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The relationship between forest productivity and site factors analyzed on the basis of forest inventory data

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Preface

This PhD thesis provides a framework for five articles dealing with forest productivity in the context of global change. Before the main text starts, I would like to give an overview of the following chapters for a better navigation between articles and PhD thesis. Basically, the thesis is separated into two sections: First, the ‘Cumulative thesis’ which summarizes the underlying articles (three first authorships, two co-authorships). Second, the main section of the thesis that provides both theoretical foundation as well as reflections on the results of the articles. In chapter 1 the motivation for investigating forest growth and mortality in dependence on site factors is elaborated and objective as well as research questions are clarified. Chapter 2 provides background knowledge on forest productivity, tree mortality and site factors. Chapter 3 provides concise summaries of the methods and main results of the five publications that compose this thesis. Chapter 4 connects the results of the different studies and discusses them jointly. In chapter 5 a conclusion is drawn from the main findings, referring back to the research questions.

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Abbreviations

ΔB	above-ground wood biomass growth
AFT	accelerated failure time
AIC	Akaike information criterion
ATP	adenosine triphosphate
AWC	available water capacity
BA	basal area
BRT	boosted regression trees
C/N	carbon-to-nitrogen
dbh	diameter at breast height
DEM	digital elevation model
dg	quadratic mean diameter
ESM	earth system model
GAM	generalized additive model
GCM	general circulation model
MAVI	mean annual volume increment
N	stem number per ha
NFI	national forest inventory
NPP	net primary productivity
PAVI	periodic annual volume increment
PH	proportional hazards
RCP	representative concentration pathway
RD	relative density
S_{100}	survival probability at age 100
SDI	stand density index
SI	site index

Summary

In many regions changes in forest productivity and increases in tree mortality have been observed and have been attributed to changing site conditions due to climate change. In order to maintain the sustainability of the important ecosystem services provided by forests, forest management does not only have to react to the changes observed, but also has to anticipate the future development of productivity and mortality, as due to the longevity of trees and forest stands current regeneration decisions have to take these developments into account. Consequently, models are needed that predict productivity and mortality in dependence on site factors with the focus on climate factors.

Therefore, this thesis aims at developing statistical models that describe the relationship between productivity or mortality and site factors, particularly climate factors. The focus lies on predictions for Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in Germany. Large-scale forest inventories provide data covering the wide climatic gradients required for model application to future climate scenarios. Thus, at the same time, this thesis explores the potential as well as the limitations of large-scale forest inventories to investigate forest growth.

First, single tree height was modelled as a function of age and site factors using a generalized additive model based on data of the 3rd national forest inventory for Bavaria. Subsequently the residuals were modelled using boosted regression trees in order to allow for regionally complex interactions between the soil variables. Second, based on top height and age estimations site index was harmonized for the German and French national forest inventories for six species (Norway spruce, Scots pine (*Pinus sylvestris* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), European beech, sessile oak (*Quercus petraea* (Mattuschka) Liebl.), and pedunculate oak (*Quercus robur* L.)). For Norway spruce and European beech, the climate dependency of site index was modeled using generalized additive models. Third, above-ground wood biomass growth of spruce dominated stands estimated based on the 2nd and 3rd national forest inventories in Germany was modeled in dependence on site factors while accounting for the effect of stand density, again using a generalized additive model. Forth, the relationship between mean or periodic annual volume increment and species richness on global scale was fitted by a power function model using a geospatial random forest while accounting for climatic, soil and topographic influences. Fifth, mortality of Norway spruce and European beech was investigated by applying survival analysis to a pan-European data set (German forest damage survey, data on crown condition from Level I and Level II plots).

Across these five studies some general findings emerged. The relationship between summer temperature or temperature during the growing season and productivity was either monotonously increasing or followed an optimum curve depending on the climatic gradients of the respective underlying dataset. Where growth was not constrained by temperature, precipitation or water supply acted as limiting factor. In addition, productivity was modified by the influence of soil texture and nutrients as well as topography in the models for Bavaria and Germany. Besides the effects of abiotic factors, a positive effect of species richness on productivity was found. Vitality and survival were mostly affected by summer temperature and species proportion. In general, mortality risk in

mixed stands was lower, whereas rising temperatures led to an increase in mortality risk. Prediction accuracy of the models was limited due to uncertainty both on the side of the response variable as well as on the side of the explanatory variables. In addition, many factors influencing productivity or mortality could not be taken into account based on the underlying data. Still, the studies outlined the potential of statistical models that are based on large-scale forest inventory data to obtain general ecological relationships and assess trends in productivity and mortality under climate change.

Zusammenfassung

Vielerorts werden Veränderungen der Produktivität der Wälder und erhöhte Mortalitätsraten mit dem Klimawandel in Verbindung gebracht. Um die Nachhaltigkeit der Ökosystemdienstleistungen der Wälder zu gewährleisten, muss die Forstwirtschaft auf die beobachteten Veränderungen reagieren. Darüber hinaus erfordert es die Langlebigkeit von Waldbäumen auch zukünftige Entwicklungen bereits heute bei der Baumartenwahl zu berücksichtigen. Dafür werden Modelle benötigt, die Produktivität und Mortalität in Abhängigkeit von Standortfaktoren, insbesondere klimatischen Faktoren, vorhersagen.

Ziel der vorliegenden Arbeit ist es daher statistische Modelle zu entwickeln, die den Zusammenhang zwischen Produktivität bzw. Mortalität auf der einen Seite und Standortfaktoren auf der anderen Seite beschreiben. Der Schwerpunkt liegt auf Vorhersagen für Fichte (*Picea abies* [L.] Karst.) und Buche (*Fagus sylvatica* L.) in Deutschland. Die Daten von großräumigen Forstinventuren decken weite Klimagradienten ab, welche die Voraussetzung für eine Anwendung der Modelle auf zukünftige Klimaszenarien bilden. Damit lotet diese Arbeit gleichzeitig sowohl die Möglichkeiten als auch die Grenzen der Verwendung großräumiger Forstinventurdaten für die Waldwachstumsforschung aus.

Die vorliegende Arbeit setzt sich aus fünf Einzelstudien zusammen: (1) Die Einzelbaumhöhe wurde als Funktion von Alter und Standortfaktoren unter der Verwendung generalisierter additiver Modelle (GAM) basierend auf der dritten Bundeswaldinventur für Bayern modelliert. Auf die Residuen wurden *Boosted Regression Trees* angewendet um regional komplexe Wechselwirkungen zwischen Bodenparametern zu berücksichtigen. (2) Für die französische nationale Forstinventur und für die deutsche Bundeswaldinventur wurden basierend auf der Oberhöhe und dem Bestandesalter harmonisierte Maße für die Bonität für sechs Arten (Fichte, Kiefer (*Pinus sylvestris* L.), Douglasie (*Pseudotsuga menziesii* (Mirbel) Franco), Buche, Traubeneiche (*Quercus petraea* (Mattuschka) Liebl.), und Stieleiche (*Quercus robur* L.)) berechnet. Für Fichte und Buche wurde die Bonität in Abhängigkeit von Klimavariablen mittels GAM modelliert. (3) Basierend auf der zweiten und dritten Bundeswaldinventur in Deutschland wurde der oberirdische Biomassezuwachs von Fichten-dominierten Beständen berechnet und in Abhängigkeit von Standortfaktoren unter Verwendung von GAM modelliert. Ein zentraler Aspekt war dabei die Berücksichtigung von managementbedingten Dichteunterschieden. (4) Der Zusammenhang zwischen mittlerem bzw. periodischem jährlichem Volumenzuwachs und Artenreichtum wurde mit einer Potenzfunktion beschrieben und mittels *Geospatial Random Forest* angepasst unter Berücksichtigung des Einflusses von Klima, Boden und Topographie. (5) Basierend auf einem europaweiten Datensatz (Waldzustandserhebung in Deutschland, Level I und Level II in Europa) wurden für Fichte und Buche Überlebenszeitmodelle angepasst.

Aus diesen fünf Studien kristallisierten sich die folgenden allgemeinen Aussagen heraus: Der Zusammenhang zwischen Sommertemperatur bzw. Temperatur während der Vegetationsperiode und der Produktivität war, abhängig vom zugrundeliegenden Klimagradienten bzw. Datensatz, entweder monoton steigend oder folgte einer Optimumskurve. Wo das Wachstum nicht von der

Temperatur begrenzt wurde, wirkte der Niederschlag bzw. die Wasserversorgung limitierend. Zusätzlich wurde das Wachstum in den Modellen für Bayern und Deutschland durch den Einfluss der Bodentextur, der Nährstoffe sowie der Topographie modifiziert. Global wurde ein positiver Effekt des Artenreichtums auf die Produktivität gezeigt. Den größten Einfluss auf das Überleben hatten Sommertemperatur und Mischung. Im Allgemeinen war das Mortalitätsrisiko im Mischbestand geringer. Steigende Sommertemperaturen erhöhten das Mortalitätsrisiko. Die Vorhersagegüte der Modelle war durch Unsicherheit sowohl auf Seiten der abhängigen als auch der unabhängigen Variablen begrenzt. Zudem konnten viele Faktoren, die Produktivität und Mortalität beeinflussen, basierend auf den zugrundeliegenden Daten nicht berücksichtigt werden. Dennoch zeigten die Studien das Potential statistischer Modelle, die auf großräumigen Forstinventuren basieren, allgemeine ökologische Zusammenhänge anzupassen und Trends der Produktivität und des Mortalitätsrisikos im Klimawandel abzuschätzen.

Part I - Cumulative Thesis

Publication I: Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany)

Authors: Susanne Brandl, Wolfgang Falk, Hans-Joachim Klemmt, Georg Stricker, Andreas Bender, Thomas Rötzer, Hans Pretzsch

Journal: Forests

Impact Factor: 1.956 (2017)

Contribution: The statistical analysis was mainly done by Susanne Brandl. Georg Stricker tested different modelling approaches and conducted the automatic variable selection for the GAM supervised by Andreas Bender. The manuscript was written by Susanne Brandl supported by Wolfgang Falk. Hans Pretzsch, Thomas Rötzer, Wolfgang Falk, and Hans-Joachim Klemmt supervised the study and provided support in data analysis and interpretation.

Summary:

Combining national forest inventory (NFI) data with digital site maps of high resolution enables spatially explicit predictions of site productivity. The aim of this study is to explore the possibilities and limitations of this database to analyze the environmental dependency of height-growth of Norway spruce and to predict site index (SI) on a scale that is relevant for local forest management. The study region is the German federal state of Bavaria. The exploratory methods comprise significance tests and hypervolume-analysis. SI is modeled with a Generalized Additive Model (GAM). In a second step the residuals are modeled using Boosted Regression Trees (BRT). The interaction between temperature regime and water supply strongly determined height growth. At sites with very similar temperature regime and water supply, greater heights were reached if the depth gradient of base saturation was favorable. Statistical model criteria (Double Penalty Selection, AIC) preferred composite variables for water supply and the supply of basic cations. The ability to predict SI on a local scale was limited due to the difficulty to integrate soil variables into the model.

Publication II: Static site indices from different national forest inventories: harmonization and prediction from site conditions

Authors: Susanne Brandl, Tobias Mette, Wolfgang Falk, Patrick Vallet, Thomas Rötzer, Hans Pretzsch

Journal: Annals of Forest Science

Impact Factor: 2.357 (2017)

Contribution: Susanne Brandl conducted the data preparation and analysis and the literature research and was responsible for methods, results and discussion section. Tobias Mette developed the concept, supported the literature research and was responsible for introduction and proof reading. Wolfgang Falk, Patrick Vallet, Thomas Rötzer and Hans Pretzsch were responsible for consulting and proof reading.

Summary:

Key message: Static site indices determined from stands' top height are derived from different forest inventory sources with height and age information and thus enable comparisons and modeling of a species' productivity encompassing large environmental gradients.

Context: Estimating forest site productivity under changing climate requires models that cover a wide range of site conditions. To exploit different inventory sources, we need harmonized measures and procedures for the productive potential. Static site indices (SI) appear to be a good choice.

Aims: We propose a method to derive static site indices for different inventory designs and apply it to six tree species of the German and French National Forest Inventory (NFI). For Norway spruce and European beech, the climate dependency of SI is modeled in order to estimate trends in productivity due to climate change.

Methods: Height and age measures are determined from the top diameters of a species at a given site. The SI is determined for a reference age of 100 years.

Results: The top height proves as a stable height measure that can be derived harmoniously from German and French NFI. The boundaries of the age-height frame are well described by the Chapman-Richards function. For spruce and beech, generalized additive models of the SI against simple climate variables lead to stable and plausible model behavior.

Conclusion: The introduced methodology permits a harmonized quantification of forest site productivity by static site indices. Predicting productivity in dependence on climate illustrates the benefits of combined datasets.

Publication III: Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany (under review)

Authors: Susanne Brandl, Wolfgang Falk, Thomas Rötzer, Hans Pretzsch

Journal: Forest Systems

Impact Factor: 0.96 (2017)

Contribution: Susanne Brandl was responsible for data preparation and analysis, literature research and writing. Wolfgang Falk, Thomas Rötzer and Hans Pretzsch were responsible for consulting and proof reading.

Summary:

Aim of study: (i) To estimate site productivity based on German national forest inventory (NFI) data using above-ground wood biomass growth (ΔB) of the stand and (ii) to develop a model that explains site productivity quantified by ΔB in dependence on climate and soil conditions as well as stand characteristics for Norway spruce (*Picea abies* (L.) Karst.).

Area of study: Germany, which ranges from the North Sea to the Bavarian Alps in the south encompassing lowlands in the north, uplands in central Germany and low mountain ranges mainly in southern Germany.

Material and methods: Biomass growth of the stand between the 2nd and 3rd NFI was calculated as measure for site productivity. Generalized additive models were fitted to explain biomass growth in dependence on stand age, stand density and environmental variables.

Main results: Great part of the variation in biomass growth was due to differences in stand age and stand density. Mean annual temperature and summer precipitation, temperature seasonality, base saturation, C/N ratio and soil texture explained further variation. External validation of the model using data from experimental plots showed good model performance.

Research highlights: The study outlines both the potential as well as the restrictions in using biomass growth as a measure for site productivity and as response variable in statistical site-productivity models: biomass growth of the stand is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. However, it entails the difficulty of how to deal with the influence of management on stand density.

Co-authorships

Publication IV: Positive biodiversity-productivity relationship predominant in global forests

Authors: Jingjing Liang, Thomas W. Crowther, Nicolas Picard, Susan Wiser, Mo Zhou, Giorgio Alberti, Ernst-Detlef Schulze, A. David McGuire, Fabio Bozzato, Hans Pretzsch, Sergio de-Miguel, Alain Paquette, Bruno Hérault, Michael Scherer-Lorenzen, Christopher B. Barrett, Henry B. Glick, Geerten M. Hengeveld, Gert-Jan Nabuurs, Sebastian Pfautsch, Helder Viana, Alexander C. Vibrans, Christian Ammer, Peter Schall, David Verbyla, Nadja Tchebakova, Markus Fischer, James V. Watson, Han Y. H. Chen, Xiangdong Lei, Mart-Jan Schelhaas, Huicui Lu, Damiano Gianelle, Elena I. Parfenova, Christian Salas, Eungul Lee, Boknam Lee, Hyun Seok Kim, Helge Bruelheide, David A. Coomes, Daniel Piotto, Terry Sunderland, Bernhard Schmid, Sylvie Gourlet-Fleury, Bonaventure Sonké, Rebecca Tavani, Jun Zhu, Susanne Brandl, Jordi Vayreda, Fumiaki Kitahara, Eric B. Searle, Victor J. Neldner, Michael R. Ngugi, Christopher Baraloto, Lorenzo Frizzera, Radomir Bałazy, Jacek Oleksyn, Tomasz Zawiła-Niedźwiecki, Olivier Bouriaud, Filippo Bussotti, Leena Finér, Bogdan Jaroszewicz, Tommaso Jucker, Fernando Valladares, Andrzej M. Jagodzinski, Pablo L. Peri, Christelle Gonmadje, William Marthy, Timothy O'Brien, Emanuel H. Martin, Andrew R. Marshall, Francesco Rovero, Robert Bitariho, Pascal A. Niklaus, Patricia Alvarez-Loayza, Nurdin Chamuya, Renato Valencia, Frédéric Mortier, Verginia Wortel, Nestor L. Engone-Obiang, Leandro V. Ferreira, David E. Odeke, Rodolfo M. Vasquez, Simon L. Lewis, Peter B. Reich

Journal: Science

Impact Factor: 37.205 (2016)

Contribution: Jingjing Liang developed the concept, conducted the analysis and wrote the manuscript. Susanne Brandl contributed by preparing the German NFI data, by advising on the evaluation and interpretation of the German NFI data and by proofreading the manuscript.

Summary: The biodiversity-productivity relationship (BPR) is foundational to our understanding of the global extinction crisis and its impacts on ecosystem functioning. Understanding BPR is critical for the accurate valuation and effective conservation of biodiversity. Using ground-sourced data from 777,126 permanent plots, spanning 44 countries and most terrestrial biomes, we reveal a globally consistent positive concave-down BPR, showing that continued biodiversity loss would result in an accelerating decline in forest productivity worldwide. The value of biodiversity in maintaining commercial forest productivity alone—US$166 billion to 490 billion per year according to our estimation—is more than twice what it would cost to implement effective global conservation. This highlights the need for a worldwide reassessment of biodiversity values, forest management strategies, and conservation priorities.

Publication V: Climate change and mixed forests: how do altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech?

Authors: Carola Paul, Susanne Brandl, Stefan Friedrich, Wolfgang Falk, Fabian Härtl, Thomas Knoke

Journal: Annals of Forest Science

Impact Factor: 2.357 (2017)

Contribution: Carola Paul, Wolfgang Falk and Thomas Knoke conceived the original concept. Susanne Brandl carried out the statistical analysis of tree mortality data. Stefan Friedrich and Fabian Härtl supported with preparation of climate and economic data. Carola Paul applied statistical analysis to study site and carried out economic analyses. Carola Paul wrote the manuscript. All others jointly discussed and revised the text of the manuscript.

Summary:

Key message: Economic consequences of altered survival probabilities under climate change should be considered for regeneration planning in Southeast Germany. Findings suggest that species compositions of mixed stands obtained from continuous optimization may buffer but not completely mitigate economic consequences. Mixed stands of Norway spruce (*Picea abies L. Karst.*) and European beech (*Fagus sylvatica L.*) (considering biophysical interactions between tree species) were found to be more robust, against both perturbations in survival probabilities and economic input variables, compared to block mixtures (excluding biophysical interactions).

Context: Climate change is expected to increase natural hazards in European forests. Uncertainty in expected tree mortality and resulting potential economic consequences complicate regeneration decisions.

Aims: This study aims to analyze the economic consequences of altered survival probabilities for mixing Norway spruce (*Picea abies L. Karst.*) and European beech (*Fagus sylvatica L.*) under different climate change scenarios. We investigate whether management strategies such as species selection and type of mixture (mixed stands vs. block mixture) could mitigate adverse financial effects of climate change.

Methods: The bio-economic modelling approach combines a parametric survival model with modern portfolio theory. We estimate the economically optimal species mix under climate change, accounting for the biophysical and economic effects of tree mixtures. The approach is demonstrated using an example from Southeast Germany.

Results: The optimal tree species mixtures under simulated climate change effects could buffer but not completely mitigate undesirable economic consequences. Even under optimally mixed forest stands, the risk-adjusted economic value decreased by 28 %. Mixed stands economically outperform block mixtures for all climate scenarios.

Part II - Thesis: The Relationship between Forest Productivity and Site Factors Analyzed on the Basis of Forest Inventory Data

1 Introduction

1.1 Motivation

Productivity and mortality risk determine tree species suitability at a given site. Both aspects depend on environmental conditions: Climate and soil decide whether a tree survives and grows at a site or not. In addition, productivity and mortality risk depend on stand characteristics. Therefore, to a certain extent, forest management can influence tree species suitability (Fig. 1). Furthermore, biotic factors not explicitly considered in this thesis, like the presence of mycorrhiza, insects or fungi in an ecosystem, influence tree species suitability as well.

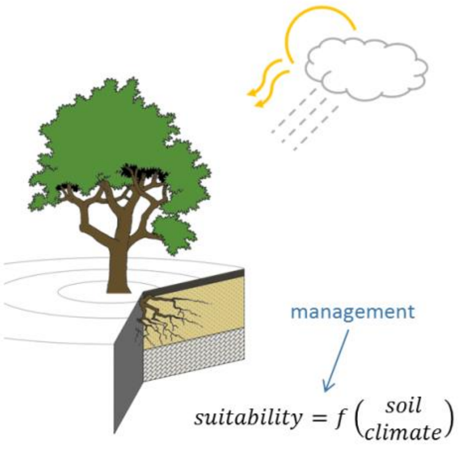

Fig. 1: Schematic representation of the influences on tree species suitability considered in the thesis.

Traditionally, tree species selection has been based on knowledge gained from experience or from the evaluation of experimental plots. For instance, knowledge about productivity obtained from experimental plots has been summarized in yield tables (e.g. Vannière 1984; Schober 1995). Both expert knowledge and yield tables are valid as long as site conditions remain the same (Skovsgaard & Vanclay 2013). However, due to global change, site conditions are changing. For Germany, climate models predict rising temperatures and changes in the precipitation regime (Brasseur et al. 2017). These changes will affect both productivity as well as mortality risk (Fig. 2).

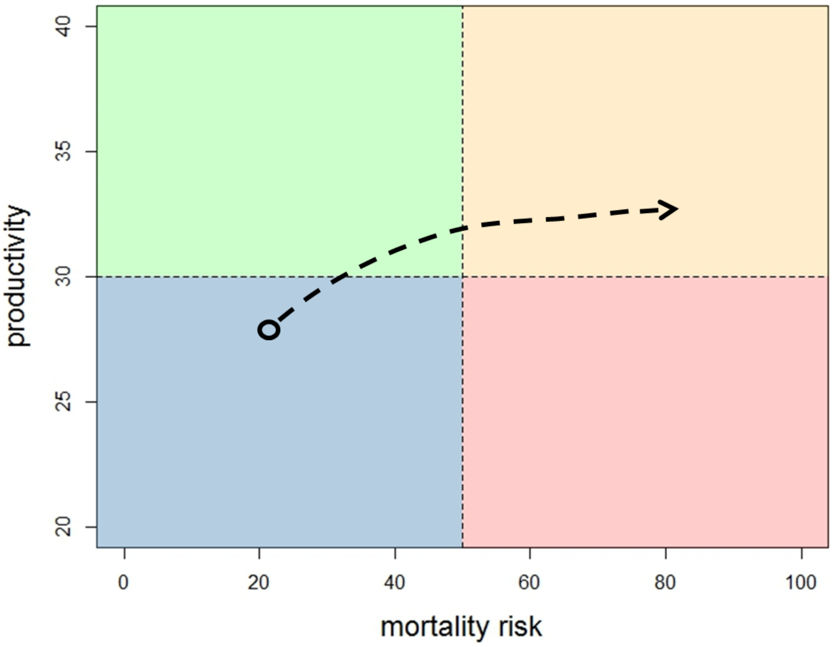

Fig. 2: Schematic representation of how productivity (e.g. site index in m) and mortality risk (in %) at a site might develop from the present (starting point) to the future (arrowhead).

Because of the longevity of trees and forest stands projected changes in site conditions have to be taken into account now when making regeneration decisions. Today's decisions do not only affect the sustainability of timber production but also the sustainable provision of other important ecosystem services of forests, e.g. recreation, biodiversity, water supply and protection from avalanches. Therefore, it is essential to estimate the effects of climate change on productivity and mortality risk of a tree species.

But how, for instance, can we assess the reaction of Germany's native tree species to temperatures and precipitation patterns that have not been observed so far in Germany? One option is to develop statistical models that describe the relationship between productivity or mortality risk and site factors and can thus predict trends in productivity or mortality risk under climate change. Ideally, these models are based on data that encompass the whole distribution range of the species including regions that already today experience the climate that is expected for Germany in the future: so-called climate analogies (Fig. 3; Kölling et al. 2016). Wide climatic gradients that cover the warm and dry margin of a species' distribution reduce the extrapolation range of the models when making predictions for the future.

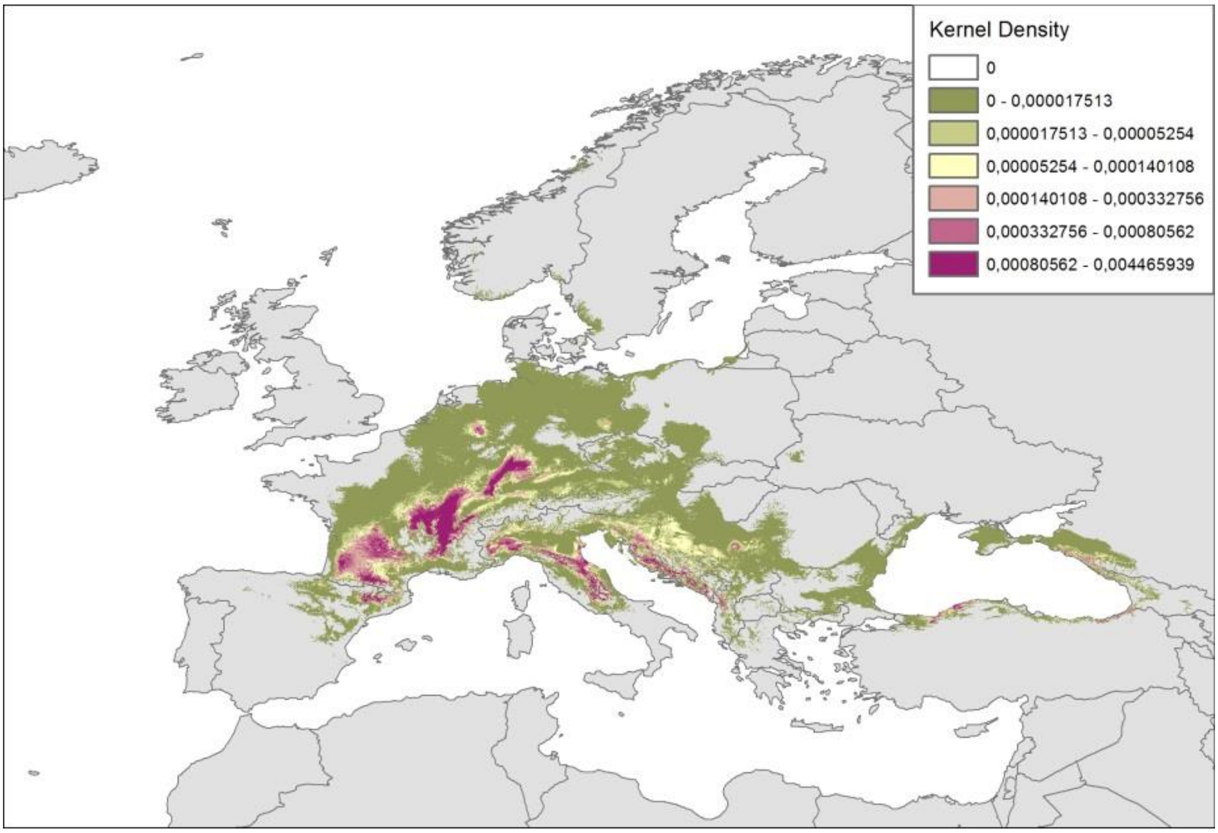

Fig. 3: Regions in Europe are colored that already today experience the climate that is predicted for Germany in the period 2061-2080: The higher the value of the Kernel Density the higher the probability that Germany will experience climate conditions (characterized by summer temperature and precipitation as well as winter temperature) in the future that are present already today in the respective region. Dark magenta marks the most likely climate analogies.

In general, these wide climatic gradients are obtained when using data that cover large geographic regions, although this is not a necessary requirement. Large-scale forest inventories provide this kind of data. Therefore, in the last decades large-scale forest inventories have gained in importance. In contrast, traditional forest growth and yield science has mainly been based on experimental plots.

