing of the manuscript with substantial input from all co-authors. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.213gk3r> (Hilmers et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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D Publication list

Publication list of the three articles include in this thesis.

Published

Hilmers, T., Avdagić, A., Bartkowicz, L., Bielak, K., Binder, F., Bončina, A., Dobor, L., Forrester, D.I., Hobi, M.L., Ibrahimspahić, A., Jaworski, A., Klopčič, M., Matović, B., Nagel, T.A., Petráš, R., del Rio, M., Stajić, B., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H. (2019) The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry (Lond)* 92, 512–522. <https://doi.org/10.1093/forestry/cpz035>

Hilmers, T., Friess, N., Bäessler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J. (2018) Biodiversity along temperate forest succession. *Journal of Applied Ecology* 55, 2756–2766. <https://doi.org/10.1111/1365-2664.13238>

Considered for publication pending minor revisions:

Hilmers, T., Biber, P., Knoke, Th., Pretzsch, H. (minor revisions needed) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in Mountain areas. *European Journal of Forest Research*

Publication list of further articles published in peer-reviewed and non-peer-reviewed journals during the time span of this thesis.

Articles in peer-reviewed journals

Hilmers, T., Bässler, C., Friess, N., Heurich, M., Müller, J., Seifert, L. (2018). Changes in forest structure in the Bavarian Forest National Park – an evaluation after 10 years of the BIOKLIM-Project. *Silva Gabreta* 161–170.

Torresan, C., del Río, M., **Hilmers, T.**, Notarangelo, M., Bielak, K., Binder, F., Boncina, A., Bosela, M., Forrester, D.I., Hobi, M.L., Nagel, T.A., Bartkowicz, L., Sitkova, Z., Zlatanov, T., Tognetti, R., Pretzsch, H. (2020) Importance of tree species size dominance and heterogeneity on the productivity of spruce-fir-beech mountain forest stands in Europe. *Forest Ecology and Management*

Pretzsch, H., **Hilmers, T.**, Biber, P., Avgadić, A., Binder, F., Bončina, A., Bosela, M., Dobor, L., Forrester, D.I., Lévesque, M., Ibrahimspahić, A., Nagel, T.A., del Rio, M., Sitkova, Z., Schütze, G., Stajić, B., Stojanović, D., Uhl, E., Zlatanov, T., Tognetti, R. (submitted) Evidence of elevation specific growth changes of spruce, fir, and beech in European mixed mountain forests during the last three centuries *Canadian Journal of Forest Research*

Sommerfeld, A., Rammer, W., Heurich, M., **Hilmers, T.**, Müller, J., Seidl R. (submitted) Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? *Journal of Ecology*

Articles in non-peer-reviewed journals

Hilmers, T., Knoke, Th., Biber, P., Pretzsch, H. (2017) Simulation verschiedener Waldumbauszenarien im Bergmischwald und deren Effekte auf verschiedene Waldfunktionen. Beiträge zur Jahrestagung. DVFFA – Sektion Ertragskunde

Hilmers, T., Avdagić, A., Bartkowicz, L., Bielak, K., Binder, F., Bončina, A., Dobor, L., Forrester, D.I., Hobi, M.L., Ibrahimspahić, A., Jaworski, A., Klopčič, M., Matović, B., Nagel, T.A., Petráš, R., del Rio, M., Stajić, B., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H. (2018) Zur Produktivität von Bergmischwäldern aus *Picea abies*, *Abies alba* und *Fagus sylvatica* in Europa. Beiträge zur Jahrestagung. DVFFA – Sektion Ertragskunde

Hilmers, T., Steinacker, L., Pretzsch, H. (2019) Zur Abhängigkeit der Zuwachsverteilung im Plenterwald von der Art und Größe der Bäume. Beiträge zur Jahrestagung. DVFFA – Sektion Ertragskunde