Generally, there is a trade-off between information content and precision on the one hand and spatial representation and generality on the other hand. Experimental plots provide long time series with high temporal resolution and extensive measurements. The history of the plots is known and boundary conditions are controlled for. However, "[p]ermanent sample plots, while providing a decisive and renewed contribution in contrasted forest contexts worldwide […], rely on restricted and hardly representative sampling designs" (Bontemps & Bouriaud 2014). In contrast, large-scale forest inventories have the advantage of high spatial representation: The sampling design is usually based on a systematic grid that covers a wide variety of combinations of site conditions (Bontemps & Bouriaud 2014). A major caveat is that the history of sample plots is generally unknown. Thus, total yield cannot be calculated. Furthermore, information on tree and stand characteristics is incomplete or only approximated. For instance, the assessment of stand structure is sometimes based only on a few trees and age is sometimes only an approximation (Sharma et al. 2011). In summary, whereas experimental plots enable the deduction of principles that govern growth under varying stand structures and management regimes, the climatic gradients encompassed are mostly not large enough to assess the influence of climate change on growth. There lies the advantage of large-scale forest inventory data: Wide climatic gradients are covered. Adopting a space-for-time approach (Pickett 1989) the effects of changing climate conditions can be analyzed. Thus, findings based on large-scale forest inventory data can complement the insights on forest growth and yield gained from experimental plots.

Many large-scale studies are based on national forest inventories (NFI). Since 10–15 years ago, more and more countries have made their NFI data publically available. This offers a huge potential considering the need for wide climatic gradients explained above. However, when joining NFI data of various sources harmonization is needed. A joint effort to harmonize national forest inventories, focusing mainly on forest carbon and biodiversity estimation, has been undertaken in Tomppo et al. (2010) and McRoberts et al. (2012). Pan-European data of forest damage surveys (Level I) as well as data of intensive monitoring sites (Level II) have been collected and provided by the ICP Forests network (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) (ICP Forests 2018).

Although, facing climate change, linking forest productivity to site factors has moved into focus, “[t]he preoccupation for linking explicit site factors to site productivity is nevertheless ancient and has been regularly emphasized” (Bontemps & Bouriaud 2014). One central question is how to define and estimate forest site productivity. “Although essential, the estimation of forest site productivity has remained a central problem in forestry, inherent to the perennial nature of forest stands, and the subsequent needs to document harvests and mortality and capture the effect of ontogenetic trends” (Bontemps & Bouriaud 2014). The most common measure of forest site productivity is site index (SI), i.e. height at a given age. SI has become so well-established in forest research and practice that it is often taken as the true productivity rather than simply an indicator that may or may not reflect the site potential (Skovsgaard & Vanclay 2008). For instance, Assmann found that the total volume production of stands of the same age and SI can still vary ± 15 % in dependence on site characteristics (Pretzsch 2009). Moreover, the trend to structurally diverse mixed stands and thinning from above reduces the informative value of SI (Pretzsch 2009). Therefore, the need for alternative and more comprehensive measures of site productivity has been emphasized and it has been proposed to establish direct productivity-environment relationships based on NFI data (Bontemps & Bouriaud 2014).

This thesis relies on statistical models in order to capture the relationship between productivity and site factors. In contrast to process-based models that try to simulate cause-and-effect chains statistical models are fundamentally correlative analyses. This has to be kept in mind when interpreting the results of statistical models, especially when inferring causal relations (Bontemps & Bouriaud 2014). Nevertheless, statistical model techniques present a useful tool to investigate the relationship between productivity and site conditions. The more so, as so far process-based models in forest growth are afflicted with many shortcomings (Bontemps & Bouriaud 2014). Establishing the link between the indicator (a mere descriptive assessment of the site) and site factors, statistical models improve our ecological insight. As site factors themselves can serve as geocentric indicators of forest site productivity, the approach presented in this thesis can be viewed as explaining a phytocentric measure geocentrically (Bontemps & Bouriaud 2014). There are good reasons to do so: "From a forest management and planning perspective, the main advance in replacing direct site index measurements by predictions from a biophysical regression model is to allow inference on site productivity out of the restraining locations/range of presence of a given species and to allow comparisons across several species. From an ecological perspective, site index may also be viewed as reflecting an adaptive growth feature of tree species. Focusing on the key biophysical predictors of height growth may thus give indications on the fundamental constraints of tree species ecological niche and improve our understanding of tree species distribution" (Bontemps & Bouriaud 2014). Therefore, over the last decades, it has become very popular to develop statistical models that explain site productivity in dependence on environmental variables at varying spatial scales. Many of these models are based on national forest inventories. Although mostly SI is the measure of site productivity (e.g. Germany: Albert & Schmidt 2010; Nothdurft et al. 2012; France: Seynave et al. 2005; Seynave et al. 2008), a variety of other measures has been used as well, e.g. stand basal area increment (Charru et al. 2010; Charru et al. 2014), mean annual volume increment (Gustafson et al. 2003; Watt et al. 2010; Condés & García-Robredo 2012) or net primary productivity (NPP) (Wang et al. 2005).

As for Bavaria no productivity model existed so far, the first study of this thesis (Brandl et al. 2014) aimed at developing a model at the scale of Bavaria in order to take advantage of the high-resolution digital soil maps available for this federal state. However, the ability to predict future productivity is limited due to comparably small climatic gradients. This motivated the second study of this thesis (Brandl et al. 2018). Like the studies mentioned above, larger studies are still mostly constrained to national scale. Very few studies based on NFI data move to the transnational scale (e.g. Vilà et al. 2013; Avitabile & Camia 2018), as this involves dealing with the question of how to best derive a harmonic site productivity measure from different inventory sources. An approach is presented to derive a harmonized site index from German and French NFI as response variable in the productivity model. As most studies that are based on NFI data, this study relies on SI as indicator for site productivity. So far, attempts to derive more comprehensive measures of productivity from NFI data are rare. In the third study (Brandl et al. 2019, under review) an attempt is made to derive a more direct and comprehensive measure of productivity as response variable. Many studies have detected a positive effect of species richness or mixture on productivity (Paquette & Messier 2011; Vilà et al. 2013). However, the forth study (Liang et al. 2016) presented in this thesis is the first to show such an effect on a global scale.

Facing climate change the second aspect of tree species suitability, risk, becomes more important: In some regions climate conditions will change from optimum conditions to conditions closer to the warm and possibly dry margin of a tree species' distribution. Moreover, besides changing average climate conditions, extreme events become more likely and pronounced (Brasseur et al. 2017). An increase in stress-induced tree mortality has been observed in recent years (van Mantgem et al.

2009; Allen et al. 2010). Stress-induced tree death is usually the result of complex interactions between environmental influences and the disposition of the tree (Manion 1981). Although, tree death can be abrupt, it is more often the result of a complex and gradual process (Franklin et al. 1987). This makes modelling and predicting mortality challenging. Still, statistical model techniques that are commonly used to model mortality have been successfully applied in forest research. Leaving process-based models aside (overview in Adams et al. 2013), mortality is usually modeled in dependence on explanatory variables using logistic regression (e.g. Rich et al. 2007; Adame et al. 2010) or survival analysis. Logistic regression is based on a dichotomous (alive/dead) response variable modeled over uniform time intervals, e.g. the probability for an object to die within a five-year interval. Survival analysis was originally developed for medical science, but can be applied to a variety of scientific issues when the variable of interest is time to a defined event (Mills 2011). It is likely that not all objects under investigation experience the event of interest within the observation period, which means that their full survival time is unknown (right-censored observations). Some objects might not be observed from the start of the study but enter the study later on (left-truncated observations). Survival analysis can handle these two characteristic features of survival data.

For this reason, survival models have become more and more popular in forest research. Existing studies differ in various important aspects that affect the interpretation of the results: Some studies are based on regional datasets (e.g. Ahner & Schmidt 2011; Griess et al. 2012) while other studies are based on large-scale datasets (e.g. Neumann et al. 2017). Both semi-parametric (e.g. Neumann et al. 2017) and parametric (e.g. Staupendahl & Zuchini 2011; Neuner et al. 2015) approaches have been applied. Age (e.g. Neuner et al. 2015), observation length (e.g. Neumann et al. 2017) or dbh (Woodall et al. 2005) have been used as time variable in the model. In some studies explanatory variables are independent of time (e.g. Neuner et al. 2015), whereas other studies allow for changes in explanatory variables during the observation period (e.g. Nothdurft 2013). Some studies account for hierarchical data structures (e.g. Nothdurft 2013). Some studies take the left-truncation of the data into account (e.g. Schoneberg 2017), other studies ignore it. And of course, the studies differ in the pool of explanatory variables and the implementation of these variables (categorical, linear, non-linear). Finally, the definition of the mortality event has a huge impact on the results. All in all, there are comparably few studies that aim at explaining mortality with site factors. In addition, so far there is no study based on pan-European data that applies survival models on the species scale and uses a parametric approach with age as time variable, as it is done in publication V (Paul et al. 2019).

1.2 Objective and Research Questions

The first objective of this thesis is to investigate the relationship between forest productivity and site factors based on large-scale forest inventory data. On the one hand, there is the ecological aspect: the influence of site factors on forest productivity and the changes in forest productivity that can be expected under climate change. On the other hand, there is the methodological aspect: the potential and the limitations of large-scale forest inventory data to investigate forest growth. The second objective of this thesis is to investigate the relationship between mortality and site factors.

Statistical models of forest productivity in dependence on site factors are developed. These models permit to predict forest productivity under changing site conditions. One crucial question is how to define and estimate forest productivity, i.e. the response variable in the statistical model, from inventory data. Four options are presented here: In the first study mere single tree height is used as response variable. Thus, in addition to site factors single tree age is included as explanatory variable. In the second study the indicator of forest productivity is site index (SI), i.e. top height of the stand at age 100. The method developed to estimate site index can easily be applied to any inventory data that comprises height and age information of single trees. Thus, the use of site index permits to harmonize different inventory data and therefore to expand the environmental gradient of the data used for model fitting. In the third study annual above-ground wood biomass growth of the stand (ΔB) is tested as a more direct and comprehensive measure of forest productivity.

The three models have in common that the main interest is on the effects of climate and soil variables on productivity, although stand or tree characteristics may be included. However, forest productivity also depends on stand characteristics. For instance, it has been shown that species mixture affects productivity (Mina et al. 2018). Therefore, a study is presented that investigates the relationship between mean (and periodic) annual volume increment (MAVI) of the stand and species diversity.

As under climate change risk becomes more important, it is not enough to look at mere potential productivity to assess tree species suitability. Therefore, although the main focus of this thesis is clearly on productivity, another study is presented that analyzes the influence of site and stand characteristics on mortality risk. In contrast to ΔB and MAVI, the two measures on stand level that implicitly take mortality into account, mortality risk is analyzed separately. Subsequently, survival probabilities can be integrated into growth simulations or combined with predictions from productivity models. This approach enables to differentiate between regular and irregular mortality and facilitates a better understanding of the contributions of growth and mortality to overall yield. Combining predictions of productivity and risk (Fig. 2) can give a more complete picture of tree species suitability in the future and can serve as a tool for adaptive forest management (Benito-Garzón et al. 2013; Märkel & Dolos 2017).

All studies have in common that they use large-scale forest inventory data in order to develop statistical models that enable to predict forest productivity or mortality under changing site conditions. They differ in the scale of the underlying data, and thus in the scope of the respective model, going from regional (Bavaria: single tree height model), national (Germany: biomass growth model), transnational (Germany + France: site index model), continental (Europe: mortality model) to global (productivity-diversity model) (Fig. 4, Table 1). The scale of the model and the choice of the productivity indicator are mutually dependent. For instance, in contrast to SI, ΔB could not have been calculated for France, as ΔB requires repeated measurements that are currently not available in the

French NFI. Generally, a larger scale of the inventory data goes in line with a lower resolution and precision of the environmental data available. If the aim is to predict site productivity on a scale that is relevant for local forest management, a regional dataset combined with high quality environmental data permits to elaborate the regional differentiation of productivity without attempting to explain productivity in the entire distribution of the species. In contrast, geographically extensive studies have the advantage of larger climatic gradients and predictions for changing climate conditions become more reliable.

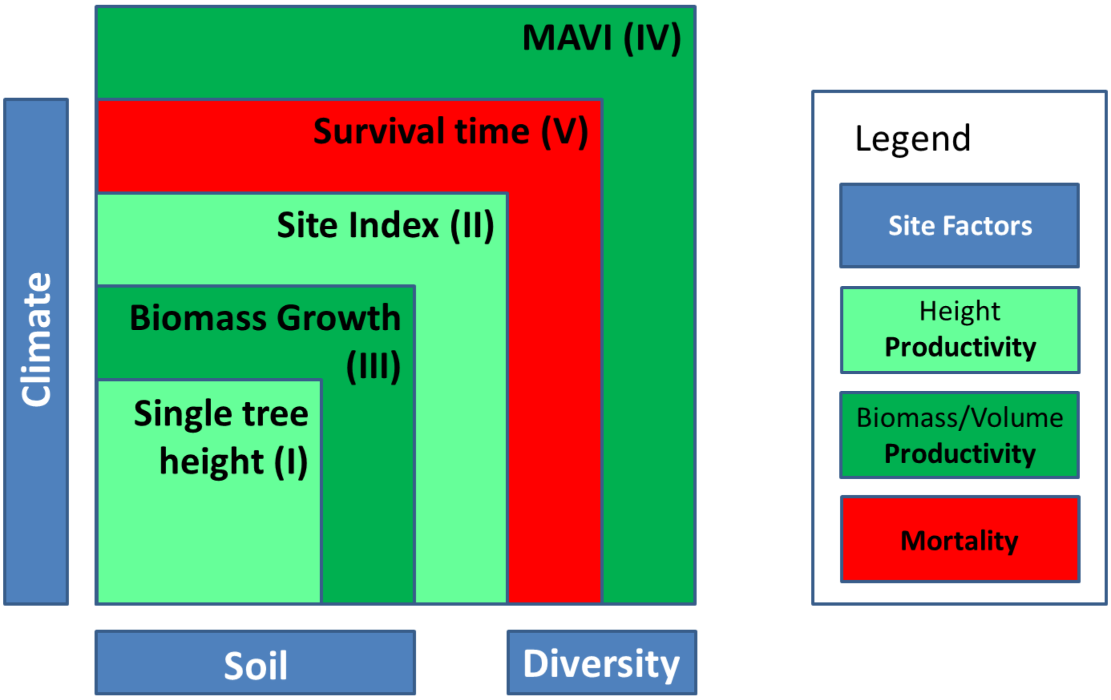

Fig. 4: Overview of the approaches presented in this thesis. The larger the square the larger the geographic range covered (not proportional). Height productivity is represented by light green color, whereas biomass or volume (MAVI) productivity of the stand is represented by dark green. Red represents mortality. The blue bars show which site factors are included in the final models.
The roman numbers refer to the underlying publications:
Publication I: Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany); Publication II: Static site indices from different national forest inventories: harmonization and prediction from site conditions; Publication III: Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany; Publication IV: Positive Biodiversity–Productivity Relationship Predominant in Global Forests; Publication V: Climate change and mixed forests: How altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech.

The following main research questions and hypotheses have been formulated:

Research questions:

- How much variance in height can be explained by spatially explicit environmental data?
- Can we predict height on a scale that is relevant for local forest management, i.e. with high local precision?

- How can we derive a harmonized measure for site productivity from different national forest inventories?
- Is it possible to derive a more comprehensive measure of site productivity than mere height from NFI data and explain it in dependence on site conditions?
- How is the influence of soil and climate on forest productivity?
- What are the trends in productivity due to climate change?
- How does diversity affect productivity and mortality?
- How is mortality risk affected by climate conditions?
- What are the advantages and disadvantages, i.e. the potential and the limitations, of NFI data to investigate forest growth?

Hypotheses:

(1) Productivity increases with rising temperatures until a certain threshold value is reached.
(2) Below a certain threshold value water supply acts as a limiting factor on productivity.
(3) Where temperature and water supply are not limiting, the influence of soil nutrients on height growth becomes apparent. Therefore, high-resolution soil variables improve height growth models.
(4) Biomass growth of the stand derived from NFI data is a better proxy for productivity than height growth or site index.
(5) Productivity of mixed stands is higher.
(6) Average climate conditions (30 year averages) act as predisposing factors: Mortality risk is higher at sites with high summer temperature. Mortality risk is higher at sites with low summer precipitation.
(7) Mortality risk is reduced in mixed stands.

Table 1: Overview of the publications, stating the aspect of tree species suitability (P: productivity, M: mortality) that is investigated, the response variable in the model, the model type, the scale of the study and the main data sources;
Publication I: Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany); Publication II: Static site indices from different national forest inventories: harmonization and prediction from site conditions; Publication III: Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany; Publication IV: Positive Biodiversity–Productivity Relationship Predominant in Global Forests; Publication V: Climate change and mixed forests: How altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech.

Publ.	**Aspect**	**Response variable**	**Model type**	**Scale**	**Inventory data**	**Climate data**	**Soil data**
I	P	single tree height (spruce)	GAM	Bavaria	German NFI (BMEL 2014; Riedel et al. 2017; BMEL 2019)	regionalized data of Germany's National Meteorological Service (DWD) (Hera et al. 2013)	Bavarian digital site information system BaSIS (Beck & Kölling 2013)
II	P	site index (spruce & beech)	GAM	Germany & France	German NFI (BMEL 2014; Riedel et al. 2017; BMEL 2019) & French NFI (IGN 2016)	WorldClim 1.4 (Hijmans et al. 2005)	France: NFI Germany: Soil Profile Database at NFI plots (Benning et al. 2019)
III	P	biomass growth (spruce)	GAM	Germany	German NFI (BMEL 2014; Riedel et al. 2017; BMEL 2019)	regionalized data of Germany's National Meteorological Service (DWD) (Dietrich et al. 2019)	Regionalized soil data (von Wilpert et al. 2016)
IV	P	PAVI or MAVI (all species)	power function model using geospatial random forest	global	various forest inventories worldwide	WorldClim 1.4 (Hijmans et al. 2005) CGIAR-CSI (Trabucco & Zomer 2009)	WISE30sec v.1 (Batjes 2015)
V	M	survival time (spruce & beech)	survival analysis	Europe	German Crown Condition Survey (Wellbrock et al. 2018), Level I and Level II (UNECE ICP Forests 2016; ICP Forests 2018)	WorldClim 1.4 (Hijmans et al. 2005)	-

GAM: generalized additive model; NFI: national forest inventory; MAVI: mean annual volume increment; PAVI: periodic annual volume increment

2 Theoretical Background

2.1 Forest Site Productivity

First, definitions for some terms used throughout the thesis are provided. Second, some basic concepts of yield science are presented.

2.1.1 Definitions

A *site* is a geographic location that is considered homogeneous in terms of its physical and biological environment (Skovsgaard & Vanclay 2008).

Site quality refers to the combination of physical and biological factors characterizing a site regarding their potential to sustain tree growth (Skovsgaard & Vanclay 2008).

Site potential is the capability of the site to produce plant biomass, irrespective of how much of this potential is utilized by the vegetation. It is determined by climatic and soil conditions (Skovsgaard & Vanclay 2008).

Forest site productivity is the production that can be realized at a certain site with a given genotype and a specified management regime, i.e. it is a quantitative estimate of the site potential realized by the concrete stand at the given site. Thus, forest site productivity depends both on climatic and soil factors inherent to the site and on management-related factors (Skovsgaard & Vanclay 2008). In contrast to this realized forest site productivity, *potential (forest site) productivity* refers to the productivity a "standard" stand would have at the given site. Thus, potential productivity solely depends on climatic and soil conditions and allows to compare sites regarding their site potential irrespective of the actual stand and management.

2.1.2 Indicators of Site Productivity

A basic distinction can be drawn between geocentric and phytocentric indicators of site productivity. Phytocentric indicators are based on characteristics of the vegetation, whereas geocentric indicators are based on physical characteristics of the site (climate, topography, soil). However, it is difficult to derive a quantitative measure of site quality from environmental characteristics and "[s]ince estimates of the potential productivity based on soil characteristics and climate are afflicted with high uncertainty, it is necessary to rely on measures of the growing stand itself" (Assmann 1961: 154). Therefore, in forestry dendrocentric indicators, a subcategory of phytocentric indicators, prevail: one or a combination of several easily measured tree or stand variables are used to indicate forest site productivity (Skovsgaard & Vanclay 2008).

2.1.2.1 Height

The classic dendrocentric indicator is height. Already von Baur (1881) postulated that mid height is "the most precise and only correct indicator not solely for the assessment of a […] stand but for its site class." The use of height as an indicator for forest site productivity is based on Eichhorn's rule, one of the fundamental tenets of yield science. It states that "independent of the site, a certain mid height corresponds to a certain stand mass". It is based on the following three relationships (Pretzsch 2009: 432):

The first relationship states that a forest stand at a given site follows a particular height development with age.

$$height = f(age)$$

The second relationship states that, independent of the site, a certain total volume yield corresponds to a given height.

$$Total\ volume\ yield = f(height)$$

Based on the first and second relationship the third relationship expresses total volume yield as a site-dependent function of age.

$$Total\ volume\ yield = f(age)$$

Assmann (1961) substituted mid height by top height, a modification that made Eichhorn's rule more stable against thinning, especially from below.

2.1.2.2 Site Index

The use of height as an indicator of forest site productivity relies on the belief that (in even-aged stands) the height growth of the largest trees is roughly independent of the stem number. Top height at a certain age, i.e. site index (SI), can then be used to assess and compare site productivity. The most common definition of SI is top height at age 100. The SI for a given stand can be derived based on either strip methods, indicator methods or yield tables. The construction of yield tables relies on longitudinal data. Thus, site index curves represent the true mean height growth over time of the underlying stands (Fig. 5). In contrast, strip methods do not require longitudinal observations, but only large data sets of age-height measurements (Fig. 6). Lower and upper boundary age-height curves are defined and the age-height spectrum is then divided into even spaced age-height curves (Pretzsch 2009: 436f). Unlike the yield tables, these static height curves do not represent true trajectories of the stands' height development, as a space-for-time approach is biased when site conditions are changing (Yue et al. 2016; Pickett 1989). However, the static height curves effectively lead to a balanced site index distribution over the age spectrum and make site index models stable against age trends. The indicator method relies on growth series obtained from stem analysis of individual sample trees. Knowing the height growth over time at a certain site it can be assigned to a determined growth series. One limitation of this approach is that the overall stand might not develop in the same way as the sample trees (Pretzsch 2009: 436f).

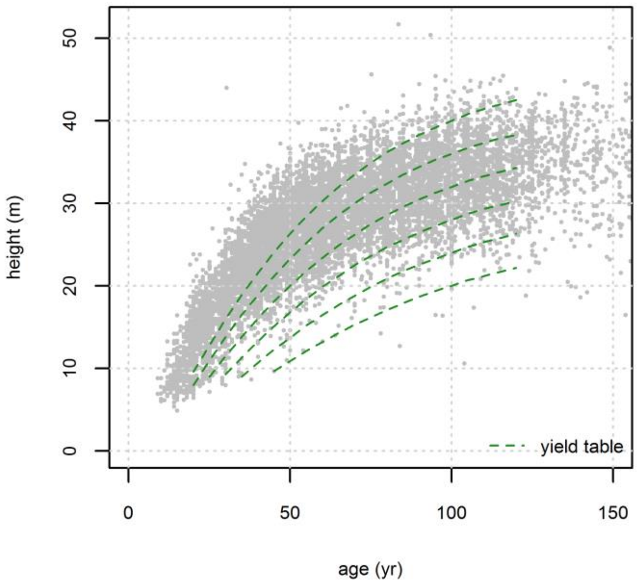

Fig. 5: Green lines: age-height development for different site classes of spruce yield tables from 1963 (Assmann & Franz). In the background age-height measurements of dominant Norway spruce trees in the 3rd German National Forest Inventory 2012 are plotted in grey: While old stands stay well within the height frame of the yield tables, young stands clearly exceed the given height frame. This is not because younger stands have been systematically planted at better sites but because they have experienced better growing conditions on the same sites. This example illustrates the difficulty in deriving a site index from yield tables under changing site conditions. From Brandl et al. (2018).

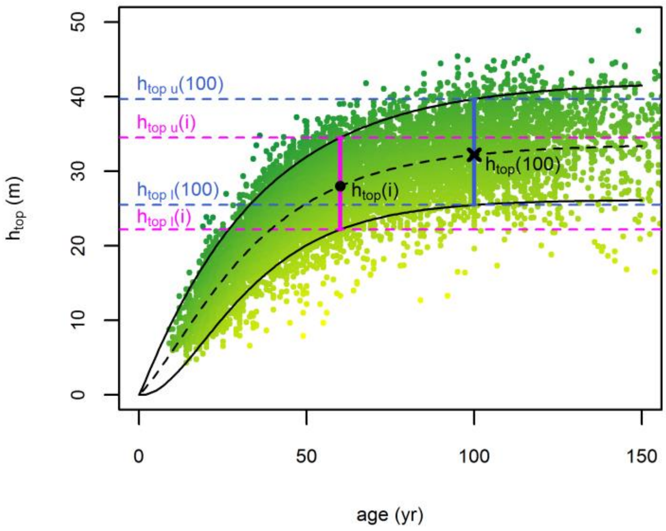

Fig. 6: Application of the strip method to NFI spruce plots (green points). The solid black curves mark lower and upper boundary age-height curves. The top height h_{top}(i) of a species in a stand at age i is translated to the corresponding height h_{top}(100) at the reference age of 100 years, i.e. the SI; The black dot marks an example stand at age 60 with a top height of 28 m. The black cross marks its translation to h_{top} at age 100, resulting in a SI of about 32 m. From Brandl et al. (2018).

2.1.2.3 Beyond Site Index (more direct and comprehensive measures of forest site productivity)

The use of SI as an indicator of productivity is based on Gehrhardt's first refinement of Eichhorn's rule stating that the relationship between total volume production of a tree species and stand height is identical for all site indices referred to as general yield level. However, later Gehrhardt specified different relationships between total volume production and stand height for each site index referred to as special yield level. Later, Assmann found that the total volume production of stands of the same age and SI can still vary ± 15 % in dependence on site characteristics referred to as subdivided special yield level (Pretzsch 2009). This implies that SI does not completely capture site productivity and in some cases more direct and comprehensive measure of forest site productivity might be preferable (Bontemps & Bouriaud 2014).

Forestry is focused on timber. Therefore, growth and yield are quantified traditionally in terms of stem-wood or merchantable wood volume, in units of m^3 (yield) or $m^3\ yr^{-1}$ (growth) per tree and hectare (Pretzsch 2009: 41).

Periodic annual increment (PAI, sometimes referred to as periodic annual volume increment PAVI) is one growth characteristic often used. It can be calculated based on repeated inventories:

$$PAI = \frac{V_{2\,remain} - V_{1\,remain} + V_{removed}}{t_2 - t_1}$$

The gross yield in volume is then:

$$Y_{V\,gross} = \int_{t=t_0}^{t_n} PAI\ dt$$

The mean annual increment (MAI, sometimes referred to as mean annual volume increment MAVI) is defined as the gross yield at time n divided by the stand age:

$$MAI = \frac{Y_{V\,gross}}{t_n}$$

(Pretzsch 2009: 56ff)

In contrast to forestry, ecological science is more interested in processes, e.g. the relationships between gross and net primary production, allocation patterns and turnover. Growth and yield are quantified by biomass (t) and biomass production (t yr^{-1}) or in energy equivalents. They characterize the biomass and energy balance of a system and constitute a more accurate estimation of production potential (Pretzsch 2009: 41). Gross primary productivity (GPP, t ha^{-1} yr^{-1}) is defined as the total biomass produced in photosynthesis over a given time period for a given area. Net primary productivity (NPP, t ha^{-1} yr^{-1}) is the part remaining after subtracting the loss through respiration and is equivalent to gross growth (GG). Subtracting the turnover (ephemeral turnover of plant organs + long-term turnover of whole individual plants) results in net growth (NG_{total}). In forestry, the intermediate variable, net growth + turnover of individuals, is a key measure when looking at growth and yield at the stand level (Pretzsch 2009: 42f).

An exhaustive overview of the terminology and quantities used in ecology and forest growth and yield science is provided in Pretzsch (2009, chapter 2).

As described above, the classic unit of growth and yield used in forestry is volume, whereas ecology focuses on biomass. More and more efforts are being made to bridge this gap and to bring forest science closer to ecological research (Pretzsch 2009: 64). Based on published scaling factors total tree biomass, stand biomass or NPP can be estimated from wood volume (Pretzsch 2009: 64). Another approach to obtain biomass estimates is to use functions that directly describe the relationship between dbh (and height) on the one hand and biomass on the other hand. These functions are often fitted based on dbh and height measurements as well as weights of the tree compartments of sample trees (e.g. Wirth et al. 2004; Cienciala et al. 2005; Hochbichler et al. 2006). However, due to the high expenses the underlying database is limited. In publication III of this thesis functions developed by Zell (2008) are used that permit to estimate single tree biomass from dbh and height measurements. These functions are not based on a sample of measured and weighed trees, but are derived based on allometric relationships: Based on data of the 2nd national forest inventory in Germany a set of representative trees was defined. Compact wood volume of these trees was estimated based on dbh, height and d_7 (diameter at 7 m). From merchantable wood volume total aboveground wood volume was deduced. Volume was then converted into biomass assuming different densities for merchantable wood volume and the expanded aboveground wood volume. Finally, species-specific biomass functions were developed, explaining single tree biomass in dependence of dbh and height.

2.2 Mortality

2.2.1 Stress-induced Mortality

Investigating tree mortality, a first distinction may be made between regular and irregular mortality. Regular mortality refers to self-thinning due to the increasing competition for resources as the stand develops, whereas irregular mortality refers to mortality due to extreme events and disturbances. However, this distinction may fall short when investigating trends in mortality due to climate change, as the self-thinning line is related to the carrying capacity of a site which in turn is affected by changes in average climate conditions. Thus, besides mortality due to extreme events, mortality due to intensified competition for resources that are affected by climate change, e.g. water supply, has to be taken into account. Mortality due to competition for light that is most strong in the juvenile phase can be excluded.

The decline disease concept (Manion 1981) presents a useful tool to structure and interpret stress-induced tree mortality. It differentiates between predisposing, inciting and contributing factors. Predisposing factors comprise climate and soil conditions, nutrient supply, genetic disposition, air pollutants and competition. These factors reduce vitality and growth in the long term. Inciting factors may be insect defoliation, frost, storms, drought and mechanical injury. They affect the physiological functioning of the tree and reduce its vitality and potential for pathogen defense in the short term leading to a rapid growth decline. Contributing factors may be bark beetles, fungi or viruses. They act in the short or long term. Contributing factors are often crucial and decide, whether the tree actually dies or not. All in all, stress-induced tree death is usually the result of an interaction between these factors and thus a complex and gradual process (Fig. 7) which means that the timing of tree death is highly variable and unpredictable (Franklin et al. 1987).

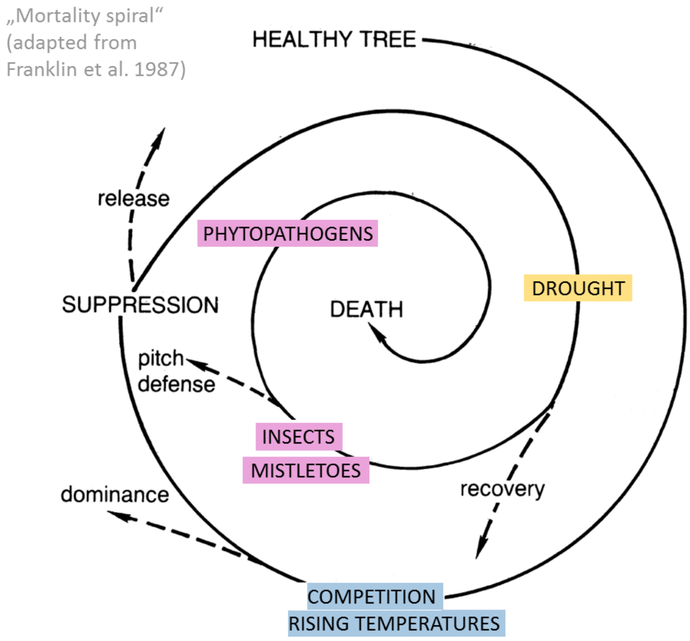

Fig. 7: Illustration of how predisposing (blue), inciting (yellow) and contributing (pink) factors can interact using as an example the study of Bigler et al. (2006) on Scots pine decline in the Valais in Switzerland: In the beginning, there is a healthy Scots pine tree. Competition and rising temperatures act as long-term predisposing factors and weaken the tree. Droughts further reduce its vitality and act as inciting factors. As a consequence of severe water stress, Scots pine lowers the resin content and the defense potential is reduced. Thus, it is more susceptible to contributing factors like mistletoe, insects, additional drought and phytopathogens. There is also an interaction between predisposing and contributing factors: Rising temperatures are likely to have favored insect development rates and increased their populations. Still, at each stage a tree might escape this spiral: for instance, suppression might be released or after a drought conditions might be more favorable and the tree recovers.

2.2.2 Survival Analysis

In short, survival analysis is the study of survival times and of the factors that influence them (Moore 2016). In many medical studies the variable of interest is the time between a treatment and the death of the patient. However, a variety of other questions can be investigated as well. For instance, in social science the time between marriage of a couple and their first baby might be analyzed (Broström 2012). In summary, survival analysis can be applied to a variety of scientific issues when the variable of interest is time to a defined event. However, not all objects under investigation might experience the event during the observation period, either because they are still alive at the end of the observation period or because they have dropped out of the study during the observation period for other reasons. This means that their true survival time is unknown. It is only known until what time they at least survived. These observations are right-censored. It is also possible that study objects are not observed from the beginning of the study but enter the study later on. These observations are left-truncated. Survival analysis can handle these two characteristic features of survival data (Fig. 8).

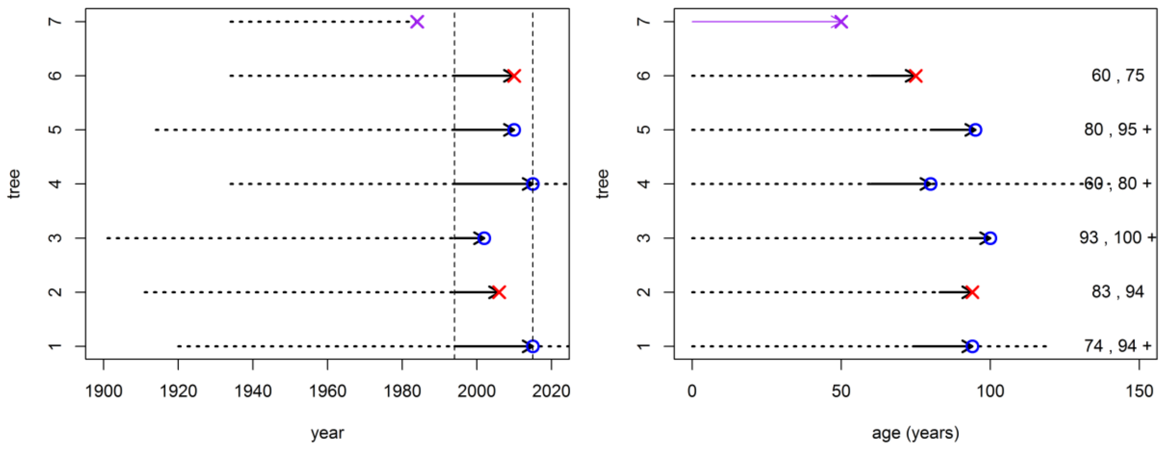

Fig. 8: Illustration of how the sampling design of a typical survival study can be applied to data of the forest damage survey. (a) There is a subplot of six trees. Observation goes from 1994 until 2015. The same trees are assessed annually. Concerning survival status there are three options: (1) The tree dies during the observation period. The event of interest (death) occurs (tree 2 and tree 6, marked with red crosses). (2) The tree survives, i.e. is still alive at the last survey in 2015 und thus right-censored (tree 1 and tree 4, marked with blue circles). (3) The tree is harvested during the observation period and is thus right-censored, as it cannot be known when it would have died naturally (tree 3 and tree 5, marked with blue circles). (b) Instead of observation time the age of the tree can serve as time variable in the survival analysis. Now the age at death matters or, if the event does not occur, the age until a tree at least survived (second number; if it is right-censored, this is denoted by a plus sign). Using age as time variable, there is no common survey start anymore, as the (hypothetical) study begin is now at age zero. The trees are observed for the first time at different ages, i.e. enter the study at different ages (first number). Data are left-truncated now. It is important to take this left-truncation of the data into account, as otherwise there would be a survivorship-bias. This is illustrated by tree 7. This tree has never been observed, because it died before the first survey. If a tree counted as living for ages younger than the youngest age it was observed, this would lead to a bias, as all the surviving trees would be considered but not the trees that died before the observation start.

Survival analysis depends on the distribution of survival times. There are two key ways of describing and modeling the distribution: the survival probability S(t) and the hazard rate h(t) (Moore 2016). The survival probability S(t) is the probability of an individual to survive to a time t. The hazard rate h(t) is the probability that an individual that is under observation at a time t has an event at that time, i.e. it is the instantaneous event rate for an individual who has already survived to time t (Fig. 9). S(t) and h(t) determine each other (Clark et al. 2003):

$$h(t) = -\frac{d}{dt}\log[S(t)]$$

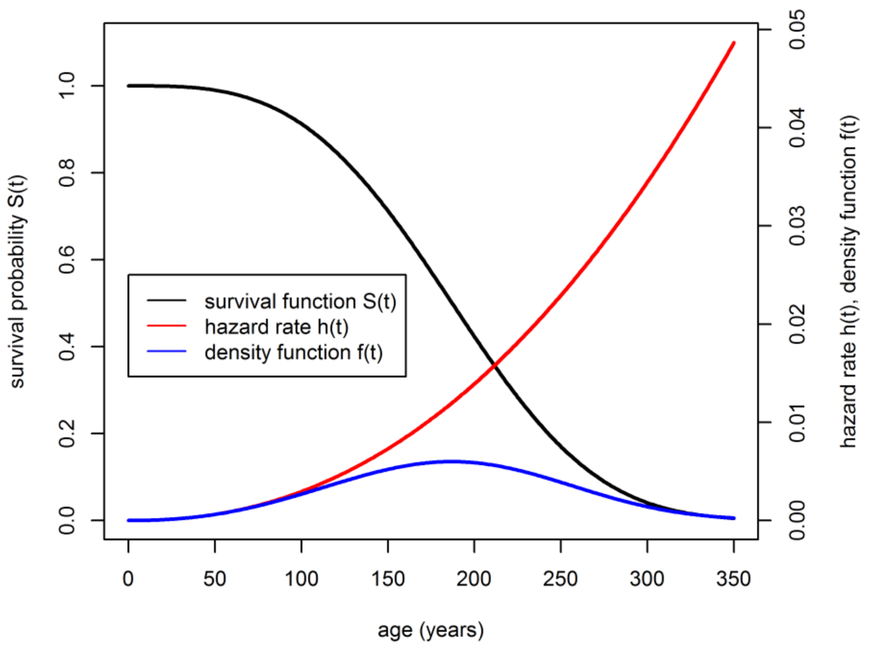

Fig. 9: Survival function S(t), hazard rate h(t) and density function f(t) for Weibull-distributed survival times. If one of the functions is known, the others are automatically determined.

Kaplan-Meier Estimator

The survival probability can be estimated non-parametrically from observed survival times using the Kaplan-Meier method (Clark et al. 2003). This estimator also provides the basis for graphical methods that are often used in the validation of parametric models. Under the assumption that events occur independently of each other, the cumulative survival probability is obtained by multiplying the probabilities of surviving from one time interval to the next (Clark et al. 2003). Table 2 and Fig. 10 illustrate the calculation of the Kaplan-Meier estimate.

$$S(t) = \prod_{t_i \le t} \frac{n_i - d_i}{n_i} = \prod_{t_i \le t} 1 - \frac{d_i}{n_i}$$

$$n_{i+1} = n_i - d_i - c_i$$

S(t): survival probability

t_i: time

n_i: observed individuals

d_i: dead individuals

c_i: censored individuals

Table 2: Illustration of how the Kaplan-Meier estimator is derived.

Age (t)	Observed trees (n)	Dead trees (d)	Censored trees (c)	Survivability (S(t))
1	0	0	0	1
2	6	0	0	1
…	…	…	…	…
7	85	1	24	0.988
8	68	0	5	0.988
…	…	…	…	…
12	141	1	8	0.981
…	…	…	…	…
15	207	6	28	0.953
…	…	…	…	…

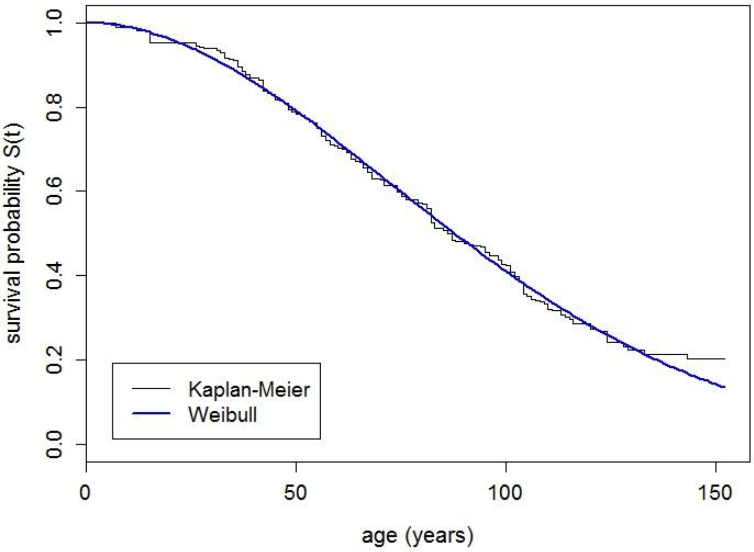

Fig. 10: Kaplan-Meier survival probabilities (step function). The blue line shows the fit of a Weibull distribution to the underlying survival times.

The Effect of Covariates on Survival

When modelling the effect of covariates on survival semi-parametric or parametric models are used. In parametric models survival time is assumed to follow a particular distribution e.g. a Weibull or log-normal distribution. They can be divided into proportional hazards models (PH) and accelerated failure time models (AFT). PH models assume a constant hazard ratio over time and covariates act multiplicatively on the hazard rate. The most commonly used approach in survival analysis is the semi-parametric Cox PH model, where the effect of covariates on the hazard rate is modelled parametrically but the baseline hazard remains unspecified (Kleinbaum & Klein 2012).

Accelerated Failure Time Models

In contrast to proportional hazard models, which estimate the baseline hazard function, AFT-models estimate the baseline survival function. Survival times are assumed to follow a distribution. The estimated covariates are multiplicative with respect to survival time.

The natural logarithm of the survival time is expressed as a linear function of the covariates (x_1, x_2, … x_p):

$$\log(T) = b_0 + b_1x_1 + b_2x_2 + \ldots + b_px_p + \varepsilon$$

where ε is a measure of residual variability in the survival times (Bradburn et al. 2003). The distributional form of this error term determines the regression model.

For Weibull distributed survival times the probability of survival S at a certain time t can be described by:

$$S(t) = exp\left[-\left(\frac{t}{\beta}\right)^{\alpha}\right] \; with\, t \geq 0$$

with α being the shape and β being the scale parameter. The shape parameter α represents the development of the hazard over time. A value of one expresses a constant risk over time, whereas smaller or larger values express a decreasing or increasing hazard rate over time, respectively. Covariates act on the scale parameter β. It is reparametrized for different values of coefficients using the following formula:

$$\beta_{\mathrm{reparametrized}} = \frac{\beta}{exp(b_1x_1) * exp(b_2x_2) * \ldots * exp(b_px_p)}$$

where b denotes the coefficient and x the value of the corresponding explanatory variable (Staupendahl & Zucchini 2011).

The exponentiated estimated coefficients correspond to ratios of survival times for any fixed value of S(t) and are also called acceleration factors. When the time ratio is greater (less) than one the covariate indicates a decrease (increase) of time to death – in other words it leads to a shrinking (stretching) of the baseline survivor function along the x-axis (Kleinbaum & Klein 2012).

2.3 Site Factors

“As a first aspect, biophysical predictors should be selected to covering abiotic factors relevant to tree growth, climate or soil related, which include their nutritional, energetic and water requirements […]. The perennial nature of tree species also comes along with some specific abiotic control to be acknowledged, e.g. related to winter climate in temperate and boreal ecosystems […]. This control may generally vary with the biomes considered […], with tree species phenology […], or with their other functional characteristics […]” (Bontemps & Bouriaud 2014).

Another aspect is the form of the relationship between the productivity indicator and the site factor. The growth of a tree follows a unimodal dose-effect curve when the site factor increases under ceteris paribus conditions (Fig. 11). The position and range of the ecological amplitude, the position of the optimum and the curve division into progressive and regressive branches depend on the site factor and the species. The path of the curve in the progressive or regressive branches can be assumed as linear, as monotone ascending or descending with or without inflection point (Pretzsch 2009: 381f).

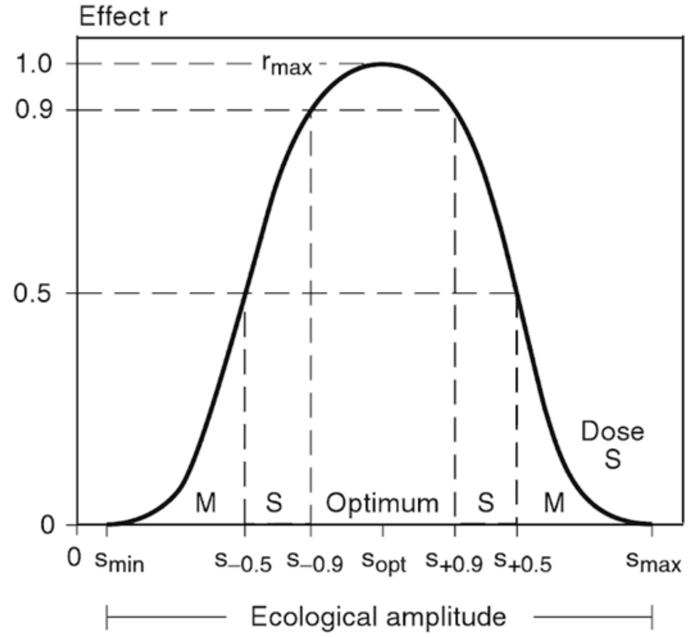

Fig. 11: Dose-effect curve. Ranges of optimum, suboptimum (S) and minimum or maximum (M) supply respectively within the ecological amplitude are indicated. From Pretzsch (2009: 382).

In practice, sometimes only the progressive or regressive branch of the dose-effect curve is relevant. For instance, data might only cover the range from the minimum to the optimum of a resource or the dose of a site factor that would be damaging simply does not occur naturally. Thus, a positive linear effect or a saturation curve might provide the best fit. For instance, the temperature modifier in the process-based stand growth model 3PG has the form of a unimodal dose effect curve, whereas the effect of relative available soil water is described by a saturation curve (Landsberg & Sands 2011). This also illustrates why statistical models should not be used for extrapolations beyond the range of the training data.

If in the interpretation of the results of this thesis the ecological plausibility of response curves is discussed, it refers to these general relationships between dose and effect.

A third aspect is the possibility of interactions between site factors. An interaction occurs when the effect of one explanatory variable (here: site factor) on the response variable depends on the value of a second explanatory variable (Fig. 12). In statistical models an interaction is introduced by including the product of the site factors as an additional covariate. Interaction terms can account for compensation or enhancement among site factors (Pretzsch 2009: 386). However, the lack of uniform coverage of all site factor combinations often leads to factor confounding. Therefore, in practice it might be difficult to fit interaction effects.

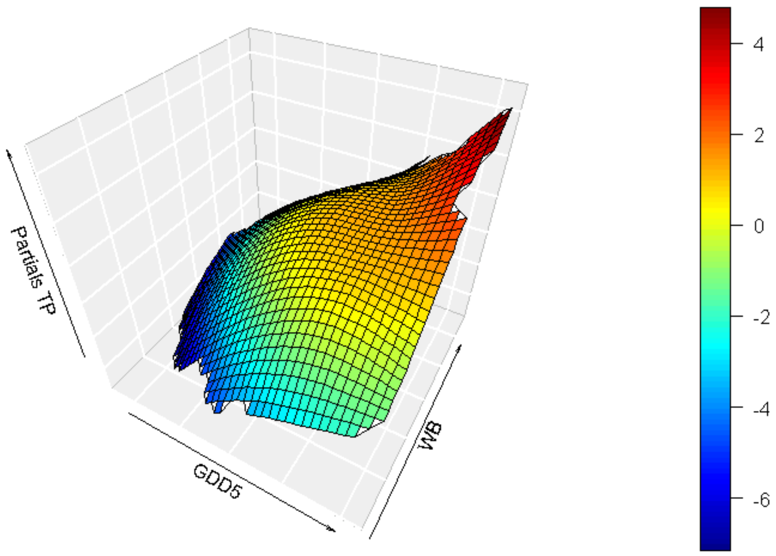

Fig. 12: Interaction effect between water supply (WB) and growing degree days (GDD5) fitted for the single tree height model (publication I). Partial effects of the tensor product on height (in m) are greatest, i.e. greatest heights are reached, when both WB and GDD5 are high. If one of the two factors is limited, greatest heights cannot be reached irrespective of the other factor. From Brandl et al. (2014).

2.3.1 Climate

Growth is determined by underlying physiological processes. The external conditions that affect the rates of these processes include, besides nutrients and water, the weather variables solar radiation, air temperature, humidity and wind (Landsberg & Sands 2011). Between these variables there are usually strong correlations. For instance, solar radiation is usually lower on cloudy or wet days, whereas humidity is usually lower when it is warmer (Landsberg & Sands 2011). In the geographical range considered in publications I, II and III solar radiation is strongly correlated with temperature.

Therefore, only temperature is used to explain growth. “Temperature is a key determinant of the rate of metabolic processes and hence has a major impact on plant growth, especially on carbon balance through its influence on photosynthesis and respiration. It also affects plant development, for example through effects of temperature on the timing of bud burst and flowering. Temperature affects the water balance of the plant, and the dynamics of soil water storage, through its effects on evaporation and transpiration. Finally, extreme temperature induces leaf damage that affects plant growth, disrupts enzyme systems, or induces extreme water stress and loss of turgor” (Landsberg & Sands 2011).

As forests do not occur in low rainfall regions of the world, water is obviously another essential controlling factor. The water balance of stands depends on precipitation, interception, run-off, evaporation and drainage. It determines canopy conductance and the ability of the trees to absorb CO_2 for photosynthesis (Landsberg & Sands 2011). Therefore, precipitation is an essential factor determining growth.

In this thesis climate averages are used. As the productivity indicators summarize growth over time it makes sense to explain this overall growth response in dependence on average conditions (publication I, II, IV, V: 30 year averages; publication III: averages over the measurement period between 2nd and 3rd German NFI). Of course, productivity and even more mortality risk are also influenced by extreme weather events like droughts. However, the influence of extreme weather events is difficult to capture given the database. Therefore, explanatory variables in the mortality models are constrained to predisposing factors, i.e. average climate conditions. For instance, warm and dry conditions over a long period can weaken trees and predispose them to inciting and contributing factors. Furthermore, a correlation between average climate conditions and extremes can be assumed: For instance, regions with higher average temperature possibly experience more drought events and thus the probability of a bark beetle outbreak is higher.

Future climate projections are based on the calculations of general circulation models (GCM). A GCM models the general circulation of the planetary atmosphere or the ocean. Recently, GCMs are applied more and more often as components of Earth system models (ESM). Besides atmosphere, ocean, land surface and sea ice, ESM take the carbon cycle and other interactive components like aerosols into account. Regional models are used to downscale their output in order to enable a more detailed and realistic prediction at the regional scale (Brasseur et al. 2017). For the 5th IPCC report (IPCC 2014) four representative concentration pathways (RCP) have been selected for climate modeling, i.e. as input for ESMs. Representative concentration pathways are greenhouse gas concentration trajectories that cause a corresponding radiative forcing. The four RCPs selected are 2.6, 4.5, 6.0 and 8.5 (named after the radiative forcing values (in W m^{-2}) in the year 2100 relative to pre-industrial values). Simulations were conducted with 40 different ESMs (Brasseur et al. 2017).

2.3.2 Soil

Chemical and physical soil properties influence growth and vitality. For instance, the water supply of the tree is not only affected by precipitation but also by soil conditions. Available water capacity (AWC) characterizes the amount of soil water that can be used by the tree. As it is laborious to measure the water retention curve and determine AWC in that way, AWC is more often estimated using pedotransfer functions based on soil texture, soil depth, density, skeletal fraction and humus (e.g. Wösten et al. 1999; Teepe et al. 2003). Sometimes the more readily available characteristics of soil texture percentage of clay, silt and sand in the soil serve as proxies of water availability (Cosby et al. 1984).

Besides water supply, a balanced nutrient supply is important. Shortage of any nutrient limits the capacity of the tree to efficiently use solar radiation and to convert photosynthates into biomass. Macro-nutrients are nitrogen, phosphorus, sulfur, calcium, magnesium and potassium. Apart from nitrogen, all nutrients originally stem from the weathering of parent minerals forming the soil. Nitrogen forms part of chlorophyll molecules and enzymes. Phosphorus is needed to build ATP. Potassium is needed to regulate the charge balance across plant membranes. Magnesium forms part of the chlorophyll molecule and plays a role in enzyme activation. Calcium forms part of cell walls, acts as an enzyme co-factor and has a function in membrane permeability (Landsberg & Sands 2011). The amount of nutrients required is determined by the growth rate of the tree. However, actual nutrient absorption rates depend on soil moisture, temperature, the effectiveness with which the soil is exploited by roots and the presence of mycorrhiza as well as the chemical availability of the nutrients (Landsberg & Sands 2011).

3 Methodology and Results

3.1 The Relationship between Single Tree Height and Site Factors (Publication I)

Tree and stand characteristics were derived from data of the 3rd German NFI (2012) for the federal state of Bavaria. Dominant Norway spruce trees of the Kraft classes 1 and 2 with height measurements and within an age range of 30 to 150 years were selected from the angle count sample with basal area factor 4. Basal area (BA) was estimated from the angle count sample with basal area factor 1. Terrain data were derived from a digital elevation model (resolution 50 m). Monthly means of temperature and precipitation for the period 1971-2000 were calculated from climate data that had been regionalized to a 50 m grid based on weather stations of Germany's National Meteorological Service (DWD). Soil data were provided by a digital site information system developed at the Bavarian State Institute of Forestry. The study consisted of two parts: (1) an exploratory data analysis and (2) a model of single tree height in dependence on age and site factors. (1) In order to make the heights of trees of varying ages comparable, the heights were divided by the fit of a 95 %-quantile regression of height against age resulting in scaled heights. Environmental variables were grouped according to the quartiles of scaled height distribution and tested for significant differences between the groups. In order to identify the environmental variables that best separate the 10 % of plots with lowest heights from the 10 % of plots with greatest heights a hypervolume analysis was conducted. (2) Height was modeled as a function of age, environmental variables and basal area of all trees using generalized additive models (GAM). Variable selection was done in three steps: double penalty selection on the smooth terms, AIC backwards selection and checking the ecological plausibility of the partial effects. Relative root mean squared prediction error (RMSPE) was calculated based on 10-fold cross-validation. In order to allow for regionally complex interactions between soil variables the residuals of the GAM were modeled using boosted regression trees (BRT).

(1) Highest and lowest growth could be separated best by 6-dimensional hypervolumes defined by temperature during growing season (T_5to9), water balance during growing season (WB), soil calcium (Ca), potassium (K), magnesium (Mg) and clay content. T_5to9 showed a positive effect on height growth, at the cold margin it acted as limiting factor. There was a trend to greater heights with better water supply. On Bavarian scale, it was difficult to identify a clear effect of soil nutrients on tree height. However, there was a weak positive effect of K on height growth and the medians of scaled heights for the five types of the depth gradient of base saturation followed an optimum curve. (2) Besides age and BA, the interaction between growing degree days (GDD5, threshold: 5 °C) and WB, base saturation as well as the relief parameters mass balance index (MBI) and soil moisture index (SMI) were included in the GAM (adjusted $R^2 = 65.2$ %, RMSPE = 0.976 m). BA had a positive effect on height. Greatest heights were predicted when both GGD5 and WB were high, whereas both variables acted as limiting factors at low values. High BS had a negative effect on height. For SMI an optimum relationship was fitted. The model predicted greater heights for lower slopes and valleys (MBI < 0) and lower heights for upper slopes (MBI > 0). Applying BRT to the residuals resulted in

ecologically plausible smoothed response curves for the soil variables nitrogen, silt content, K and Mg. The correlation coefficient between calculated and predicted residuals was 0.25. Adding the predicted residuals to the heights predicted by the GAM increased the R^2 to 67.5 %. The final model was used to generate a site index map for Bavaria. Highest growth was predicted for the southern part especially the west of the tertiary hill country (Swabia) and the Spessart in the northwest. In contrast the eco-regions “Fränkische Platte” and “Frankenalb” and the northeastern part of Bavaria were not very favorable for spruce growth. The model allows to estimate local trends in productivity due to climate change (Fig. 13).

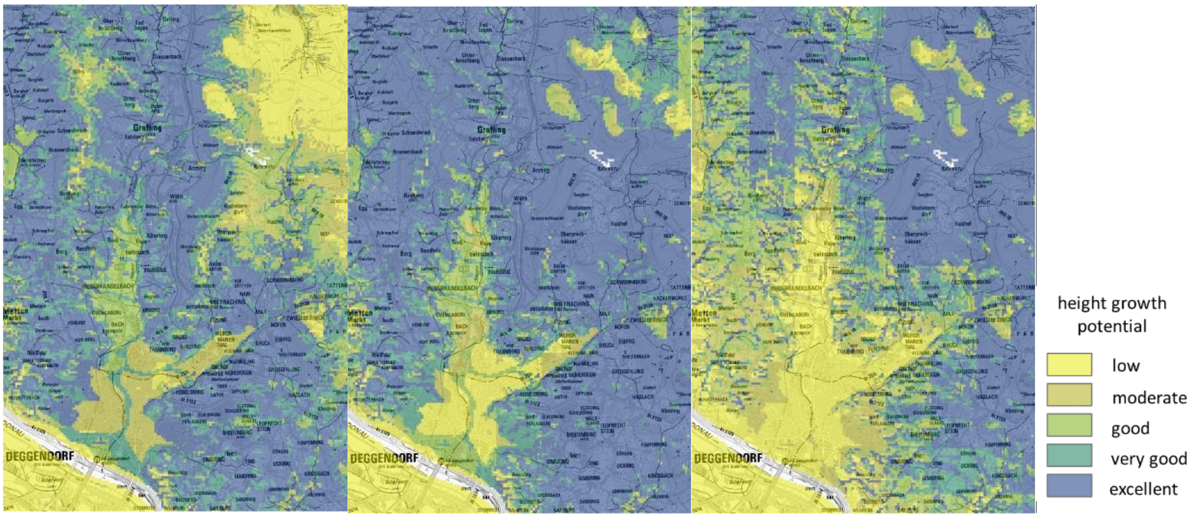

Fig. 13: Height growth potential of Norway spruce as predicted by the model in the present, near future (WETTREG B1 2031-2060) and distant future (WETTREG B1 2071-2100) for a region in the northeast of Deggendorf. This example shows how climate change affects height growth potential along elevation gradients. From Brandl et al. (2016).

3.2 The Relationship between a Static Site Index and Site Factors (Publication II)

Site indices (SI) were harmonized for the national forest inventories (NFI) of Germany (3^{rd} NFI 2012) and France (2006 until 2013) for six species: Norway spruce, Scots pine, Douglas-fir, European beech, sessile oak and pedunculate oak. Inventory plots in regular forests where the investigated species accounted for ≥ 70 % of the plot basal area and the coefficient of variation of age was ≤ 0.25 were included. The root mean square diameter of the top 100 diameters (d_{top}) of a tree species on a site was calculated. The corresponding top height (h_{top}) was derived from species-specific height-diameter curves and the corresponding age determined. In order to obtain the SI, the Chapman-Richards function was fitted to the 5 and the 95 % quantiles of the age-height spectrum creating a lower and upper boundary line. The SI was determined by translating the position of $h_{top}(i)$ between lower and upper boundary height of a species in a stand at age i to the corresponding height $h_{top}(100)$ at the reference age of 100 years (strip method). Virtual stands, which were simulated based on yield tables of Norway spruce, were used to assess the uncertainties in deriving the SI. For spruce and beech SI was modeled in dependence on climate parameters (WorldClim 1.4) using generalized additive models (GAM) with a gamma error distribution and log-link function. Climate could be characterized by mean annual temperature or summer temperature, winter temperature, precipitation, and continentality. Elevation was used as an additional explanatory variable. The influence of soil parameters was taken into account only by removing plots where the climate signal was likely to be confounded by extreme soil characteristics. The intercept could differ between Germany and France in order to account for possible effects of differences in inventory design not yet considered. Adjusted R^2 and AIC served as selection criteria.

The top height proved as a stable height measure that could be derived harmoniously from German and French NFI. The boundaries of the age-height frame were well described by the Chapman-Richards function. Tests made on virtual data ensured that there were no big or systematic deviations resulting from the two NFI sampling methods and that h_{top} was relatively stable with respect to effects of density. The effect of age errors on SI estimation decreased with increasing age. SI of spruce was modeled as a function of temperature from May to September (T_5to9), January temperature (T1), annual precipitation (P) and the country factor (adjusted R^2 = 19.1 %). T_5to9 had the strongest explanatory power. Until approximately 15 °C, SI increased strongly with rising temperatures. A further increase in T_5to9 led only to a very slight increase in SI. Overall SI decreased with rising T1. There was a steep increase in SI with increasing P until saturation was reached at a threshold value of about 750 mm. The effect of the country factor was rather small. SI of beech was modeled as a function of temperature of the warmest quarter (T_wq), precipitation sum from May to September (P_5to9), elevation and the country factor (adjusted R^2 = 40.1 %). For T_wq a curve with a wide optimum range between about 14 and 18 °C was fitted. Applying monotonicity constraints a saturation curve could be fitted for P_5to9 which flattened at a threshold value of about 570 mm. Elevation had a strong effect on SI. It increased from sea level to 200 m and then continuously decreased. The effect of the country factor was rather strong. The models were used to create maps of SI for current and future climate (climate scenario RCP 4.5 for the period 2061–2080 based on WorldClim MPI-ESM) (Fig. 14). As under the chosen climate scenario a clear increase in temperature but not much change in precipitation is predicted, changes in SI were mainly temperature-driven. Under current conditions high SI for spruce were predicted for Southern Germany due to a favorable combination of mean T_5to9, T1, and P, whereas in the Alps SI was limited by T_5to9. Under future conditions the model predicted an increase in SI in the mountains and for Southern Finland and Norway as T_5to9 increases and no longer limits height growth while T1 is still rather low. In Germany, the model predicted slightly lower SI for the future mainly due to rising T1. For beech, under current climate low SI were predicted for mountainous regions. In Southern Europe, low SI were due to elevation and low precipitation, whereas summer temperature mostly does not reach values that seriously limit height growth. In the South of Germany, environmental conditions were found very favorable for beech and SI were high. In the predictions for the future, rising temperatures caused a clear shift to the north for regions of high SI and a decrease in SI for Southern Germany. However, in the future maps the strong effect of elevation in the beech model became apparent: Despite rising temperatures, SI remained low in the mountains.

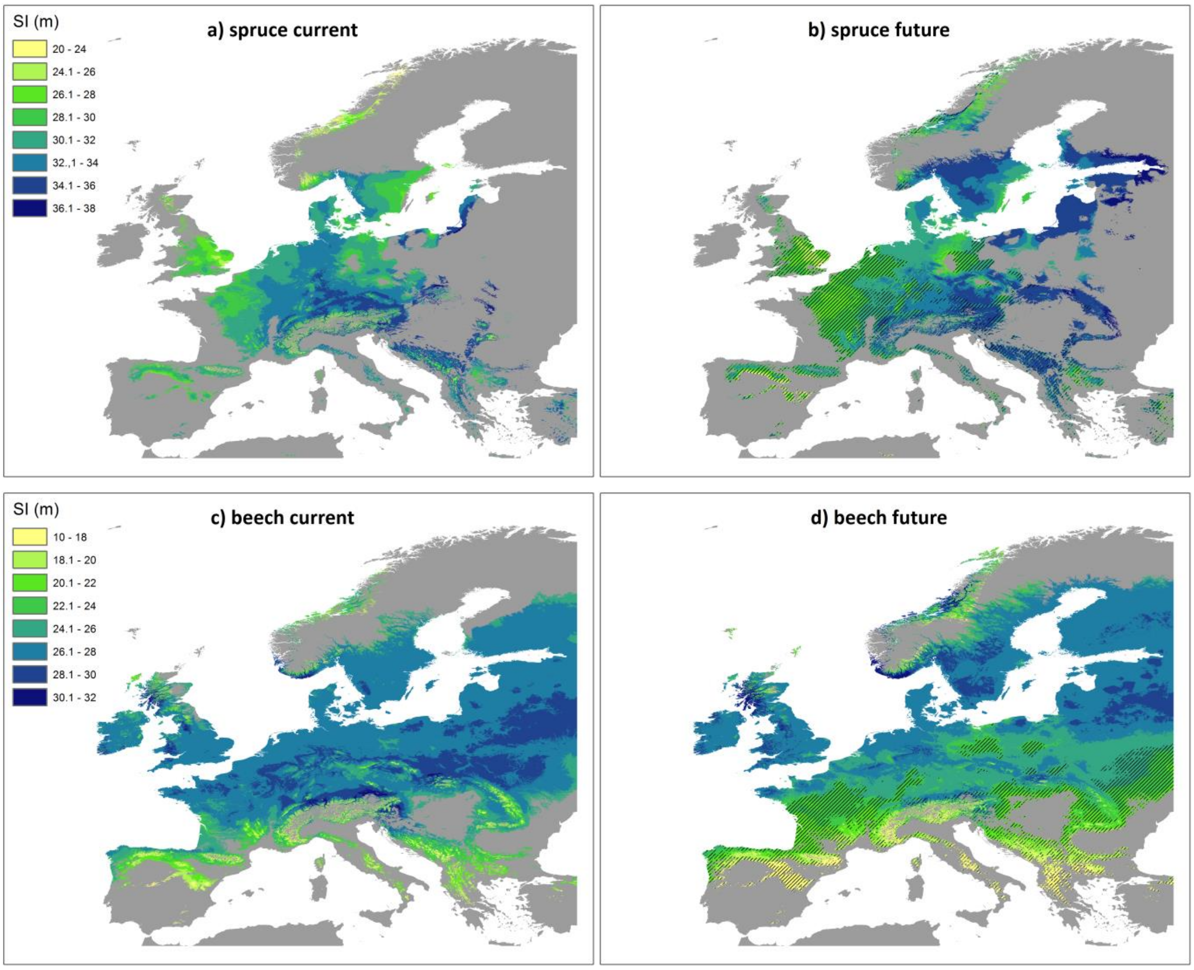

Fig. 14: Map of predicted SI of Norway spruce and European beech for present and future climatic conditions (limitations due to soil conditions are not taken into account). The gray areas mask the extrapolation range of the models. Predictions for the future are hatched when current climatic conditions are present in the training data, but future climatic conditions fall into the extrapolation range. From Brandl et al. (2018).

3.3 The Relationship between Biomass Growth and Site Factors (Publication III)

Above-ground wood biomass was estimated for the 2nd (2002) and 3rd (2012) NFI in Germany based on the angle-count sample (factor 4) using species-specific functions of dbh and height. Biomass growth per year was determined for each tree as the difference between NFI 3 and NFI 2 divided by the period length. These values were extrapolated to 1 ha and summed up at plot-level in order to obtain above-ground wood biomass growth of the stand (ΔB). As a measure for stand density the stand density index of Reineke (SDI) was calculated. For the analysis plots with a basal area proportion of spruces ≥ 70 % and stand age between 30 and 150 years were used. Plots on gley soils, pseudogley soils and moor soils were discarded. The study consisted of two parts: (1) an exploratory data analysis and (2) a model of biomass growth (ΔB) in dependence on site factors.

(1) In order to address the question what stand variables explain the variability in ΔB for a given site index, the variation in ΔB not already explained by SI (and stand age) was explored. First, for each plot SI was determined by estimating the top height and extrapolating it to age 100 applying the Chapman-Richards function (Brandl et al. 2018). Second, a generalized additive model (GAM) was fitted explaining ΔB in dependence on SI and stand age. Third, the residuals were divided in quartiles and tested if stand (SDI, stem number, standing above-ground wood biomass and quadratic mean diameter) and tree (height, dbh and relative dbh increment) parameters differed significantly between the quartiles using Kruskal Wallis and post-hoc Nemenyi test.

(2) In order to separate the effect of environmental conditions from the effect of forest management on stand density a relative SDI was calculated: Plots of similar site conditions were identified using k-means clustering (21 clusters) of climatic and soil variables. Then, for each NFI plot the ratio of its SDI and the maximum SDI of the corresponding cluster was calculated resulting in a relative density (RD) that reflects the effect of thinning on density. Generalized additive models with a gamma error distribution and log-link function were used to explain biomass growth in dependence on stand age, RD and climate and soil variables. Variable selection was based on adjusted AIC and the ecological plausibility of the partial effects. External validation was based on an independent dataset of 78 long-term experimental plots on 14 locations in Bavaria using the increment periods which were closest to the inventory periods of the NFI.

(1) In the data there was a clear trend to larger quadratic mean diameter, dbh, standing biomass and ΔB with increasing SI. However, there was considerable variation in productivity (ΔB) that was not explained by SI and stand age. Differences in productivity were largely due to differences in stand density. Sites with greater productivity generally had a higher stem number per ha (Fig. 15a), whereas there was no clear trend for quadratic mean diameter (Fig. 15b). Standing above-ground wood biomass significantly differed between the quartiles of the distribution of the residuals and showed an increasing trend. Trees on sites with greater productivity but same SI did not have greater single tree diameters on average, but relative dbh increments were higher. There was no clear trend in single tree heights.

(2) The final model included RD, age, mean annual temperature, summer precipitation, temperature seasonality, base saturation, C/N ratio and sand content (Adjusted $R^2 = 0.758$). RD had a strong, approximately linear positive effect. ΔB decreased with increasing stand age from 30 years onwards. ΔB increased with rising mean annual temperatures. The increase was stronger in the low and medium temperature range. The effect of precipitation was smaller. Low summer precipitation clearly limited ΔB. ΔB was reduced at both extremes of temperature seasonality. Optimum ΔB was reached at medium base saturation. There was a tendency to higher ΔB with decreasing sand content and a clear negative effect of very high sand content. ΔB decreased nearly linearly with rising C/N ratio. External validation resulted in an R^2 of 0.753 of the linear relationship between measured and predicted values.

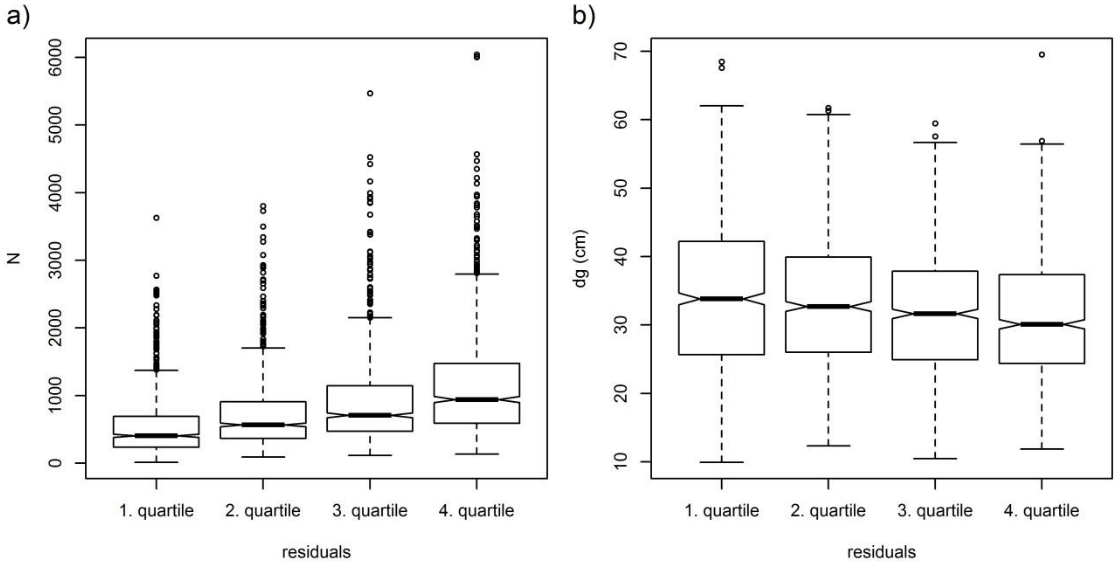

Fig. 15: Comparison of stem number per ha (N) and quadratic mean diameter (dg) between the quartiles of the distribution of the residuals of a model explaining ΔB in dependence on site index and stand age (Brandl et al. submitted). Larger residuals go in line with greater ΔB at a given site index and stand age.

3.4 The Relationship between Productivity and Biodiversity (Publication IV)

The effect of tree species richness on tree volume production was explored on a global scale based on 777,126 forest inventory plots in 44 countries and 13 ecoregions (Fig. 16). For each plot three key attributes were derived from measurements of individual trees: tree species richness (S), stand basal area (G), and primary site productivity (P). S represented the number of different tree species alive at the time of inventory. To facilitate inter-biome comparison, relative species richness (Š) was calculated as the ratio of S and local maximal species richness. G corresponded to total cross-sectional area of live trees per unit sample area and represented stand density. For plots with repeated measurements (77 % of plots) P ($m^3\ ha^{-1}\ yr^{-1}$) was estimated as periodic annual volume increment calculated from the sum of individual tree stem volume at the time of the first inventory and the second inventory, respectively. Mortality and ingrowth were accounted for. For plots without remeasurements (23 % of plots) P was measured in mean annual increment based on total stand volume and stand age, or tree radial growth measured from increment cores. Mortality was approximated based on region-specific turnover rates. The relationship between productivity and biodiversity (BPR) was approximated with a power function model using a geospatial random forest model: $P = \alpha * f(X) * S^{\theta}$, where f(X) is a function of a vector of control variables X (selected from stand basal area and 14 climatic, soil, and topographic covariates), and α a constant. The elasticity of substitution θ characterizes the shape and strength of the dependency function and measures the change in productivity resulting from one unit decline of species richness, and reflects the strength of the effect of tree diversity on forest productivity, after accounting for climatic, soil, and plot specific covariates. At the global-scale, the magnitude of BPR (as expressed by θ) was mapped using geospatial random forest and universal kriging.

A consistent positive concave-down effect of biodiversity on forest productivity across the world was found (Fig. 16).

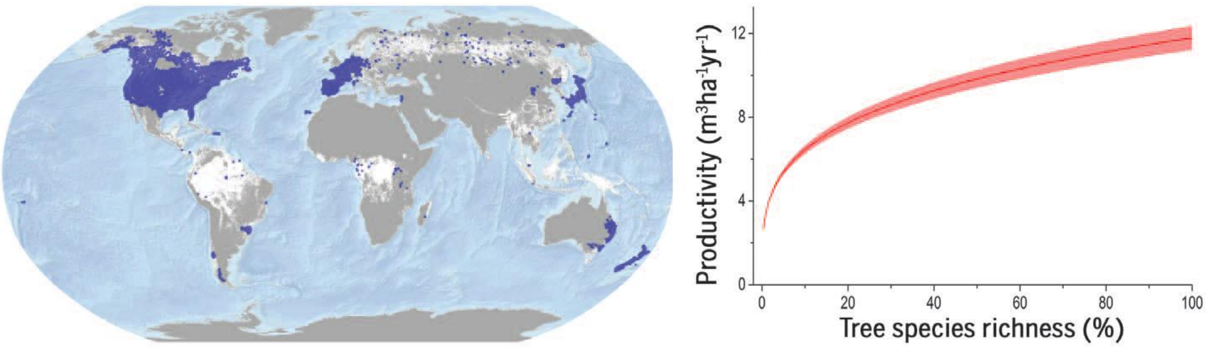

Fig. 16: The effect of tree species richness on forest productivity: Based on worldwide 777,126 permanent forest inventory sample plots (blue dots, left) a positive, concave-down relationship between tree species richness and forest productivity could be found (right). From Liang et al. (2016).

Overall, the global forest productivity increased with a declining rate ($\theta = 0.26$) from 2.7 to 11.8 $m^3 ha^{-1} yr^{-1}$ as tree species richness increased from the minimum to the maximum value. Thus, a continued biodiversity loss would result in an accelerating decline in forest productivity and thereby in a reduction of forest carbon absorption rate worldwide. The BPR showed considerable geospatial variation across the world. The same percentage biodiversity loss would lead to greater percentage productivity decline in the boreal forests of North America, Northeastern Europe, Central Siberia, East Asia, and scattered regions of South-central Africa and South-central Asia. In the Amazon, West and Southeastern Africa, Southern China, Myanmar, Nepal, and the Malay Archipelago, however, the same percentage biodiversity loss would lead to greater absolute productivity decline. The economic value of biodiversity in maintaining forest productivity was estimated at $396–579 billion per year.

3.5 The Combined Effect of Productivity and Mortality on Economic Yield (Publication V)

The study integrates empiric survival functions into a bio-economic simulation and optimization model in order to obtain predictions of economic yield that are both sensitive to forest productivity and mortality risk. Survival analysis was based on annual assessments of tree status in a pan-European data set (German Crown Condition Survey, Level I and Level II data). For Norway spruce and European beech accelerated failure time models were fitted. Climate variables (Worldclim 1.4) and mixture proportion of the respective species could act multiplicatively on survival time. Variable selection was based on prediction accuracy (brier score) in a 10-fold cross-validation. Example study site and data for the economic analysis were from Freyung, Germany. Growth data were simulated with SILVA. Two alternatives of combining the two species were defined: block mixture with no biophysical interaction between the species, and mixed stands in which stand resistance was affected in accordance with the effect of mixture proportion in the survival model and volume growth and wood quality were affected based on assumptions from previous studies. Economically optimal species composition was derived based on Modern Portfolio Theory. The allocation of forest area for different tree species reduces the standard deviation of the portfolio's return. The downside risk measure Value at Risk (VaR) was calculated as the expected portfolio return at the 5 % quantile at the undesirable, left tail of the return distribution. Maximizing VaR for block mixtures and mixed stands under current and expected future climate conditions resulted in the respective economically optimal tree species composition. For mixed stands, returns and risks were directly simulated for a range of mixtures between spruce proportions of 10 to 90 % in 10 percentage point increments. Frequency distributions of return were estimated by means of Monte Carlo simulation and 10,000 iterations. Simulations were conducted with production periods of 10 years, starting at age 0, assuming bare land. The expected portfolio return was represented by the Land Expectation Value. A constant discount rate of 1.5 % was assumed. A sensitivity analysis was conducted by comparing the magnitude of change in optimized species composition to important economic drivers other than tree species selection: investment costs, correlation of returns, discount rate and the assumed attitude towards risks.

For spruce sum of precipitation in the warmest quarter, mean temperature of the warmest quarter and share of spruce in the stand were selected as covariates influencing survival times. For beech maximum temperature of the warmest month, minimum temperature of the coldest month and share of beech were selected (Fig. 17).

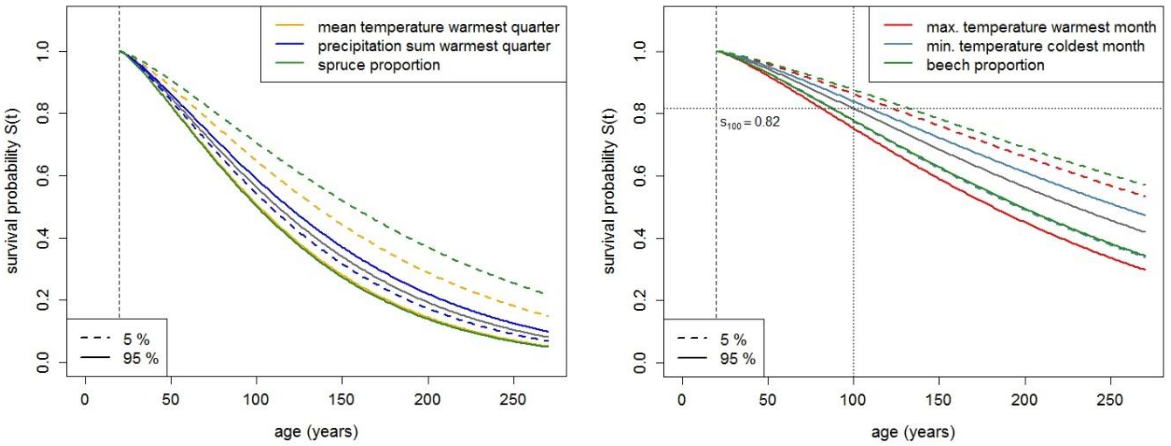

Fig. 17: Results of the AFT model for spruce (left) and beech (right): For each selected covariate survival probabilities are depicted when setting the covariate to the 5%- and 95%-quantile of its range, respectively, while fixing the remaining covariates at their means. The grey line shows the survival probabilities when all covariates are set to their mean values.

The effect of admixture on tree survival was positive for both species, whereas high summer temperature had a negative effect. The probability of a tree in pure stands to still being alive at age 100 was 0.49 for spruce and 0.80 for beech, under a constant climate at the study site. Climate change affected both species at a similar magnitude. Yet, due to the higher survival of beech under current climate, its absolute survival rates still remained at a much higher level compared to spruce. The survival probability of spruce trees could still be maintained at today's level when admixing pure spruce stands with 40 % beech. In block mixtures, despite its higher survival probabilities, beech had a much lower return and higher coefficient of variation (67 %) compared to spruce (38 %). Consequently, pure spruce stands would also give a much higher VaR (43 € ha^{-1} yr^{-1}) compared to pure beech stands (2 € ha^{-1} yr^{-1}) and the model would choose to dedicate the entire regeneration area to pure spruce stands. The consideration of the effect of climate change through altered survival probabilities only slightly reduced the economically optimal spruce proportion for a risk-averse forest owner. The increased survival probabilities found for both species when grown in mixed stands resulted in a considerably higher VaR compared to block-wise mixtures. Under a constant climate, the VaR of the economically optimal species proportion in the mixed stand design was 19 % higher compared to the highest VaR attainable in block mixture This advantage even increased to up to 57 % under the climate change scenarios. Climate change would still affect the forest owner, but compared to block mixtures and pure stands, economic consequences could be buffered considerably. The economically optimal spruce proportion in mixed tree stands was with 60-70 % generally lower compared to the ideal block mixtures. In the model, individual returns of spruce increased with an increasing admixture of beech. This was due to the higher stand resistance associated with lower hazard-induced losses and the shortening of rotation periods. The same effect was found for beech, but was less pronounced, due to the various effects of admixture on tree growth and wood quality. Consequently, given the overall higher return of spruce, this species still dominated the species portfolio of mixed stands. Species selection in mixed stands was more stable under rather extreme climate change scenarios.

In the sensitivity analysis, even moderate changes in the establishment costs of spruce, relative to beech by ±75 % (i.e. ±1500 €) reduced the share of spruce in optimized block mixtures from 100 % to only 50 %. This difference in species selection was much larger compared to the simulated effects of climate change. Furthermore, the advantage of mixed stands was reduced when assuming higher establishment costs for mixed stands compared to block mixtures. Under a higher correlation of events the advantage of having beech in the species portfolio was reduced. Changing the accepted level of risk, by decreasing the accepted shortfall probability from a moderate value of 5 % to a very risk-averse value of 1 % resulted in a much smaller optimal proportion of spruce in the block-mixture of 57 %. A moderate change in discount rate did not alter species selection in the block portfolio. The optimal species composition in mixed stands was less sensitive to changes in model assumptions. The optimal spruce proportion did not drop below 60 % (under current climate) when increasing establishment costs of spruce by 75 %, or decreasing shortfall probability to 1 %. Thus, biophysical interactions dominated species selection in mixed stands, while ideal compositions were less susceptible to other input variables.

4 Discussion

4.1 Measuring and Modeling Forest Productivity

The single tree height model is directly based on height measurements. Thus, in contrast to more comprehensive measures of productivity, it is free of any assumptions needed for upscaling. In only one step height was modeled as a function of age and site factors. The SI approach involved two steps: first, estimating top height and scaling it to age 100, the most common definition of SI, and second, modeling SI in dependence on site factors. The first step allowed a mere descriptive site (index) assessment of a stand without the uncertainty attached to modeled effects of environmental variables. Modeling the SI in dependence on site factors in a second step clearly separated the effect and explanatory power of environmental variables from the effect of age. As height and age information is generally included in inventory data and no remeasurements are required for the developed approach, SI could be successfully harmonized for different national forest inventories. Thus, subsequent modeling benefitted from large environmental gradients.

Height and SI only encompass the vertical aspect of productivity. Biomass growth of the stand additionally encompasses the horizontal aspect of productivity (i.e. dbh increment), as well as stand density and (implicitly) stand mortality. Major caveats were the need for repeated measurements (or increment cores), the uncertainty introduced due to the upscaling based on the assumptions about allometry and the need to deal with the strong influence of forest management on stand density. All the same, biomass growth could be calculated from German NFI. It was possible to separate effects of thinning and effects of site quality on stand density. Thus, the influence of site factors on biomass growth could be elaborated more clearly. On a global scale it was possible to estimate periodic (based on remeasured plots) and mean (based on plots without remeasurements) annual volume increment from various inventory sources. Despite the high uncertainty attached to these estimations, the method proved suitable to detect large-scale patterns on a global scale. However, in order to detect patterns on the national scale and make predictions that are relevant for national forest management, more exact estimations of site productivity, like the height, SI or biomass growth estimations presented in this thesis, are needed as response variables in the models.

4.2 The Effect of Environmental Conditions on Forest Productivity

4.2.1 Temperature Regime and Water Supply

The environmental variable with the highest explanatory power is temperature during the growing season. As Germany forms part of the temperate zone, potential productivity is strongly driven by length and temperature of the growing season (Nemani et al. 2003). Due to the high collinearity between variables characterizing annual temperature, summer temperature or temperature during the growing season, this can be stated across all investigated measures of productivity and species even if different specifications of temperature have been selected. At low and medium temperatures productivity strongly increases with rising temperatures due to longer growing seasons (Pretzsch et al. 2014) and higher enzyme activity (Barnes et al. 1998: 210). At the warm temperature margin uncertainty is higher. Depending on the measure of productivity, the investigated species and the study area (chapter 4.2.3) a slight further increase, a more or less constant level, or a decrease is modeled. Still, again across all investigated measures and species it can be stated that above a certain threshold rising temperatures are not beneficial for productivity anymore. This can also be interpreted in relation to the effect of water supply: At high temperatures, droughts are more likely and lead to growth reductions (Matyssek et al. 2010: 239ff).

Across all investigated measures and species water supply during the growing season acts as limiting factor. For the single tree height model for spruce in Bavaria the interaction between growing degree days (GDD5) and water balance was selected. In all other cases one of the highly correlated variables annual precipitation, summer precipitation or precipitation during the growing season was selected as explanatory variable. The effect of precipitation on productivity can be described by a saturation curve. Below a certain threshold there is a steep increase in productivity with precipitation. Above a given amount of water, precipitation is no longer the limiting factor.

For tree growth the interplay between temperature regime and water supply is decisive (Lyr et al. 1992). Ideally, i.e. based on ecological theory, the highest explanatory power should result from an interaction between temperature regime and water supply. Such an interaction is included in the single tree height model for spruce in Bavaria with the interaction between GDD5 and water balance, expressing that both factors can limit tree growth, whereas highest growth is reached if GDD5 is high and water supply is abundant. However, as the combination of both high temperatures and high precipitation rarely occurs in the data, the models could not always distinguish between effects of temperature and water supply, which led to wiggly surfaces of the interaction effect. For instance, in the single tree height model, in order to obtain a smooth, ecologically plausible surface of the interaction effect, the Alps had to be excluded. Thus, in the other models single effects were preferred.

Of course, water supply does not only depend on precipitation, but also on soil texture and depth. Available water capacity was found to be a limiting factor for height growth of spruce in Bavaria and is also integrated in the water balance that was selected as explanatory variable in the single tree height model. SI models of spruce and beech had a higher explanatory power, when filtering out inventory plots with extreme soil conditions before modeling, which indicates the influence of physical soil properties. Soil texture influenced productivity. Silt content had a positive effect on productivity, whereas very high sand content had a negative effect. Effects of soil texture can both reflect nutrient supply (chapter 4.2.2) and water supply. Soils with high silt content often have more favorable physical properties in respect to water and air balance than soils with high sand or clay contents (Scheffer & Schachtschabel 2002: 241).

4.2.2 Nutrient Supply

Between basic cation supply and productivity an optimum relationship is assumed: On acidic soils the lack of available basic cations reduces growth, whereas on calcareous sites Ca-K-antagonism (Rehfuess 1990) and immobilization of phosphor (Mellert & Ewald 2014) can occur. This is reflected in the effect of base saturation on ΔB and can also be seen when comparing single tree heights for the five types of the depth gradient of base saturation. However, in the single tree height model there is no negative effect of low base saturation. In summary, productivity is enhanced by a balanced supply of basic cations, it is strongly reduced at high base saturation, and is affected to a lesser extent by low base saturation.

The effects of silt and sand content, discussed in chapter 4.2.1 in their relation to water supply, might also be interpreted in the light of nutrient supply: Soils with high sand content are often poor in nutrients, whereas high silt contents are usually associated with nutrient-rich soils (Scheffer & Schachtschabel 2002).

In general, the variance explained by variables characterizing nutrient supply was small in comparison to the variance explained by climatic effects (chapter 4.2.3). This might be explained by Liebig's law of the minimum (von Liebig 1855). A certain nutrient only influences growth, if it is the limiting factor. In Bavaria this is generally not the case for the investigated soil nutrients. In addition, data on phosphorus which has a strong influence on tree vitality and growth (Lang et al. 2016) was not available.

4.2.3 The Importance of Scale

The geographical, or actually the environmental, range of the data used for model fitting influences both the selection as well as the modeled effects of environmental variables.

Large-scale productivity patterns are mainly shaped by temperature and water supply. That is true at the Bavarian scale, the German scale and the transnational scale. However, models based on German or Bavarian data alone do not predict a clear decline in productivity at the warm temperature margin. In contrast, based on both German and French data, and thus encompassing more plots with very high temperatures, a clear decline in productivity for rising temperatures is predicted.

The effect of precipitation is weaker in the models based on German or Bavarian data alone, as water is, except in extreme drought years, not generally the growth limiting factor in spruce or beech dominated NFI plots in Germany. In contrast, on a global scale water supply is a crucial variable constraining productivity (Stegen et al. 2011). When expanding the database with data of the French NFI, the influence of precipitation during the growing season already became more important. In addition, for spruce an effect of winter temperature, interpreted as an effect of continentality, was included.

Due to the small-scale heterogeneity of soil the influence of soil conditions should become apparent within regions of similar climate and explain local differences in productivity. That way, boosted regression trees allowed for regionally complex interactions of soil variables and led to a greater differentiation and a more realistic range in predicted heights for Bavaria. However, even on Bavarian scale it was difficult to elaborate a clear and strong influence of soil nutrients. On the one hand this might be due to the fact that generally in Bavaria soil nutrient supply seldom limits growth of Norway spruce. On the other hand this might be due to the uncertainty in the explanatory variables caused by the regionalization of soil properties. This idea is supported by the fact that the relief variables MBI and SMI that can be derived with high local precision from a DEM improved the model.

The small-scale heterogeneity of soil conditions makes it difficult to capture the effect of soil on transnational or European scale, as harmonized soil data of high precision are not available. An exception is the Biosoil dataset (Hiederer et al. 2011). However, this dataset covers only a part of the Level I plots.

4.3 The Effect of Diversity on Forest Productivity

Climate and soil conditions form the foundation of forest productivity. Still, forest productivity is not determined by climate and soil conditions alone, but is strongly shaped by stand characteristics. In contrast to climate and soil conditions, stand characteristics can be affected by forest management. Thus, there is potential for adaptation. In the study about the relationship between productivity and biodiversity (Publication IV) the focus is shifted from the influence of climate and soil conditions to the influence of one of the key features of a stand: species mixture or diversity. The influence of diversity on productivity could be elaborated on a global scale by accounting for environmental variables as potential confounders. (Stand characteristics were included in the single tree height model or in the biomass growth model as well. But, opposite to the study on the biodiversity-productivity relationship, they were not in the focus and were integrated to account for the potential confounding effect of stand characteristics and make the effect of the environmental variables more clear.) A positive concave-down relationship between species richness and forest productivity was detected across forest ecosystems worldwide, a pattern that is well in line with recent findings on the biodiversity-productivity relationship (Tilman et al. 1997; Cardinale et al. 2011; Reich et al. 2012; Liang et al. 2015). With increasing species richness, the rise in productivity becomes less pronounced, which is in line with observations from long-term forest experimental plots dating back to 1870 (Forrester & Pretzsch 2015; Pretzsch et al. 2015). Based on this positive concave-down relationship, a continued biodiversity loss would result in an accelerating decline in forest productivity worldwide. This would also lead to reduced carbon absorption rates. These findings underline the importance of species mixture in maintaining not only stable but also productive forests.

4.4 The Effect of Site Factors on Mortality

Besides productivity, mortality risk is an important factor influencing economic yield. As the focus of this thesis is on the influence of site factors and not on economic assessments, only the results of the survival analysis are discussed here and the economic analysis that builds up on these results is left aside.

Mortality risk of spruce and beech increased with rising summer temperature. Besides, cold winter temperatures (minimum temperature of the coldest month) had a negative effect on the survival of beech. On the one hand, hot and dry summers weaken the vitality of spruce and act as predisposing factors by making the trees more susceptible to inciting and contributing factors like bark beetles in the case of spruce. On the other hand, warm average summer temperatures are correlated with the frequency and intensity of drought events. Therefore, the modeled effect of summer temperature might also include “hidden” effects of the inciting factor drought. The effect of temperature in the model of beech is more difficult to interpret. At both extremes of the temperature range mortality is increased. One possible interpretation could be that severe frost causes damages. In the end, the two selected temperature variables in the beech model are more or less in balance. Thus, the overall effect of rising temperatures in climate change would depend on how much winter- and summer temperature will rise respectively.

One would expect that low precipitation in summer would lead to water shortage and thus increase mortality risk. However, summer precipitation only had a weak effect in the spruce model. In Europe warm summers are often associated with low precipitation, whereas the combination of high summer temperatures and high precipitation is rare. This makes it difficult for the models to differentiate between the effects of temperature and precipitation. Thus, the temperature effect might already include part of the postulated effect of precipitation.

Species admixture strongly increases survival probability: Competition is relieved due to complementarity in resource allocation (Pretzsch et al. 2015). In addition, mixed stands are more stable against calamities (Schäfer et al. 2018). Due to the inclusion of mixture effects and age, the models allow to assess the influence of silvicultural decisions on mortality risk under climate change (Fig. 18).

It is important to note that for both species confidence intervals of the effects of site factors are wide, i.e. predictions have high uncertainty. This is due to limitations of the database and the complexity and highly stochastic nature of tree mortality (chapter 2.2.1).

Single tree survival probabilities for spruce are considerably lower than for beech. For instance, when all predictors are set to their means, survivability at age 100 of spruce is 56 %, whereas survivability of beech is 82 %. These values are low in comparison with the study of Neuner et al. (2015), but are consistent with the findings of Schoneberg (2017). The differences in the level of survival probabilities result from a methodological difference. This thesis, as well as the study of Schoneberg (2017), take the left-truncation of the data into account and thus estimate lower survival probabilities especially at young ages. It has to be taken into account when interpreting these values that single tree survival probabilities have been modeled that cannot be transferred to the stand one-to-one. In many cases the loss of a single tree can be compensated by enhanced growth of the surrounding trees that soon fill the gap (Schoneberg 2017).

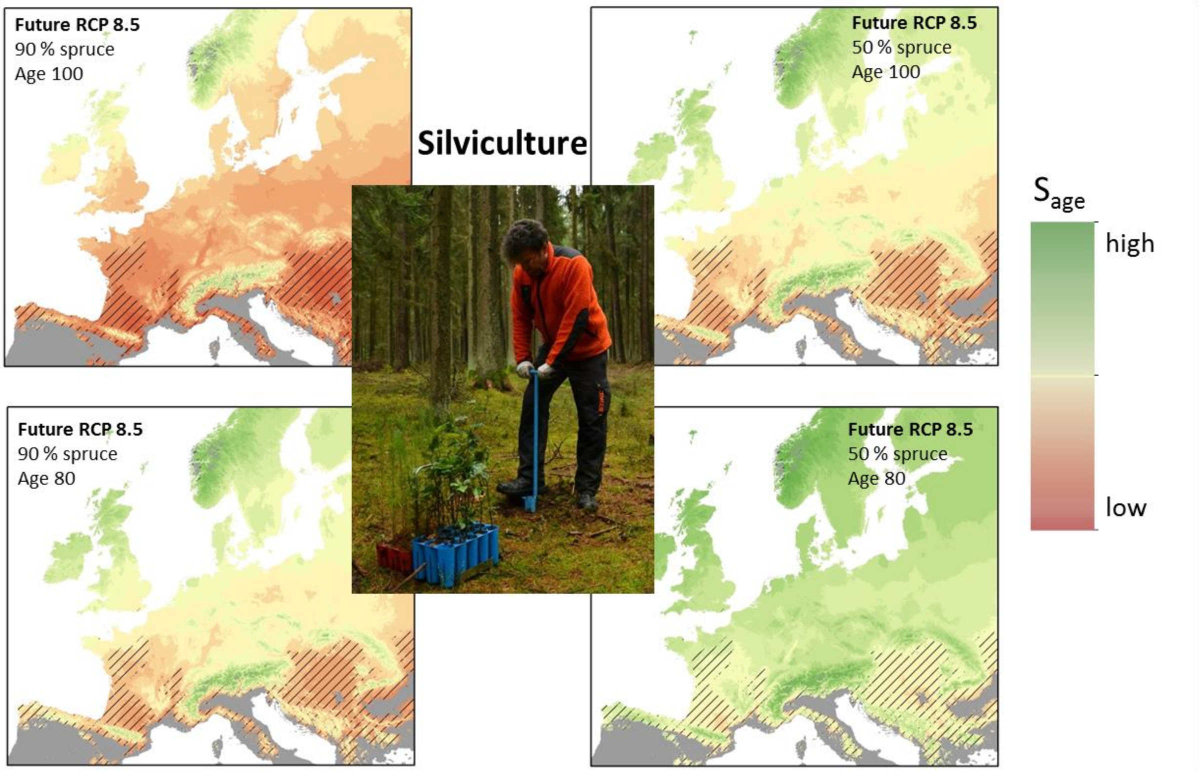

Fig. 18: Silvicultural decisions affect the mortality risk in the future. Single tree survivability (S) of Norway spruce at the respective rotation period for varying spruce proportions are mapped for one selected climate scenario (MPI-ESM RCP 8.5) for the period 2061-2080 (Worldclim 1.4). Both an increase in species admixture (top right) as well as a shortening of the rotation period (bottom left) significantly reduce risk in comparison to a stand with a spruce ratio of 90 % that is harvested at age 100 (top left). The probability to reach the rotation period decreases due to climate change. It increases with both rising mixture proportion as well as shortening of the rotation period (bottom right). The extrapolation range of the models is masked in grey (current climate of these regions not present in the training data) or hatched (future climate not present in the training data). Adapted from Brandl & Falk (2019).

4.5 Limitations of the Database and the Methodology

Both the response variable as well as the explanatory variables in the models entail uncertainty. The estimation of SI is based only on few height measurements. In addition, these height measurements already include some measurement error. Further uncertainty is introduced by upscaling height and dbh measurements to volume or biomass and/or to ha basis. In large scale forest inventories age is often only an approximation. However in both the productivity models as well as in the mortality model age is an essential variable. In the appendix of publication II the implications of potential errors in age information on site index estimation are assessed and discussed.

In contrast to experimental plots, the history of the plots in forest inventories is often unknown. Position, dimension and neighborhood of trees are often only partly assessed. Thus, for both productivity and mortality important explanatory variables, like stand structure, competition and past management are largely missing. For instance, tree dimension is an important predictor for tree mortality (Schoneberg 2017). However, information on tree dimension is missing in the Level I dataset that largely underlies the mortality models. Studies based on tree ring data can even go further and use growth rates to predict mortality risk (e.g. Bigler et al. 2006; Cailleret et al. 2014). In addition, the definition of a mortality event has a huge impact on model results and their interpretation. However, it is sometimes impossible to determine why a tree is missing in a subsequent inventory and the cause of removal at times can only be guessed.

Depending on the scale of the study, different climate data were used. However, even high-resolution data are interpolated from measurements at weather stations. Concerning future climate, there is a high variation between the outcomes of global circulation models for different concentration pathways. Therefore, predictions should actually be made for an ensemble of climate scenarios. Soil information is often not precise. Although soil characteristics are sometimes measured at inventory plots, more often information on soil has to be derived from digital site maps. As soil can be heterogeneous on a very small spatial scale modeled relationships are generally weak and do not contribute much to explaining productivity or mortality. In addition, important explanatory variables like nitrogen and phosphorus are not (consistently) available for the inventory plots and could thus not be included into the models.

5 Conclusion

This thesis investigates the relationship between forest productivity and site factors based on large-scale forest inventory data. In order to answer the research questions presented in chapter 1.2 statistical models describing productivity or mortality in dependence on site factors were developed based on data encompassing wide environmental gradients on varying spatial scales:

How much variance in height can be explained by spatially explicit environmental data?

The variance in SI explained by site factors varied between 19.1 % for spruce and 40.1 % for beech. In the single tree height model the inclusion of site factors increased the explained variance in height from 56.9 % (only age as covariate) to 67.5 %.

Can we predict height on a scale that is relevant for local forest management, i.e. with high local precision?

The ability to predict height growth potential on a local scale was limited due to the difficulty to integrate soil variables into the models. For instance, for Bavaria, the predicted large-scale pattern of SI is largely based on climate conditions. This pattern is coherent with experience and can thus be used to assess trends in productivity due to climate change and take them into account in forest planning. Using digital site maps the ability to predict SI on a local scale was improved to a certain extent but is still limited due to the difficulty of integrating metric soil variables into the model and the small explanatory power of the modeled soil variables. This leads to the conclusion that digitally highly resolved soil characteristics are an important step towards spatially explicit predictions of SI. However, up to the present they have not yet achieved high enough local accuracy. Therefore, height predictions with high local precision are not possible. In addition, detailed information on stand structure, competition and past management are largely missing in NFI data, but considerably influence local productivity.

How can we derive a harmonized measure for site productivity from different national forest inventories?

When combining different national forest inventories, the measure for productivity has to be relatively simple. The static site index presented in this thesis can be calculated whenever data allow for distinguishing a top collective and assigning height and age estimates.

Is it possible to derive a more comprehensive measure of site productivity than mere height from NFI data and explain it in dependence on site conditions?

Above-ground wood biomass growth of the stand (ΔB) is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. On the one hand, it entails the difficulty of how to deal with the influence of stand density and stand age. On the other hand, there is the advantage of encompassing at once a stand's productivity in the response variable with no need to consider the question of different yield levels later on. In conclusion, the stand-alone use of ΔB as a measure for site potential is not recommendable because many assumptions are needed when dealing with the effect of stand density. Thus, hypothesis 4 has to be rejected. Still, combining traditional SI with ΔB might result in a more accurate picture of site potential as there are sites that do not differ significantly in SI, but still differ in productivity. Using ΔB as response it was possible to fit plausible effects of site conditions, albeit these effects were small in comparison to the effects of stand structure.

How is the influence of soil and climate on forest productivity?

The results of the studies on productivity show that at first productivity increases with rising temperatures. Analyses based on larger climate gradients indicate that the relationship between temperature and growth is an optimum relationship and that beyond a certain threshold value there is no further increase in productivity with rising temperatures (hypothesis 1). Below a certain threshold value water supply acts as a limiting factor on productivity (hypothesis 2). An effect of nutrient supply and soil texture on productivity could be detected at a Bavarian scale using high-resolution digital soil maps. The inclusion of soil variables slightly improved the singe tree height model (hypothesis 3).

What are the trends in productivity due to climate change?

The chosen climate model (MPI-ESM) predicts a clear increase in temperature but not much change in precipitation for Europe. Therefore changes in productivity are mainly temperature-driven. At first, productivity increases with rising temperatures as long as water supply is not the limiting factor. Models based on larger climatic gradients indicate that at the high temperature margin productivity might increase no further but decrease with rising temperatures.

How does diversity affect productivity and mortality?

As hypothesized (hypothesis 5) it could be shown that productivity increases with increasing species richness. Thus, the positive effect of mixing tree species that had been shown in many studies based on experimental plots could also be demonstrated on a global scale. On European scale it could be shown that single tree survival probability is higher in mixed stands (hypothesis 7).

How is mortality risk affected by climate conditions?

There was a clear and strong effect of average climate conditions (30 year averages) on mortality risk of spruce and beech (hypothesis 6). Mortality risk increased at sites with high summer temperature. Therefore, high summer temperature can be interpreted as a predisposing factor. However, the hypothesized effect of summer precipitation on mortality risk was less clear which might be partly due to a confounding with temperature effects.

What are the advantages and disadvantages, i.e. the potential and the limitations of NFI data to investigate forest growth?

Despite the shortcomings discussed in chapter 4.5 large-scale forest inventory data and digital site information exhibited a huge potential for investigating forest productivity and mortality facing climate change. Ecologically plausible effects of covariates could be fitted. Moreover, statistical models allow to quantify the relationship between productivity or mortality on the one hand and site factors on the other hand. For instance, the survival probabilities predicted for spruce and beech could be integrated into economic simulations (Paul et al. 2019). Even some threshold values have been indicated. For instance, the effect of precipitation on SI of spruce indicated a threshold value of about 750 mm of annual precipitation below which productivity is strongly reduced.

In conclusion, ecologically plausible relationships between productivity or mortality respectively and site factors, with a strong focus on climatic factors, could be fitted based on large-scale inventory data using statistical model techniques. Thus, a first assessment of how climate change will affect productivity and mortality risk is possible based on the predictions of the developed models. When adapting forests to climate change it is important to consider productivity and mortality risk jointly, both for the current and future climate conditions. A first visual approach is to draw the trajectory of a stand's development from current to future conditions in a productivity-mortality-graph (Kölling et al. 2016). Fig. 19 illustrates this for spruce for a sample of European Level I plots. As the mortality model fitted a linear increasing effect of summer temperature, risk becomes higher for all inventory points. Still, many inventory points remain in the range of low risk. In contrast, productivity can increase or decrease depending on the starting point. If temperature is rather low today, increasing temperatures can lead to higher productivity in the future. But if a certain threshold is passed, there is a decline in productivity.

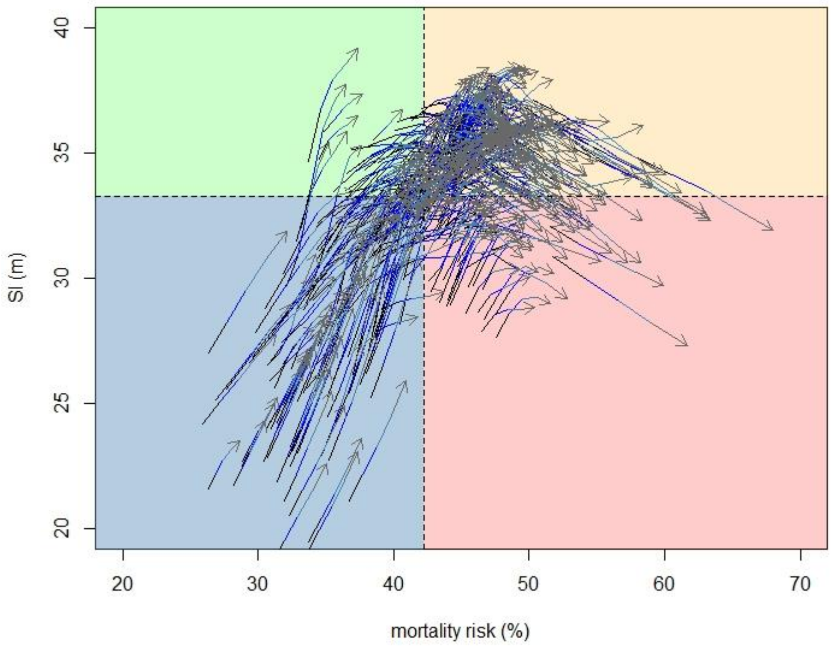

Fig. 19: Productivity-risk-trajectories of a random sample of 500 Level I plots based on model predictions of the survival model and the SI model for spruce. Productivity is described by site index (SI). The proxy for mortality risk is based on survival probability at age 100 (S_{100}). It is calculated as 1-S_{100}.

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Appendix:

Published Articles and Submitted Manuscripts

Publication I

Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany)

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Article

Possibilities and Limitations of Spatially Explicit Site Index Modelling for Spruce Based on National Forest Inventory Data and Digital Maps of Soil and Climate in Bavaria (SE Germany)

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Abstract: Combining national forest inventory (NFI) data with digital site maps of high resolution enables spatially explicit predictions of site productivity. The aim of this study is to explore the possibilities and limitations of this database to analyze the environmental dependency of height-growth of Norway spruce and to predict site index (SI) on a scale that is relevant for local forest management. The study region is the German federal state of Bavaria. The exploratory methods comprise significance tests and hypervolume-analysis. SI is modeled with a Generalized Additive Model (GAM). In a second step the residuals are modeled using Boosted Regression Trees (BRT). The interaction between temperature regime and water supply strongly determined height growth. At sites with very similar temperature regime and water supply, greater heights were reached if the depth gradient of base saturation was favorable. Statistical model criteria (Double Penalty Selection, AIC) preferred composite variables for water supply and the supply of basic cations. The ability to predict SI on a local scale was limited due to the difficulty to integrate soil variables into the model.

Keywords: climate; forest inventory; height growth; soil; statistical model

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1. Introduction

The increasing availability of spatially explicit data created by modern techniques like remote sensing or digital soil mapping enables the development of tools for forest management that promise high local precision. Combining digital site maps with traditional forest inventory data gives valuable insights into the relationship between site conditions and growth potential, a relationship which has often been investigated [1–4]. Many studies ([5], overview in [6]) are based on the data of experimental plots which have the advantage of long time series but sometimes only partly represent the environmental gradient. NFI data have the advantage of high spatial representation and can thus complement data of experimental plots [7]. They can be viewed as an experimental design that covers a wide variety of combinations of environmental variables. This makes NFI data suitable for forest growth investigation despite its short time series and age errors [8]. Using environmental variables to predict SI permits creating maps of current site productivity and predicting site productivity under changing environmental conditions. The aim of the study was predicting site productivity of spruce stands by combining NFI data with spatially explicit digital site maps on a scale that is relevant for local forest management. Thus, we focused on the regional differentiation of SI in Bavaria and not on explaining SI in the distribution of Norway spruce in entire Germany. In contrast to geographically extensive studies (e.g., [2,9]), the climatic gradient is smaller and the correlation of temperature, precipitation and elevation is higher. This minimizes the explanatory power of climatic variables, and soil variables that are difficult to capture become more influential. Nevertheless, Bavaria encompasses a distinct climatic gradient and a wide range of site characteristics. We investigated if the quality and high resolution of digital soil maps, together with the climatic data, allows creating maps of SI that can be integrated in the Bavarian Forest Information System (BayWIS) and used in forestry consulting. German NFI data—sometimes combined with data of experimental plots—and regionalized environmental variables have already been used to estimate SI (e.g., [1,10]), but with less differentiated soil information.

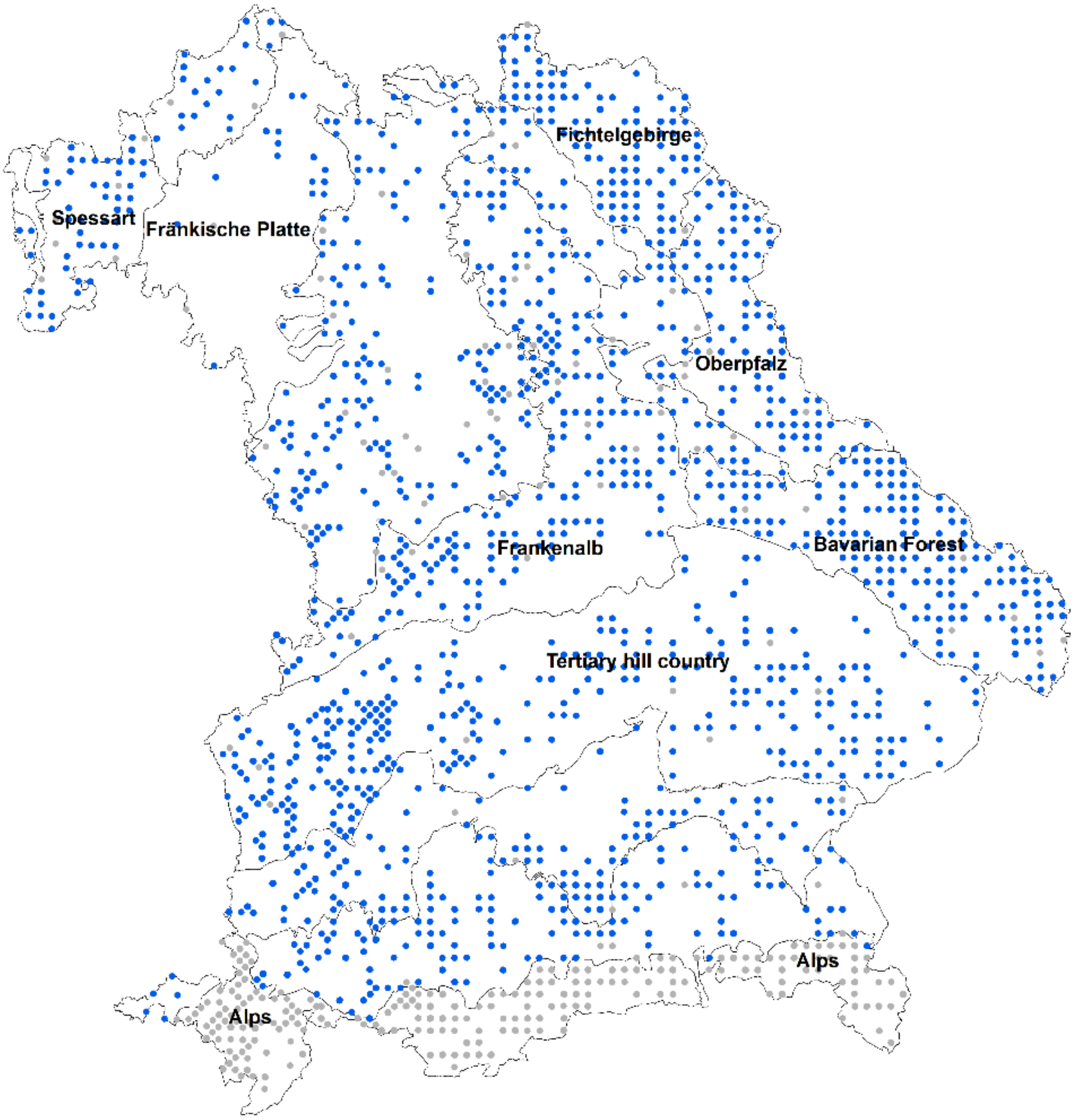
We elaborated the possibilities and limitations of NFI data and spatially explicit environmental data to analyze the dependencies of site productivity. Height at a given age served as indicator for site productivity. We focused on height as it is less affected by management than diameter at breast height (dbh), and most suitable to elaborate the effect of environmental conditions on growth [11]. Exploratory analysis helped improving the understanding of the relationship between SI and environmental variables and contributed to checking the plausibility of the statistical model. It facilitated interpreting the results of the model and understanding its limitations.

2. Methods

2.1. Study Area

Study area is the German federal state Bavaria (Figure 1) in the south-east of Germany. In forest practice, Bavaria is divided into 15 different eco-regions with varying site conditions. Geology comprises crystalline basement rocks, volcanic rocks, different triassic sedimentary rocks, limestones, tertiary molasse to quaternary fluvial, glacial, and aeolian deposits. This leads to a rich diversity in soil types. The climate varies from subatlantic lowlands at the Main river in north-west Bavaria (mean annual temperature 8.5 °C, annual precipitation sum 750 mm) to the alpine in southern Bavaria (mean annual temperature <5.5 °C, annual precipitation sum >1500 mm).

Figure 1. Map of the study area; national forest inventory (NFI) plots used in the SI-model are marked with blue dots, the remaining NFI plots containing spruces are marked with grey dots; eco-regions mentioned in the text are labeled.



2.2. Data

2.2.1. National Forest Inventory Data

NFI in Germany is based on a permanent nationwide 4 km × 4 km grid. Each grid point in forest area is the center of an angle-count sampling and sample circles with defined radii [12].

We concentrated our study on data of the third NFI (2012) for the federal state of Bavaria, because for this state harmonized high-quality site information was available. The investigated tree species was Norway spruce, as this species is the most common in Bavaria with a coverage percentage of 44.5% based on the forest area. Furthermore, the species' distribution encompasses an environmental gradient with growth limits at the cold and warm edge. Table 1 characterizes the NFI 3 dataset used in this study. Only dominant trees of the Kraft tree classes 1 and 2 were included in the analysis, as these trees are less affected by light competition and their heights at a given age reflect environmental conditions better than the heights of intermediate or overtopped trees [13]. The dataset was reduced to spruces with an age between 30 and 150 years (5318 spruces with measured heights on 3252 sample plots) (Figure 1).

For model fitting, the Alps were excluded from the dataset, because for this region large errors of height measurements occur and the estimation of age is much more insecure. Furthermore, extreme environmental conditions in the Alps bias the model, as long as not all variables relevant for growth are captured in the model, and lead to implausible predictions for the rest of Bavaria. This way, 1002 spruce plots remained.

Table 1. Characteristics of dominant spruces with height measurements in the NFI 3.

Variable	Unit	Min	Max	Mean	SD
dbh	cm	7.8	114.6	41.2	13.2
height	m	5.1	48.2	28.5	6.1
age	year	30	150	81	31

2.1.2. Environmental Data

We assigned environmental data (Table 2) from three different sources to all NFI plots. Terrain data from a digital elevation model (DEM) with a grid width of 50 m were provided by the Bavarian Survey and Geoinformation Agency (LVG). Climate data of the weather stations of Germany's National Meteorological Service (DWD) were regionalized with regression methods to a 50 m grid covering the whole of Bavaria [14,15]. Monthly means of temperature and precipitation were calculated for the period 1971–2000. Soil data were taken from a digital site information system developed at the Bavarian State Institute of Forestry [16]. Basic principle is the use of digital soil maps of the Bavarian Environmental Agency (LfU) with a scale of 1:25,000. Data gaps were filled with the help of digital soil mapping. Complex soil units were split according to relief position [17]. Thus, a finer scale of the map was derived. Soil physical and chemical properties came from reference soil profiles that were assigned to the soil units according to substrate and soil types. Chemical and physical soil properties were calculated for a depth of 1 m. Properties of different profiles within one soil unit were averaged.

Table 2. Characterization of the environmental variables for Norway spruce plots.

Type	Parameter	Abbreviation	Unit	Min	Max	Mean	SD
Climate	Average temperature during growing season from May to September	T_5to9	°C	8.7	16.3	14.1	1.4
	Precipitation sum during growing season from May to September	P_5to9	mm	249	1307	524	213
	Growing degree days (threshold: 5 °C)	GDD5	°C	541	1948	1492	260
Soil	Available water capacity	AWC	mm	5	284	135	41
	Depth gradient of base saturation	DGBS	Categorical variable (Table 3)				
	Pool of exchangeable calcium	Ca	kmol/ha	0.0	4771.0	479.2	565.1
	Pool of exchangeable potassium	K	kmol/ha	0.1	108.2	15.7	14.4
	Pool of exchangeable magnesium	Mg	kmol/ha	0.3	2374.0	166.1	221.9
	Base saturation	BS	%	2	100	49	33
	Base saturation of the first 30 cm	BS_30	%	2	100	35	34
	Pool of nitrogen	N	t/ha	0.2	39.5	6.3	4.4
	Nitrogen deposition (average of $NO_y + NH_x$ from 2004 until 2007)	N_dep	$eq \cdot ha^{-1} \cdot year^{-1}$	1225	2748	1927	241
	Clay content	clay	%	2	77	20	10
	Silt content	silt	%	4	88	37	14
	Sand content	sand	%	1	94	43	21
Relief	Soil moisture index [18]	SMI		0.27	0.61	0.49	0.04
	Mass balance index [19]	MBI		−2.87	2.70	0.07	0.82
Climate and soil	Water balance during growing season (Precipitation – evapotranspiration + AWC)	WB	mm	−108	1169	282	257

Table 3. Definition of depth gradient of base saturation and number of spruce plots for each type.

DGBS-Type	Definition	Number of Plots
11	BS > 80% in the whole profile with high stocks of Ca, Mg and K, no soil acidification	154
12	BS > 80% in the whole profile with high stocks of Ca and Mg and low stocks of K (<400 kg ha^{-1}), no soil acidification	381
2	high BS with high stocks of Ca, Mg and K, slight acidification in the top soil	903
3	medium BS with medium stocks of Ca, Mg and K, stronger acidification in the top soil	888
4	low BS with low stocks of Ca, Mg and K, deep soil acidification, increase of BS > 20% not until 1 m depth	628
5	low BS (<20%), low stocks of Ca, Mg and K, deep soil acidification	298

2.3. Exploratory Data Analysis

We explored which variables have a decisive influence on height growth and how these variables are best integrated into the model. The exploratory analysis was based on biological hypotheses: (i) the large-scale pattern of height growth of spruce stands is mainly shaped by temperature and water supply, (ii) in addition, height growth is regionally improved if the supply of basic cations is balanced, (iii) statistical height models can be improved by considering interactions of environmental variables. The exploration of the database served as justification and the variable selection as basis for a statistical SI-model.

2.3.1. Quantile Regression

In order to be able to compare trees of varying ages their heights have to be scaled. This is necessary because usually there were too few trees of similar age at the investigated sites. A 95%-quantile regression was applied to a function describing height as a fourth order polynomial of age with $\alpha = -4.4985$, $\beta_1 = 1.2841$, $\beta_2 = -0.0156$, $\beta_3 = 0.0001$ and $\beta_4 = 0.0000$ (Equation (1)).

$$\text{height} = \alpha + \beta_1 \cdot \text{age} + \beta_2 \cdot \text{age}^2 + \beta_3 \cdot \text{age}^3 + \beta_4 \cdot \text{age}^4 \quad (1)$$

The result is interpreted as the maximum height that can be reached at a certain age if environmental conditions are not limiting. Then, each tree's height was divided by the predicted value of the 95%-quantile regression for its age. The resulting value, hereafter called scaled height, can be interpreted as the percentage of the maximum height a tree can reach. Under favorable environmental conditions, a tree will reach a greater percentage than under unfavorable conditions. In order to have a safer basis for the analysis and not to give outliers too much influence a 95%-quantile regression was used instead of simply drawing an envelope curve. This means that some trees have a scaled height greater than 100%, which, however, does not impair comparisons. Additionally, the scaled height has the advantage that we can compare the height of each tree with a reference of the same age. Thus, we avoid mixing a time effect with site effects as described e.g., by [20]. The concept of scaled height was applied only in exploratory data analysis.

2.3.2. Significance Tests

We grouped environmental variables according to the quartiles of scaled height distribution and tested for significant differences between the groups using Kruskal Wallis and Pairwise Wilcoxon Rank Sum Tests (significance level $p = 0.05$), as the data were not normally distributed.

2.3.3. Hypervolumes

N-dimensional hypervolumes define species niches using *n* environmental variables. It is possible to measure hypervolumes by multidimensional kernel density estimates and thus compare the hypervolumes of different species [21]. We applied this concept to growth data by selecting the 10% of plots with lowest heights and the 10% of plots with greatest heights and interpreting them as two different species. We aimed at separating highest and lowest growth in the best possible way. The pool of potential environmental variables consisted of T_5to9, P_5to9, AWC, WB, BS_30, Ca, K, Mg, clay, silt and sand (see Table 2). If two environmental variables were highly correlated only one of them was chosen. Criteria for the selection of the environmental variables were (i) to minimize the percentage of intersection of the two hypervolumes; (ii) to maximize the percentage of the hypervolume, where only highest growth occurs on the hypervolume of highest growth and (iii) to maximize the percentage of the hypervolume, where only lowest growth occurs on the hypervolume of lowest growth.

In order to compare how big the environmental space is where lowest or highest growth can occur we calculated the percentage of the hypervolumes of plots with lowest growth and with highest growth on the hypervolume of all spruce plots in Bavaria.

2.4. Statistical SI-Model

We modelled height in dependence on age, the environmental influences and the basal area of all trees which are included in the angle-count sampling with factor 1 (BA_{ACS1}) as density measure using a generalized additive model (GAM). Variable selection was done in three steps. In the first step, double penalty selection was performed on the smooth terms [22]. In the second step, AIC backwards selection was done for the parametric terms. AIC (Akaike Information Criterion) is a measure of the relative quality of a statistical model for a given data set. It rewards goodness of fit and penalizes complexity. The third criterion was the ecological plausibility of the partial effects of the smooth terms. Beforehand different modeling approaches had been compared by 10-fold cross validation and calculation of the relative root mean square prediction error (RMSPE). To predict SI age was set to 100 years and the density measure was fixed at an intermediate value.

Finally, BRT were applied on the scaled residuals of the SI-model to allow for regionally complex interactions between the soil variables. BRT are a suitable tool for modeling residuals as they take interactions into account and can detect patterns that are otherwise undiscovered [23]. The chosen model setting included a gaussian distribution, a learning rate of 0.001, a maximum number of trees of 20,000 and a tree complexity of four.

2.5. Software

All analyses were done in R (version 3.0.1) using the libraries cvTools, gbm, hypervolume, mgcv and quantreg and the method for BRT provided by [24].

3. Results

3.1. Exploratory Data Analysis

3.1.1. Exploring the Environmental Space

Highest and lowest growth could be separated best by 6-dimensional hypervolumes defined by T_5to9, WB, Ca, K, Mg and clay content which differentiated stronger than 2-dimensional water supply and temperature only hypervolumes. This is expressed by a smaller intersection and higher percentages of only highest and only lowest growth (Table 4).

Table 4. Separation of plots with highest and lowest growth using hypervolumes constructed by different combinations of environmental variables.

Criteria for Separation of Highest and Lowest Growth		**Hypervolume Constituted by**	
		T_5to9, WB	**T_5to9, WB, Ca, K, Mg, clay**
Percentage of	intersection of the hypervolumes of highest and lowest growth	51	15
	only highest growth on the hypervolume of highest growth	5	19
	only lowest growth on the hypervolume of lowest growth	48	85
	highest growth on the Bavarian hypervolume	48	7
	lowest growth on the Bavarian hypervolume	86	38

3.1.2. Effect of Temperature and Water Supply on Height Growth

Temperature during growing season has a positive effect on height growth and can act as a limiting factor as greatest heights cannot be reached where temperature during growing season is low (Figure 2). Growth of Norway spruce is improved by a better water supply. AWC can be a limiting factor, as greatest heights cannot be reached when AWC is below a threshold of approximately 50 mm (Figure 3). There is a trend to greater heights with increasing precipitation if the Alps are eliminated from the data. Precipitation is strongly negatively correlated with temperature. In the Alps precipitation is higher, but temperature regime limits growth at higher elevations. Heights in the fourth quartile are still reached when precipitation during growing season is low. However, only 122 of 857 plots in the warm and dry (T_5to9 ≥ 3. quartile and WB ≤ 1. quartile) regions of Bavaria contain spruces. Spruce plots there are characterized by significantly higher AWC, precipitation and WB and lower temperature during growing season than the plots without spruce. The mixture proportion of spruce in plots of warm and dry regions with a mean of 55% is significantly lower than in the remaining Bavarian spruce plots with a mean of 70%.

Figure 2. Boxplot of temperature during growing season for the quartiles of scaled height distribution; mean temperature during growing season for the fourth quartile is significantly higher than for the first and second quartile.

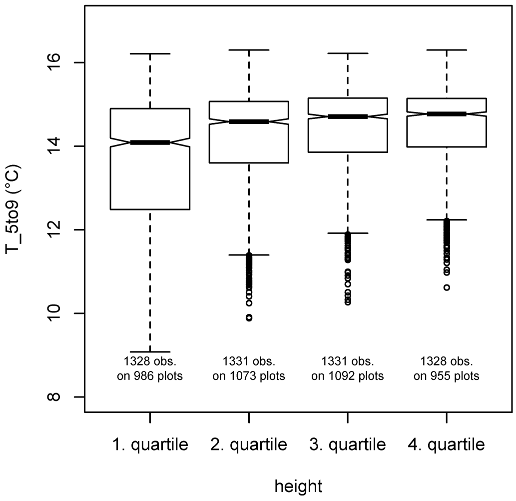
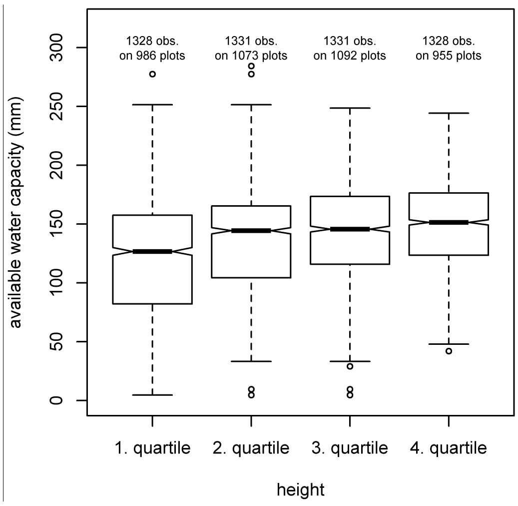
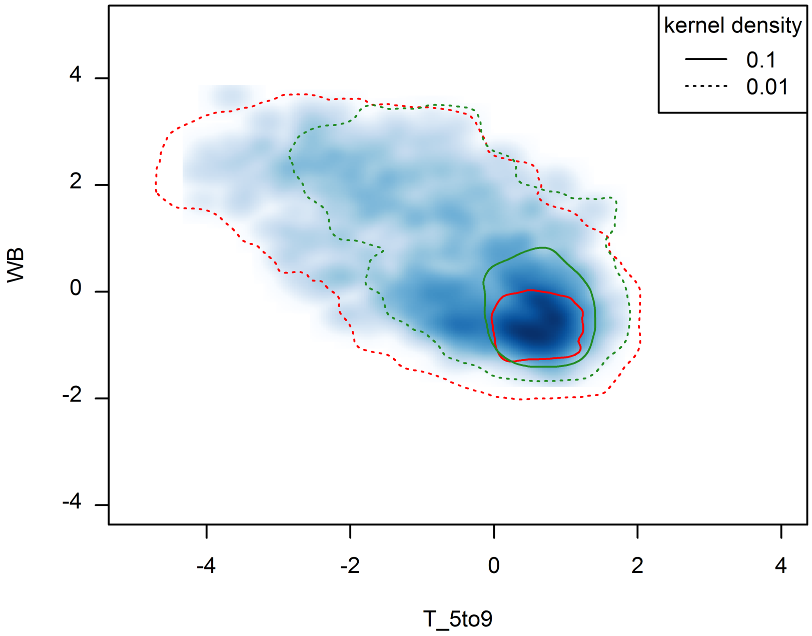


Figure 3. Boxplot of AWC for the quartiles of scaled height distribution; differences in means are significant.



The impact of the interaction between temperature and water supply on spruce growth can be visualized by comparing the densities of the 10% of plots with lowest and the 10% of plots with greatest heights (Figure 4). A particular combination of high temperatures and good water supply favors best growth. Both water supply and temperature can limit height growth. Figure 4 also illustrates that a great part of the data is concentrated in a rather small region, which explains why not only the kernel density of best growth but also the kernel density of lowest growth is high (≥0.1) at these points.

Figure 4. Green lines show the kernel densities of the hypervolumes where highest growth (best 10%) occurs, red lines show the kernel densities of the hypervolumes where lowest growth (worst 10%) occurs in a 2-dimensional projection (WB and T_5to9); in the background a smooth scatter of all spruce plots is plotted.

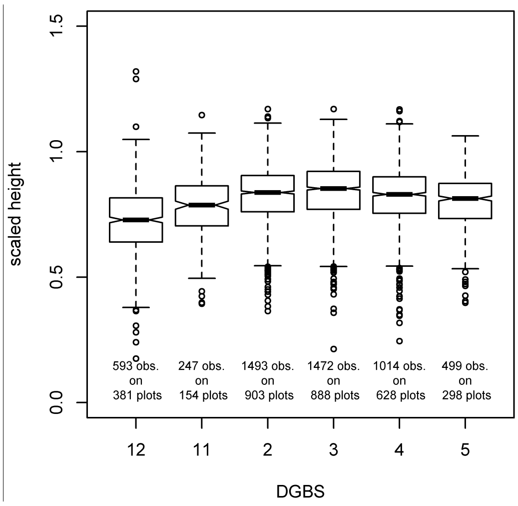


3.1.3. Additional Modifying Effect of Nutrients

On Bavarian scale, it is difficult to identify a clear effect of soil nutrients on tree height. There is an—albeit weak—effect of soil K on height growth. Mean stock of soil K is significantly higher for the fourth quartile (highest growth) of the height distribution than for the first and second quartile and mean content of soil K for the third quartile (second highest growth) is still significantly higher than for the first quartile (lowest growth).

The distributions of scaled heights for the DGBS-types are coherent and the medians follow an optimum curve (Figure 5).

Figure 5. Boxplots of scaled heights for the DGBS-types.



It has to be noted though that in Bavaria DGBS-type 1 often coincides with an unfavorable temperature regime or scarce water supply and DGBS-type 5 with low temperatures. Thus, the effects are mixed with climatic effects.

In order to detect a limiting effect of soil nutrients, regions where temperature regime and water supply are not likely to limit growth have to be chosen. However, in these climatically favored regions (T_5to9 ≥ median and WB ≥ median) nutrient supply is good: K-, Mg- and N-stock is significantly higher on spruce plots in these favored regions than in the remaining spruce plots. Furthermore, only 33 of 751 plots there have the unfavorable DGBS-type 12 and only two plots the unfavorable DGBS-type 5. Therefore, soil nutritional factors do not seem to be limiting and no significant trends can be detected by comparing them for the quartiles of height distribution. However, scaled heights for the DGBS-type 12 are significantly lower than scaled heights for the DGBS-types 11, 2, 3 and 4, whereas temperature does not differ significantly and water supply is even significantly better on the plots with the DGBS-type 12.

A limiting effect of N on tree growth cannot be detected by comparisons of means. Best growth is possible over the whole range of N-stocks.

According to [25], nutrient supply has a crucial influence on tree growth in the Alps. They identified N and P as the main limiting nutrients. To support this hypothesis sites with different geological and soil properties but no significant differences in elevation, temperature and precipitation during growing season were chosen and their scaled heights compared. These are significantly higher at flysch-sites (northern fringe of the Alps predominated by sandstone, mudstone and marl) with an average of 0.82 compared to calcareous sites with an average of 0.69.

3.2. SI-Model

The selected main model can be described with:

$$y_{height}(\mu) = \beta_0 + f(age) + \beta_1 BA_{ACS1} + f(BS) + f(MBI) + f(SMI) + f(GDD5, WB) + \varepsilon \quad (2)$$

The interaction between temperature regime and water supply has the strongest environmental effect on height (Table 5). T_5to9 was replaced by GDD5 as the later yielded slightly better results. High BS has a negative effect on height (Figure 5).

Table 5. Detailed summary of the main model (GAM).

Variable	**Estimate**	**Standard Error**	***T*-Statistic**	***p*-Value**
Intercept	27.092	0.151	178.800	2×10^{-16}
BA_{ACS1}	0.04099	0.003	11.750	2×10^{-16}
	edf	***df* residuals**	***F*-statistic**	***p*-Value**
f(age)	7.655	8.503	839.360	2×10^{-16}
f(BS)	3.379	4.148	20.880	2×10^{-16}
f(MBI)	5.034	6.170	22.340	2×10^{-16}
f(SMI)	3.543	4.446	5.410	1.48×10^{-4}
f(WB,GDD5)	9.687	11.028	33.280	2×10^{-16}
Adjusted R^2		0.652		
Relative RMSPE (crossvalidation)		0.976		

By including BS into the model the effect of temperature and water supply becomes apparent more clearly and the surface of the interaction effect becomes smoother (Figure 6). A negative influence of very low BS on growth, which would be ecologically plausible, is too weak to be modeled in a GAM probably due to the small sample of plots with extremely low BS. The inventory method angle-count sampling makes it difficult to calculate indices for stand density or competition. The best proxy appeared to be the basal area of trees included in the angle-count sampling with factor 1 as it is the most comprehensive sample of the site. Stand density has a positive effect on height. The model can be improved by including the relief parameters MBI and SMI resulting in an optimum curve for SMI and higher growth for lower slopes and valley areas (MBI < 0) and lower growth for upper slopes and crests (MBI > 0) (Figure 7). Variable selection by statistical model criteria prefers composite variables to single predictors, like WB to AWC and precipitation and BS to K and Mg.

The residuals of the main model were modeled in dependence of the soil variables N, silt, K and Mg using BRT (Figure 8). Choosing these variables to characterize soil nutrient status resulted in ecologically plausible smoothed response curves. Most important predictor is N, but silt, K and Mg are important predictors as well and lie in a similar range. The correlation coefficient between calculated and predicted residuals is 0.25.

Adding the predicted residuals to the site indices predicted by the main model (GAM) increases the R^2 to 0.675. The final SI-model is used to generate a SI-map for Bavaria (Figure 9). Highest growth can be expected in the southern part especially in the west of the tertiary hill country (Swabia) and in the Spessart in the northwest. In contrast the eco-regions "Fränkische Platte" and "Frankenalb" and the northeastern part of Bavaria are not very favorable for spruce growth.

Figure 6. Partial effects of the tensor product (in m) of the interaction between WB and GDD5 on height of Norway spruce.

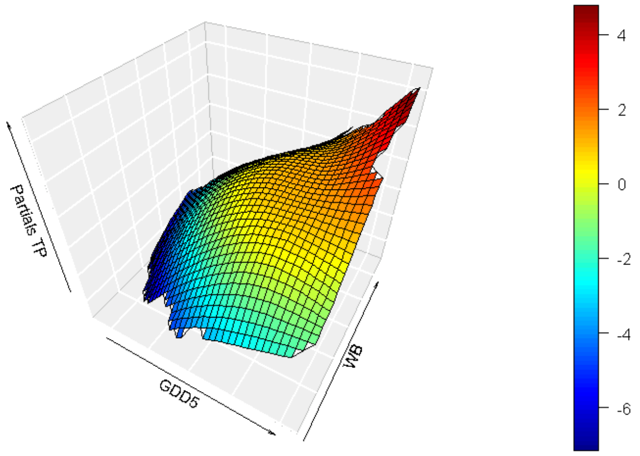


Figure 7. Partial effects of age, BS, MBI and SMI on height of Norway spruce. Dashed lines comprise 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate.

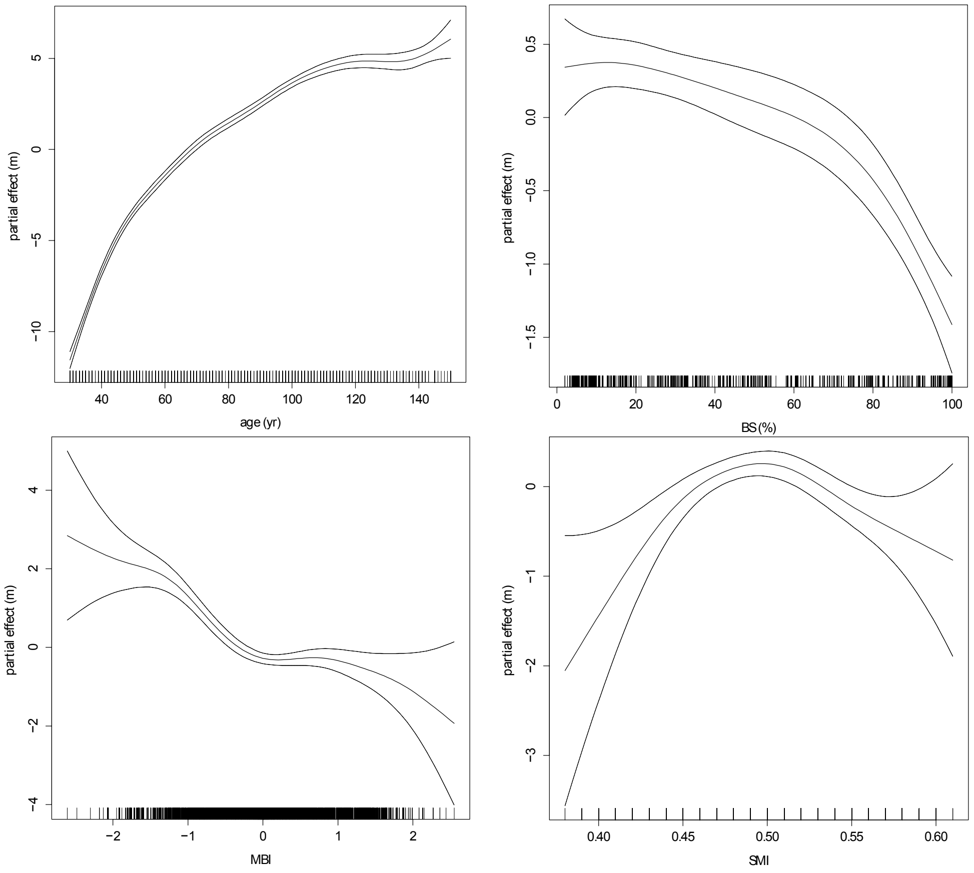


Figure 8. BRT-model of the residuals: effects of N, silt, K and Mg variables on the residuals of the main model (response); the red lines are smoothed response curves; the percentages correspond to the relative importance of the variable.

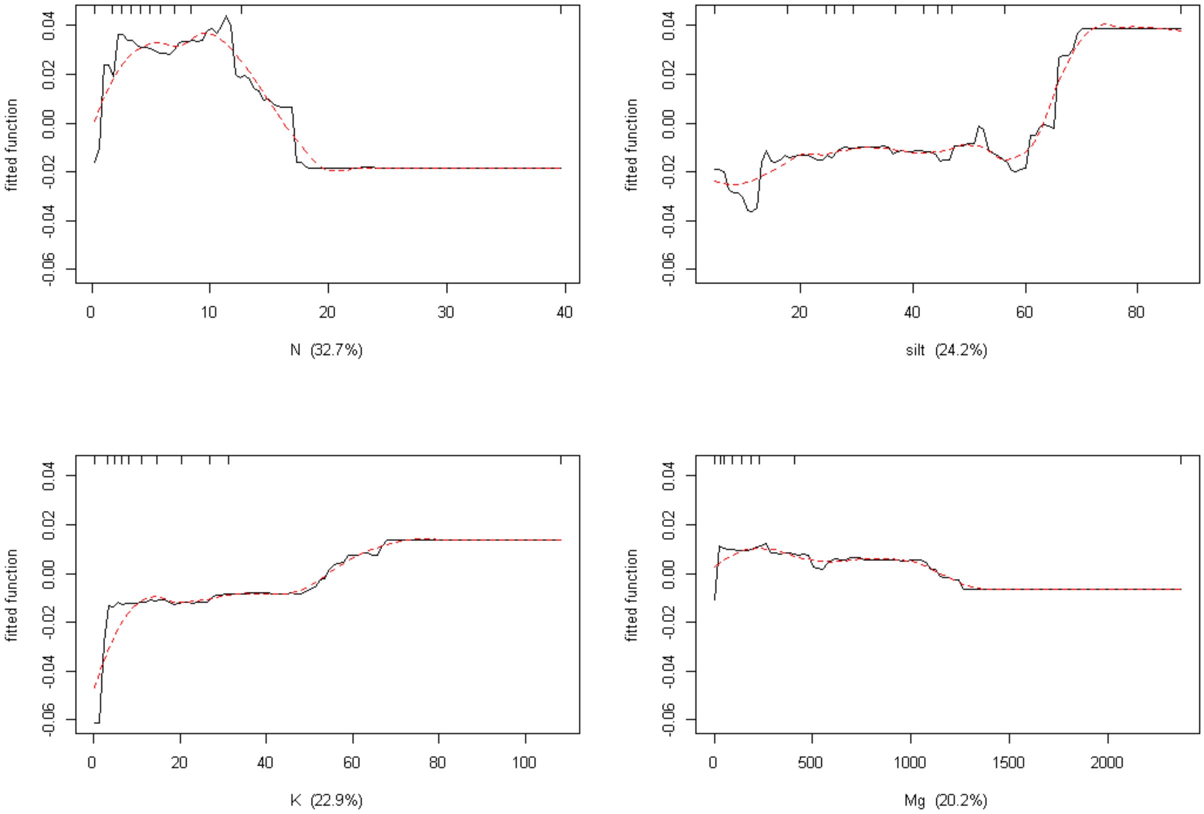
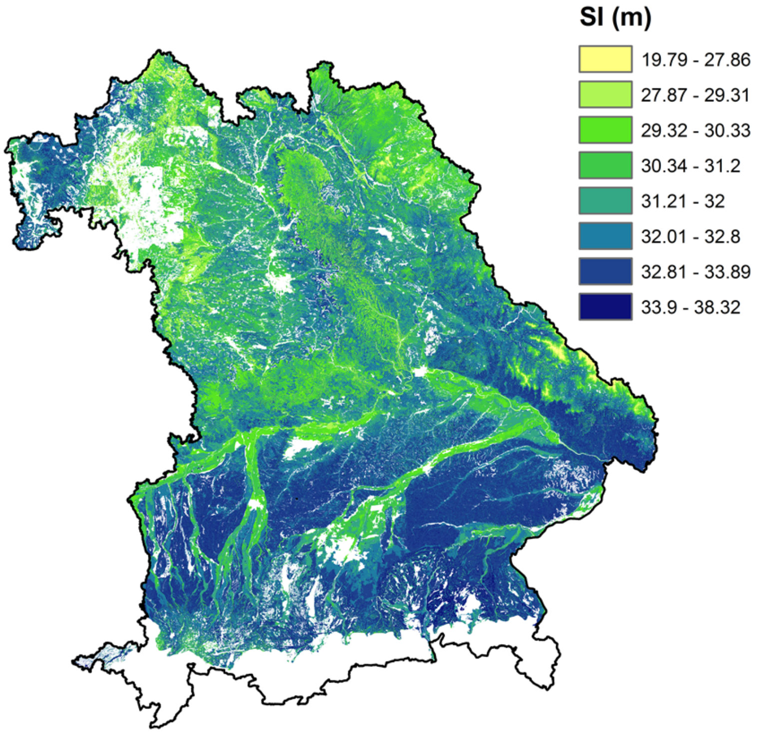


Figure 9. Modeled SI for Bavaria (Alps are excluded).



4. Discussion

4.1. Confirmation of the Ecological Hypotheses

4.1.1. Large-Scale Pattern of Tree Growth in Bavaria

On a Bavarian scale growth patterns are mainly shaped by temperature and water supply [26]. Exploratory data analysis using BRT identifies temperature during growing season and water supply as the most important environmental variables explaining height. The densities of plots with highest and lowest growth show, that highest growth is more likely in regions with warm temperatures and sufficient water supply, whereas in regions with a shortage of one of these factors lower growth rates can be expected. In the Alps, but also at high elevations in the Bavarian forest or the Fichtelgebirge, growth is limited by both temperature during growing season and the length of growing season. Sufficient water supply is essential for the growth of Norway spruce and often acts as limiting factor in regions, where temperature is not restricting. As great heights are still possible when precipitation during growing season is low, in Bavaria precipitation limits height growth only in combination with other factors like high temperatures and low available water capacity. This is also reflected in the SI-model where WB which combines these influences is selected as explanatory variable and not precipitation.

4.1.2. Additional Modifying Effect of Nutrients

Regarding soil properties Norway spruce is less demanding than other species [27]. Nevertheless, if temperature and water supply are not limiting an effect of soil nutrients, growth can be expected [28,29]. In this study, the contribution of soil nutrients compared to variables characterizing temperature and water supply was small. It was difficult to elaborate their influence on a Bavarian scale. This might be due to the fact that generally in Bavaria soil nutrient supply seldom limits growth of Norway spruce [30].

However, for the DGBS slight growth responses can be observed on a Bavarian scale and thus summarized over different temperature- and water-regimes. DGBS seems to be a meaningful parameter characterizing the soil nutrient status [31]. This emphasizes that a balanced supply of basic cations is important for a tree's nutrient supply and not the quantity of a specific nutrient alone. It is not surprising that no positive effect of Ca could be detected, as in Bavaria there is hardly ever a shortage of Ca [30]. Exploratory data analysis by BRT suggests a negative effect of Ca. At calcareous sites an imbalance of nutrients is possible leading to Ca-K-antagonism [32] and the immobilization of P [25]. Additionally, in Bavaria soils rich in Ca are often shallow (e.g., Rendzic Leptosols) and therefore tend to be dry [30]. There are only few sites with shortages in Mg-supply, but some of these sites may have been limed. Consequently, it is difficult to find an effect of Mg. On a Bavarian scale a weak effect of K only for trees at age 100 could be detected and exploratory data analysis by BRT suggested that very low K values limit growth, but the overall influence was very small.

Still regions that do not differ significantly in temperature and water supply differ in growth, which sometimes can be traced back to the soil nutrient status. For instance in the Alps spruces at flysch-sites are much higher than spruces at calcareous sites, when comparing sites that do not differ significantly in temperature, precipitation and elevation. This can be explained besides by a higher AWC by a more balanced supply of basic cations and a higher availability of P at flysch-sites. It supports the findings of [25] that in the Alps nutrient supply has a leading influence on growth.

Sites with highest growth (best 10% of plots) can be differentiated better from sites with lowest growth (worst 10% of plots) if variables characterizing the nutrient supply are added (hypervolume-analysis). This indicates that specific combinations of temperature regime and water supply with nutrient variables are necessary to reach greatest heights.

4.2. SI-Model

The predicted pattern of site indices for Bavaria is coherent with experience. The most important environmental predictor for height is the interaction between temperature regime and water supply, expressing that both factors can limit tree growth, whereas highest growth is reached if GDD5 is high and water supply is abundant. The effect of BS is mainly plausible, as high BS can limit growth. However, the GAM does not detect any limiting effect for very low BS which would be ecologically plausible. The positive effect of stand density on the one hand can be due to the fact that trees invest more in height growth if competition is stronger [33], while on the other hand it can be due to the fact that at favorable sites higher stand density is possible.

The variance in height explained by age and the selected environmental variables is 65.2%, whereas age alone explains 56.9%. Studies that encompass larger environmental gradients achieve higher explanatory power of environmental variables [2,9]. The SI predictions exhibit a regression towards the mean. This is natural for a model, but in particular high site indices are not predicted well. Hypervolume-analysis showed that very high and very low growth cannot be separated easily. If in the same environmental space (hypervolume) both high and low growth occur, the model is going to fit an average value for this combination of environmental variables and is not going to predict very high or low values. Hypervolume-analysis showed that there are more regions with only low growth than regions with only high growth. This explains why predictions for favorable sites exhibit a stronger regression towards the mean.

Exploratory analysis indicated that the overall influence of nutrient supply is small in comparison with temperature regime and water supply. Still, nutrient supply might influence height growth at a local scale and therefore we applied BRT on the residuals. The GAM has the advantage that the overall effect of temperature and water supply can be elaborated clearly, checked for ecological plausibility and therefore used for predictions under varying climate scenarios. BRT allow for regionally complex interactions of soil variables and lead to a greater differentiation and a more realistic range in predicted site indices. This approach assumes that the pattern in the residuals is stable with respect to climate change. Modeling the residuals in dependence of soil variables renders ecologically plausible trends and helps accentuating the predicted site indices locally. Silt content can be interpreted as a proxy for soils which have more favorable physical properties in respect to water and air balance than soils with high sand or clay contents. It is ecologically plausible that low N and very low K limit height growth, whereas high Mg contents often coincide with shallow gypsum soils that limit growth.

4.3. Limitations of SI Predictions

The variables with highest explanatory power are temperature regime and water supply. Nevertheless, regions exist which are very similar in this respect but exhibit great variation in height growth. Hypervolume-analysis showed that highest and lowest growth can be separated better, if along with temperature and water supply soil nutrients and soil texture are taken into account. However, in a GAM this effect cannot be represented well as these variables are not significant and are not chosen by variable selection or render implausible response curves. Hypervolume-analysis was applied only to the 10% of plots with greatest heights and the 10% of plots with lowest heights, whereas for the model all data were used. Using all data the noise is bigger and hinders the detection of clear effects.

Thus a lot of variation in SI remains unexplained. There are two possible explanations for this: missing factors influencing height growth and quality of the database.

4.3.1. Missing Factors Influencing Growth

The influence of soil on growth might be too complex to be described in correlations between the soil variables used in this study and tree height. This complexity might be captured better by explanatory variables that summarize the physiological effects of soil like vegetation data and species indicator values [9,25], by classifying soils into eco-series [34] or creating complex site factors following empirical rules [35].

Besides average environmental conditions extreme events like droughts and disturbances and/or pathogens can influence tree growth [36–38]. Furthermore, the impact of drought depends on species composition and forest structure [39]. Another source of variation in height growth might be the genetic diversity within Norway spruce [40], though provenances in Bavaria do not seem to differ greatly [41]. Furthermore phosphorus could have a strong influence on growth [42,43]. Phosphorus availability is optimal in the slightly acid to neutral pH range. In highly acid soils phosphorus is precipitated as highly insoluble Fe- or Al-phosphates or adsorbed to oxide surfaces, whereas in calcareous soils phosphorus is immobilized as di- and tri-calcium phosphates [44]. A relationship between base saturation or the DGBS-types respectively and growth could be detected in the data. The form of this relationship would be in accordance with an influence of phosphorus as well. Greatest heights are reached for intermediate DGBS-types (Figure 5), whereas high base saturation has a negative effect on height (Figure 7). However, for Bavaria regionalized data for plant available phosphorus are not available to model the effect of phosphorus and separate it from the effect of the supply of basic cations. Sometimes unexplained differences in height may not be due to site conditions but may be artifacts. For instance in some regions of Bavaria like e.g., the “Fichtelgebirge” browsing damage is very common, which might explain low tree heights [45]. Furthermore, in some regions snow damage can affect height growth. Another possible artifact is the historical use of humus layer in the “Oberpfalz”, which led to strongly reduced growth probably due to P-deficits. Older trees still have this signal in their growth history [46].

4.3.2. Quality of the Database

The suitability and accuracy of the data can be questioned both on the side of the response and on the side of the explanatory variables.

NFI data have a high sampling quality and cover a wide range of site conditions. Thus they are a valuable data source for validating data created by digital site mapping or remote sensing. Still they have some shortcomings. Age sometimes is only estimated. There might be a bias in age estimation by estimating greater ages for better growing trees which partly levels out the influence of site conditions. For this analysis the environmental variables were treated as if they are stable. However a tree may have experienced changes in environmental conditions during its lifetime [47]. Older trees may have grown under different environmental conditions in their youth than do young trees today. Management effects [48] cannot be considered adequately and it is difficult to account for competition and density effects as complete neighborhood information is not available due to angle-count sampling [49].

The suitability of SI, *i.e.*, the height at a certain age, as an indicator of site productivity can be discussed [47]. On unfavorable sites stand density has a considerable effect on height whereas on favorable sites this effect is much less pronounced [6]. As sites with the same SI can still differ in biomass production [47], biomass production might be a more adequate site potential indicator than mere height.

For spatially explicit predictions for entire Bavaria, we had to use modeled explanatory variables (digital site maps) along with measured ones. Relationships between modeled soil variables like AWC, DGBS and nutrient stocks and growth could be detected. However, the relationships are generally weak and do not contribute much to explaining SI. Modeled soil data might not be sufficiently accurate to picture the relations between soil variables and SI as soil can be heterogeneous on a very small spatial scale. The relief variables MBI and SMI that can be derived with high local precision from a DEM improve the GAM. This emphasizes the importance of small-scale heterogeneity.

5. Conclusions and Outlook

In summary, NFI data are a useful and valuable basis for investigating the relationship between forest growth and site characteristics. The dependency of height growth as derived from NFI data on site characteristics based on climatic data and modeled soil maps could be demonstrated. Applying a variety of exploratory tools for variable selection prior to modeling improves the understanding of the relationship between site productivity and site characteristics and contributes to checking the plausibility of the model and understanding its limitations. For Bavaria, the predicted large-scale pattern of SI is coherent with experience and can be projected into the future by applying climate scenarios. The limited environmental gradient leads to a limited explanatory power of the SI-model. Using digital site maps the ability to predict SI on a local scale was improved to a certain extent but is limited due to the difficulty of integrating metric soil variables into the model and the small explanatory power of the modeled soil variables. This leads to the conclusion that digitally highly resolved soil characteristics are an important step towards spatially explicit predictions of SI. However, up to the present they have not yet achieved high local accuracy.

To improve local predictions of site potential, both response and explanatory variables can be addressed. Instead of SI as height at age 100, site potential should probably be characterized by biomass growth. As in this study, the GAM tends to select aggregated variables, while ecophysiological quantities like NPP derived from process-based models can be tested as explanatory variables.

Acknowledgments

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Author Contributions

The statistical analysis was mainly done by Susanne Brandl. Georg Stricker tested different modelling approaches and conducted the automatic variable selection for the GAM supervised by Andreas Bender. The manuscript was written by Susanne Brandl supported by Wolfgang Falk. Hans Pretzsch, Thomas Rötzer, Wolfgang Falk, and Hans-Joachim Klemmt supervised the study and provided support in data analysis and interpretation.

Conflicts of Interest

The authors declare no conflict of interest.

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Publication II

Static site indices from different national forest inventories: harmonization and prediction from site conditions

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RESEARCH PAPER

Static site indices from different national forest inventories: harmonization and prediction from site conditions

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Abstract

• ***Key message*** **Static site indices determined from stands' top height are derived from different forest inventory sources with height and age information and thus enable comparisons and modeling of a species' productivity encompassing large environmental gradients.**

• ***Context*** Estimating forest site productivity under changing climate requires models that cover a wide range of site conditions. To exploit different inventory sources, we need harmonized measures and procedures for the productive potential. Static site indices (SI) appear to be a good choice.

• ***Aims*** We propose a method to derive static site indices for different inventory designs and apply it to six tree species of the German and French National Forest Inventory (NFI). For Norway spruce and European beech, the climate dependency of SI is modeled in order to estimate trends in productivity due to climate change.

• ***Methods*** Height and age measures are determined from the top diameters of a species at a given site. The SI is determined for a reference age of 100 years.

• ***Results*** The top height proves as a stable height measure that can be derived harmoniously from German and French NFI. The boundaries of the age-height frame are well described by the Chapman-Richards function. For spruce and beech, generalized additive models of the SI against simple climate variables lead to stable and plausible model behavior.

• ***Conclusion*** The introduced methodology permits a harmonized quantification of forest site productivity by static site indices. Predicting productivity in dependence on climate illustrates the benefits of combined datasets.

This article is part of the topical collection on *Environmental data for the German NFI*

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Contribution of the co-authors
Susanne Brandl: 55 % data preparation and analysis, literature research, responsible for methods, results, and discussion. Tobias Mette: 25 % concept, literature research, responsible for introduction, and proofreading. Wolfgang Falk: 5 % consulting and proof reading. Patrick Vallet: 5 % consulting and proof reading. Thomas Rötzer: 5 %, consulting and proof reading. Hans Pretzsch: 5 % consulting and proofreading

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1 Introduction

Forest site conditions are not static. Changes in site conditions due to climate change lead to changes in potential productivity. As potential productivity constitutes key information for timber-oriented forestry or the estimation of carbon stocks, it is important to estimate future trends. Prerequisites for this are databases containing large environmental gradients and a suitable measure for potential productivity. In the history of forestry, phytocentric approaches have dominated (Bontemps and Bouriaud 2014) as formulated, e.g., in Assmann (1961: 154): "Since estimates of the potential productivity based on soil characteristics and climate are afflicted with high uncertainty, it is necessary to rely on measures of the growing stand itself". The German forest scientist von Baur postulated already in 1881 that mid height is "the most precise and only correct indicator not solely for the assessment of a […] stand but for its site class [German: *Standortbonität*]." This postulate meant a remarkable change in forest growth and yield science: the *yield* development is estimated through *height and age* information. What helped to manifest von Baur's postulate was that Eichhorn (1902) showed for silver fir experimental plots in South-West Germany that "independent of the site, a certain mid height corresponds to a certain stand mass" [in forestry, at that time, mass was a synonym for volume yield]. The law of Eichhorn was amended by Gehrhardt (1909), who recommended substituting yield by total yield (including thinnings), and by Assmann (1961), who recommended substituting mid height by top height. Both modifications made Eichhorn's law more stable against thinning, especially from below (for summaries see Skovsgaard and Vanclay 2008; Pretzsch 2009; Bontemps and Bouriaud 2014).

Since the late eighteenth century, thousands of yield tables for hundreds of species have been compiled all over the world (e.g., Schober 1995; Vannière 1984). Common to all yield tables is the differentiation of site classes defined by a spectrum of age-height trajectories. The site index refers to the height at a specific reference age. For long-lived temperate forestry species, the reference age is typically 100 years. Yield tables were designed to represent regional growth behavior of a species and to allow estimating the site index of a given stand. However, for a long time, it was not considered that site conditions change, especially climate conditions.

While old stands stay well within the height frame of the yield tables, young stands clearly exceed the given height frame (Fig. 1; see also Röhle 1997, resp. Pott 1997 in Pretzsch 2009, pp. 557 resp. 584). This is not because younger stands have been systematically planted at better sites but because they have experienced better growing conditions on the same sites. Any model that relates a site index based on yield tables to recent site condition data would be afflicted with an age trend: on the same site, young stands would be assigned a higher yield class and thus a better site quality than old stands. The realization that site conditions are not constant and that non-table conforming growth is rather the rule than the exception, questions how reliably a site can be classified by yield tables (Skovsgaard and Vanclay 2013; emphasis on enhanced growth due to climate change: Spiecker 1999; Pretzsch et al. 2014).

Against this background, we derive a *static* site index. By <static>, we refer to the idea of generating false or pseudo age-height trajectories from momentary data of different ages (as in von Baur's original strip method; in German: *Streifenbonitierung*). This is done by dividing large data sets of age-height measurements into even spaced age-height curves. Unlike the yield tables, these static height curves do not represent true trajectories of the stands' height development since, under changing site conditions, a space-for-time substitution is biased (Yue et al. 2016; sensu *lato* Pickett 1989). However, the static height curves effectively lead to a balanced site index distribution over the age spectrum and make site index models stable against age trends.

Over the last decades, it has become very popular to develop statistical models that explain site index in dependence on environmental variables with varying spatial scales (Bontemps and Bouriaud 2014; e.g., Germany: Albert and

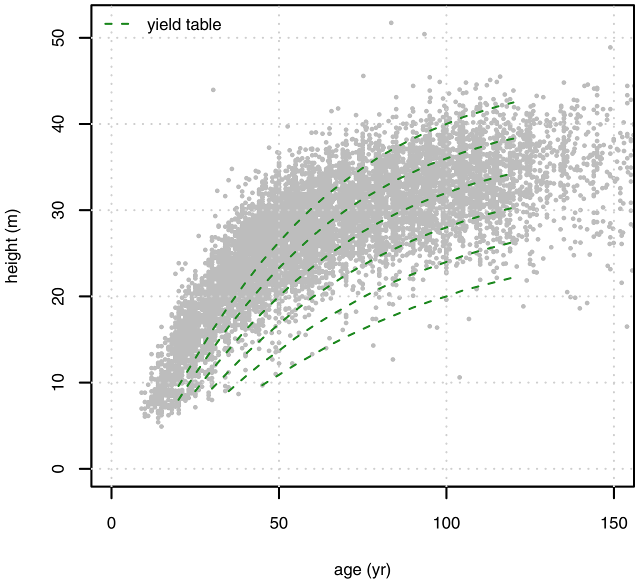

Fig. 1 Age-height measurements of dominant Norway spruce trees in the third German National Forest Inventory 2012 along age-height development for different site indices of spruce yield tables from 1963 (Assmann and Franz)

Schmidt 2010; Nothdurft et al. 2012; France: Seynave et al. 2005; Seynave et al. 2008). Many large-scale studies are based on national forest inventories. Since 10–15 years ago, national inventories have provided an increasingly accessible data source of high quality and representation. A joint effort to harmonize national forest inventories has been undertaken in McRoberts et al. (2012) and Tomppo et al. (2010). The methods and methodologies developed focused mainly on forest carbon and biodiversity estimation.

This study relates to these efforts as we harmonize site indices and the underlying height and age measures of two publicly accessible NFI data sets: Germany and France. We harmonized site indices for six species: Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Mattuschka) Liebl.), and pedunculate oak (*Quercus robur* L.). Then, we pushed forward the analyses for two species, spruce and beech, to analyze their SI modulation by environmental variables. The methodology that we introduce is transferable to other species and inventory designs as well. The combination of different inventories is extremely promising as it can cover substantially larger parts of a species' distribution and distribution limits than a single inventory alone (Brus et al. 2012; Nabuurs et al. 2013; Dolos et al. 2016). This is an important premise to derive stable species-specific models that predict the site index as a measure of growth potential from site conditions.

In summary, the aims of the study were (1) to derive a harmonized static site index based on German and French NFI data and (2) to estimate trends in productivity due to climate change.

2 Material and methods

2.1 National forest inventory data

In Germany, the NFI is based on a permanent nationwide 4 km × 4 km grid (regionally densified). Each grid point represents an inventory cluster of four inventory points laid in a square of 150 m edge length. Each inventory point in forest area is the center of an angle-count sampling and sample circles with defined radii (BMELV 2011). In this study, the data of the third NFI (2012) are used. In France, since 2010, the NFI is based on a 1 km × 2 km grid surveyed over a 5-year rotation. Each grid point is the center of three subplots of 6, 9, and 15 m, respectively, where trees that reach certain diameter thresholds are included (IGN 2016). In this study, data from 2006 until 2013 are used. From the NFI data, we selected all inventory plots where the investigated species accounted for ≥ 70% of the plot basal area. Plots in forests with no defined structure and coppice plots were discarded as well as plots with a coefficient of variation of age > 0.25. For Norway spruce, this resulted in 10,552 plots in Germany and 914 plots in France. For European beech, 5247 plots in Germany and 1595 plots in France were selected. Trees with top or crown breakage or other severe damages were not counted among the dominant trees.

2.2 Top height and age

The top height h_{top} is defined as the height corresponding to the root mean square diameter d_{top} of the top 100 diameters of a tree species on a site (Kramer and Akça 1995). The estimate of h_{top} depends in the first place on the representativeness of the sampled trees for the entire stand. Each sample tree stands for a certain number of trees per hectare, which depends on the tree's DBH. Arguing that each sample tree represents a DBH distribution rather than a single value, a density function was laid over the DBH distribution, i.e., a bandwidth filter was applied to the DBH histogram (Fig. 2). The bandwidth scales the width of this distribution and equals the standard deviation of the normal function in a Gaussian kernel (Venables and Ripley 2002). The corresponding h_{top} was derived from species-specific uniform height-diameter curves (Dahm 2006).

In the German NFI, the age of all sample trees is given, but the source and quality of the age information differ (records of planting, increment boring, estimation etc.). In the French NFI, only the age at breast height of one or two dominant trees is determined by increment boring. The age corresponding to d_{top} and h_{top} was calculated as the mean age of the top 100

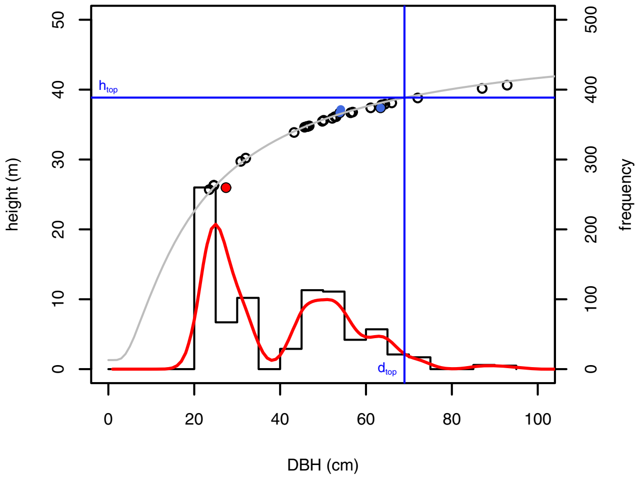

Fig. 2 d_{top} and h_{top} estimation visualized for an exemplary spruce plot of the German NFI: The circles mark height and DBH of trees included in the sample. Trees with measured heights are plotted blue. The red dot corresponds to a tree with crown breakage. The uniform height-diameter-curve is overlaid in gray. The histogram shows the number of trees per hectare represented by the sampled tree of a certain DBH. The red line shows the density of the DBH distribution

trees of the investigated species for the German NFI sample. For the French NFI sample, the age at breast height of the trees of the investigated species with age measurements was averaged and adjusted for the missed tree rings between 0 and 130 cm height according to previous measurements from the French NFI.

2.3 Static site index determination

To obtain the site index (SI), the age-height spectrum has to be divided into infinite sets of adjacent age-height curves. To do so, we fitted the Chapman-Richards function (Richards 1959) to the 5 and the 95% quantiles of heights creating a lower and upper boundary line (Fig. 3).

$$h_{top\ (i)} = A*\left(1-e^{-k*age_i}\right)^p \quad (1)$$

The SI is determined by scaling the position of $h_{\mathrm{top}}(i)$ between lower and upper boundary height at age i with the ratio of the span between lower and upper boundary height at age 100 and the span between lower and upper boundary height at age i:

$$\hat{SI} = h_{top\ l(100)} + \left(h_{top\ (i)} - h_{top\ l(i)}\right)\cdot\frac{h_{top\ u(100)} - h_{top\ l(100)}}{h_{top\ u(i)} - h_{top\ l(i)}} \quad (2)$$

with $h_{\mathrm{top}l}$ and $h_{\mathrm{top}u}$ as the lower and upper boundary height at the respective age.

As indicated in the introduction, we did not develop a height growth model here. Our aim was to determine stable lower and upper boundary lines of the age-height distribution in the data in order to determine the SI of each stand by comparing its top height with a reference of the same age. We employed the Chapman-Richards function instead of polynomials because its properties allow a stable fit of lower and upper boundary lines over the whole age range. However, these lines represent true trajectories of the stands' height development over time only if growth conditions are assumed to be stable. If we assume improving growth conditions over the last century—for which evidence is ample (cf. introduction)—young stands will grow faster, i.e., with higher site indices, than old stands which experienced less favorable growing conditions when young. The static site index thereby avoids an age trend in the site indices and makes young and old stands on similar sites comparable.

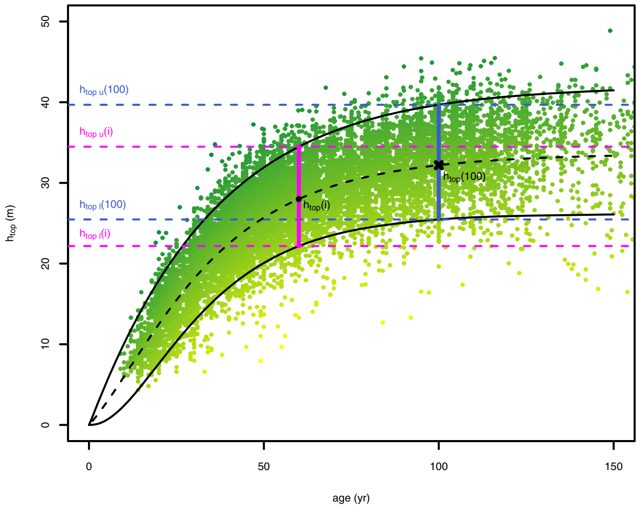

Fig. 3 Illustration of translating the top height $h_{\mathrm{top}}(i)$ of a species in a stand at age i to the corresponding height $h_{\mathrm{top}}(100)$ at the reference age of 100 years, i.e., the SI; green points mark heights and ages of NFI spruce plots; the solid black curves show the fit of the Chapman-Richards function to the 5 and 95% quantiles; the black dot marks an example stand at age 60 with a top height of 28 m. The black cross marks its translation to h_{top} at age 100, resulting in a SI of about 32 m

2.4 Error estimation from virtual data

We used virtual stands, which were simulated based on yield tables of Norway spruce, to assess the uncertainties in deriving the static site index. A detailed description of methods and results as well as a discussion of the uncertainties associated with the static site index formation are presented in Appendix 1.

2.5 Modeling site index in dependence on environmental variables

The second aim of the study was to model SI in dependence on climate parameters and predict the potential productivity of a tree species under climate change. We used the climate data of WordClim which cover the study area with a resolution of 30 arcseconds, i.e., approximately 1 km (Hijmans et al. 2005). Climate variables (Table 1) were grouped into variables characterizing mean annual temperature or summer temperature, winter temperature, precipitation, and continentality. Elevation was used as an additional explanatory variable. In order to prevent high correlations, only one variable could be selected from each group.

We did not include soil parameters in the models, since it is difficult to derive comparable soil parameters for the German and French inventory plots. The influence of soil parameters was taken into account only by removing plots where the climate signal was likely to be confounded by extreme soil characteristics (gley soils, pseudogley soils, moor soils, extremely shallow soils (depth < 35 cm), and soils with skeleton content > 90%). For Germany, the soil data were raised within the project "Forest productivity, Carbon sequestration, Climate change". For France, information on soil parameters forms part of the NFI data. We compared the differences in model performance caused by applying these soil filters.

We fitted generalized additive models with a gamma error distribution and log-link function (Wood 2006; Pya

Table 1 Characterization of the environmental variables for spruce and beech plots used for model fitting

			Spruce		Beech	
			Mean	SD	Mean	SD
Summer/annual temperature	Mean annual temperature (°C)	T	7.4	1.1	8.4	1.2
	Mean temperature warmest quarter (°C)	T_wq	15.4	1.2	16.1	1.1
	Mean temperature May to Sept. (°C)	T_5to9	14.1	1.2	14.7	1.1
	Max. temperature warmest month (°C)	Tmax_wm	21.3	1.5	22.1	1.4
	Mean July temperature (°C)	T7	16.2	1.2	16.8	1.1
Winter temperature	Mean January temperature (°C)	T1	−1.5	1.4	−0.2	1.6
	Min. temperature coldest month (°C)	Tmin_cm	−4.2	1.5	−2.9	1.5
Precipitation	Annual precipitation sum (mm)	P	882	176	831	147
	Precipitation sum warmest quarter (mm)	P_wq	270	54	238	42
	Precipitation sum May to Sept. (mm)	P_5to9	420	80	382	63
Continentality	Continentality index (Conrad 1946)	ci	36.5	3.8	35.7	3.6
	Tmax_wm–Tmin_cm (°C)	Txn_range	25.6	1.7	25	1.6
	T_wq–T1 (°C)	T_range	17	1.2	16.3	1.3
Elevation	Elevation (m)	Elevation	564	278	472	315

and Wood 2015) using R version 3.3.2 and the R packages mgcv and scam. For model fitting, only plots with mean ages of the top 100 trees between 30 and 150 years were used. The intercept could differ between Germany and France in order to account for possible effects of differences in inventory design not yet considered. We selected the best model of all possible combinations using adjusted R^2 and AIC as criteria. We checked for trends in the residuals by plotting them against the covariates and the fitted values. Additionally, we checked for spatial trends in the residuals by mapping them.

3 Results

3.1 Static site index determination

Figure 4 displays age-height scatter plots and the fits of the Chapman-Richards function for Norway spruce and European beech from the joint data sets of the German and French NFI. Results for Scots pine, Douglas-fir, sessile oak, and pedunculate oak are presented in Appendix 2. Table 2 summarizes the function parameters for the joint data set. The asymptotes (A) of the upper boundary line are lower than the maximum top heights observed, as they were fitted with 95% quantile regressions. The fitted upper and lower boundary lines describe well the range of top heights over the whole age range, which was a prerequisite for deriving the static site index.

3.2 Error estimation from virtual data

Tests made on virtual data ensured that there are no big or systematic deviations resulting from the two NFI sampling methods and that h_{top} is relatively stable with respect to effects of density. The effect of age errors on SI estimation decreases with increasing age. Detailed results are presented in Appendix 1.

3.3 Site index dependency on environmental variables

We investigated how far environmental variables contribute in explaining the site index. Tables 3 and 4 summarize the results of SI models for Norway spruce and European beech respectively. Filtering the data for extreme soil conditions increases the adjusted R^2 (spruce: from 0.164 to 0.191; beech: from 0.335 to 0.401).

3.3.1 Spruce

The generalized additive model for spruce can be described with:

$$SI_{\text{GAM, Spruce}} = \exp(f(T\_5to9) + f(T1) + f(P) + \text{country} + \varepsilon) \quad (3)$$

Mean temperature of the growing season from May to September (T_5to9), mean temperature in January (T1), and annual precipitation sum (P) were selected to explain SI of Norway spruce. Graphical checks revealed no trends in the residuals. T_5to9 has the strongest explanatory power (Fig. 5a). It has a positive effect on SI over the whole range.

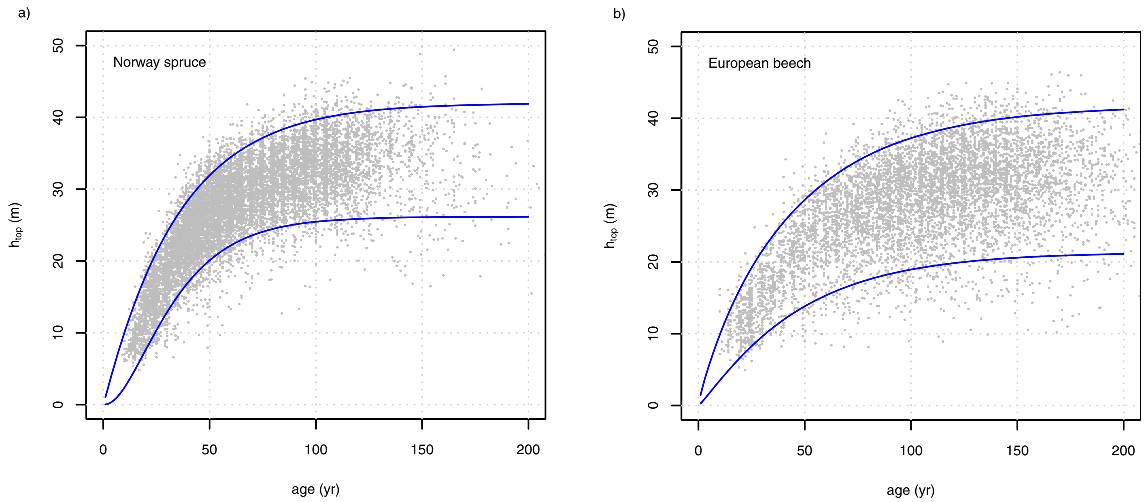

Fig. 4 Age-height scatter plots for Norway spruce and European beech in the German and French NFI data. Lines depict quantile regression for the 5 and 95% percentiles with the Chapman-Richards function

Until approximately 15 °C, SI increases strongly with rising temperatures. A further increase in T_5to9 leads only to a very slight increase in SI. The confidence intervals become wide for T_5to9>16 °C, i.e., the uncertainty in model predictions is high at the warm temperature margin. Overall SI decreases with rising T1 (Fig. 5b). For T1>− 1 °C, a continuous decrease is fitted. Due to the wide confidence intervals at the cold margin of T1, one could either assume no effect of T1 on SI below − 1 °C or a decrease in SI with rising T1 over the whole range of the variable. There is a steep increase in SI with P until a threshold value of about 750 mm is reached (Fig. 5c). Even at the very dry margin, the confidence intervals remain narrow, i.e., this effect is clearly present in the data. At the threshold value of 750 mm saturation is reached and the effect of Psum stays more or less level until a value of about 1100 mm. The effect of the country factor is rather small (Table 3).

In order to help interpret the effect of temperature on SI, we fitted the same model except that T_5to9 and T1 entered the model as an interaction term (Fig. 5d). At the cold edge (lower left corner), the contour lines are more or less vertical, i.e., only T_5to9 influences SI. Towards warmer summers, the SI increases but the increase is stronger when winters stay colder (lower right corner; continental climate) than under warm (oceanic) winter conditions (upper right corner).

Table 2 Results of fitting the Chapman-Richards function to the lower 5% and the upper 95% percentiles of the age-height distribution for the joint German and French inventory data

Quantile curve	Parameter	Spruce	Beech
Lower	*A* =	26.16	21.35
	k =	0.0448	0.0232
	p =	2.35	1.15
Upper	*A* =	42.01	41.79
	k =	0.0294	0.0208
	p =	1.05	0.86

3.3.2 Beech

The generalized additive model for beech can be described with:

$$SI_{\mathrm{GAM,Beech}} = \exp(f(T\_wq) + f(P\_5to9) + f(\mathrm{elevation}) + \mathrm{country} + \varepsilon) \quad (4)$$

Mean temperature of the warmest quarter (T_wq), precipitation sum during the growing season from May to September (P_5to9), and elevation were selected to explain SI of European beech. Graphical checks revealed no trends in the residuals. For T_wq, a curve with a wide optimum range between about 14 and 18 °C is fitted (Fig. 6a). SI increases strongly with rising T_wq until about 14 °C. There is a slight further increase in SI until about 16 °C when it is more or less level and reaches the optimum at 17.2 °C before it decreases again for T_wq>17.5 °C. A saturation curve can be fitted to P_5to9 (Fig. 6b). SI slowly starts increasing at P_5to9 =

Table 3 Site index model performance for Norway spruce

	Estimate	Standard error	*T* statistics	*p* value
Intercept	3.473	0.005	633.864	$< 2 \times 10^{-16}$
country factor (Germany)	0.029	0.006	4.749	2.12×10^{-6}
	edf	Ref. df	*F* statistics	*p* value
s(T_5to9)	4.943	6.077	87.48	$< 2 \times 10^{-16}$
s(T1)	6.058	7.131	14.28	$< 2 \times 10^{-16}$
s(P)	7.906	8.667	12.94	$< 2 \times 10^{-16}$
Adjusted R^2	0.191		Deviance explained	19.6%

edf estimated degrees of freedom

Table 4 Site index model performance for European beech

	Estimate	Standard error	*T* statistics	*p* value
Intercept	3.228	0.030	106.4	$< 2 \times 10^{-16}$
Country factor (Germany)	0.131	0.009	15.0	$< 2 \times 10^{-16}$
	edf	Ref. df	*F* statistics	*p* value
s(T_wq)	6.250	7.197	9.684	4.1×10^{-12}
s(P_5to9)	2.743	3.048	24.544	9.07×10^{-16}
s(elevation)	7.919	8.593	40.596	$< 2 \times 10^{-16}$
Adjusted R^2	0.4013		Deviance explained	41.6%

edf estimated degrees of freedom

300 mm. Between 380 and 520 mm, there is a steep increase, which flattens at a threshold value of about 570 mm. The effect of P_5to9 or variables characterizing precipitation in general is not as clear as the effects of the other variables. Monotonicity constraints had to be applied to fit ecologically plausible curves that can be used for predictions. A smooth term without any constraints would lead to an increase in SI between 300 and 520 mm, followed by a slight decrease and a further increase until approximately 630 mm. This is in line with the constrained fit. However, a model without constraints would predict a very high SI for very low P_5to9 (≈ 200 mm) and for high P_5to9 (> 630 mm) a steep decrease. Both the dry and the wet margin are barely supported with data, which is also reflected in wide confidence intervals. Therefore, it seems justified to constrain the fit to ecologically plausible behavior at the data margins. Elevation has a strong effect on SI of beech (Fig. 6c). SI is highest at an elevation of about 200 m. It increases from sea level to 200 m and then continuously decreases. At 400 m, the same SI is reached as that at sea level. Between 450 and 600 m, the otherwise strong decrease is less pronounced. In spite of the high explanatory power of the climate variables and elevation in the model for beech, the

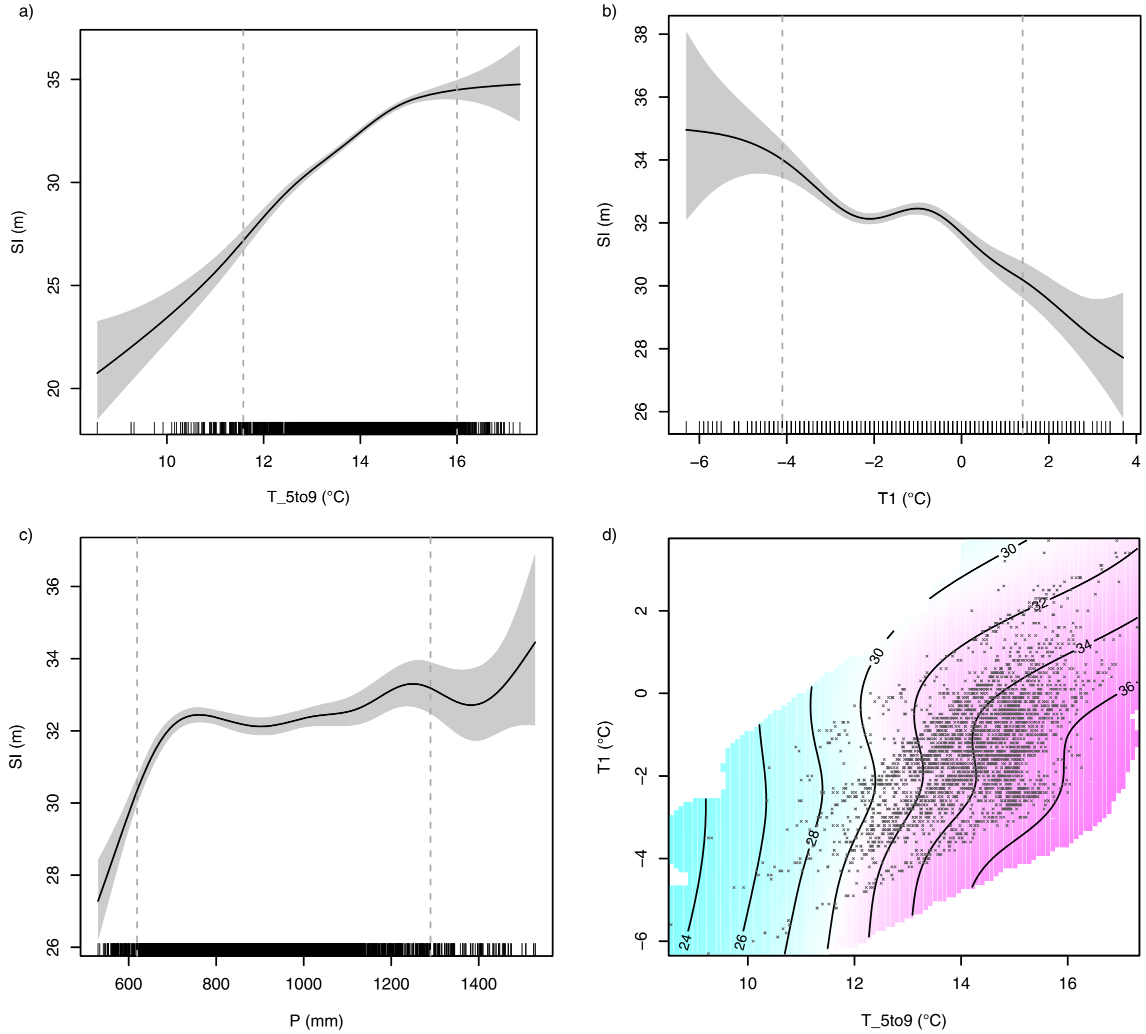

Fig. 5 Effects of T_5to9 (a), T1 (b), and P (c) on SI of Norway spruce. The gray area comprises 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate. The vertical dashed lines mark the 5 and 95% quantiles of the covariate's distribution. The contour plot (d) shows the result of the alternative model fitted with an interaction between T_5to9 and T1

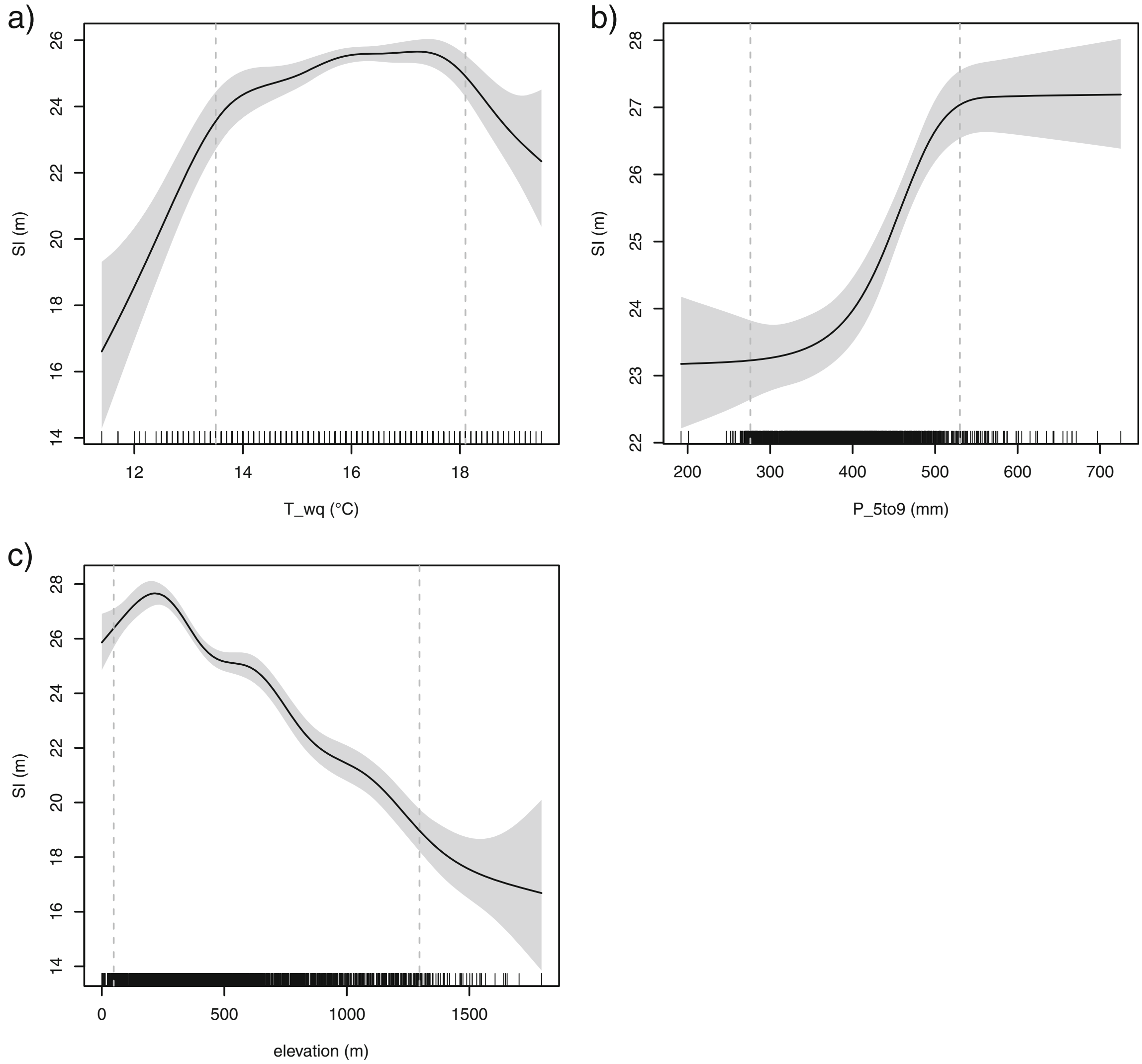

Fig. 6 Effects of T_wq (a), P_5to9 (b) and elevation (c) on SI of European beech. The gray area comprises 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate. The vertical dashed lines mark the 5 and 95% quantiles of the covariate's distribution

effect of the country factor is rather strong (Table 4), predicting approximately 14% higher SI for Germany under the same environmental conditions.

3.3.3 Prediction maps

The models were used to create maps of SI (Fig. 7) for current and future climate (climate scenario RCP 4.5 for the period 2061–2080 based on WorldClim MPI-ESM). After removing plots with extreme soil conditions, we modeled the effect of climate and, in the case of beech, elevation on SI. Thus, prediction maps show the climate-driven SI. We masked the extrapolation range of the models. In these areas, the species can occur but the corresponding climatic conditions were not present in the French and German NFI data used for model fitting (gray areas). Areas in the future maps are hatched when current climatic conditions are present in the training data, but future climatic conditions fall into the extrapolation range.

3.3.4 Spruce—current climate

High SI are reached in Southern Germany due to a favorable combination of mean temperature during growing season, temperature in January, and precipitation sum. In the Alps, T_5to9 strongly limits height growth. T_5to9 also acts as a limiting factor in Southeast Finland. The model predicts lower SI for France than for Germany, which is mainly an effect of higher T1. In Eastern Germany P limits height growth. In the Balkans, high SI are predicted in mountain areas because of low T1 and P greater than the modeled threshold value of about 750 mm and suitable T_5to9, but at the highest elevations again, T_5to9 is too low to reach high SI.

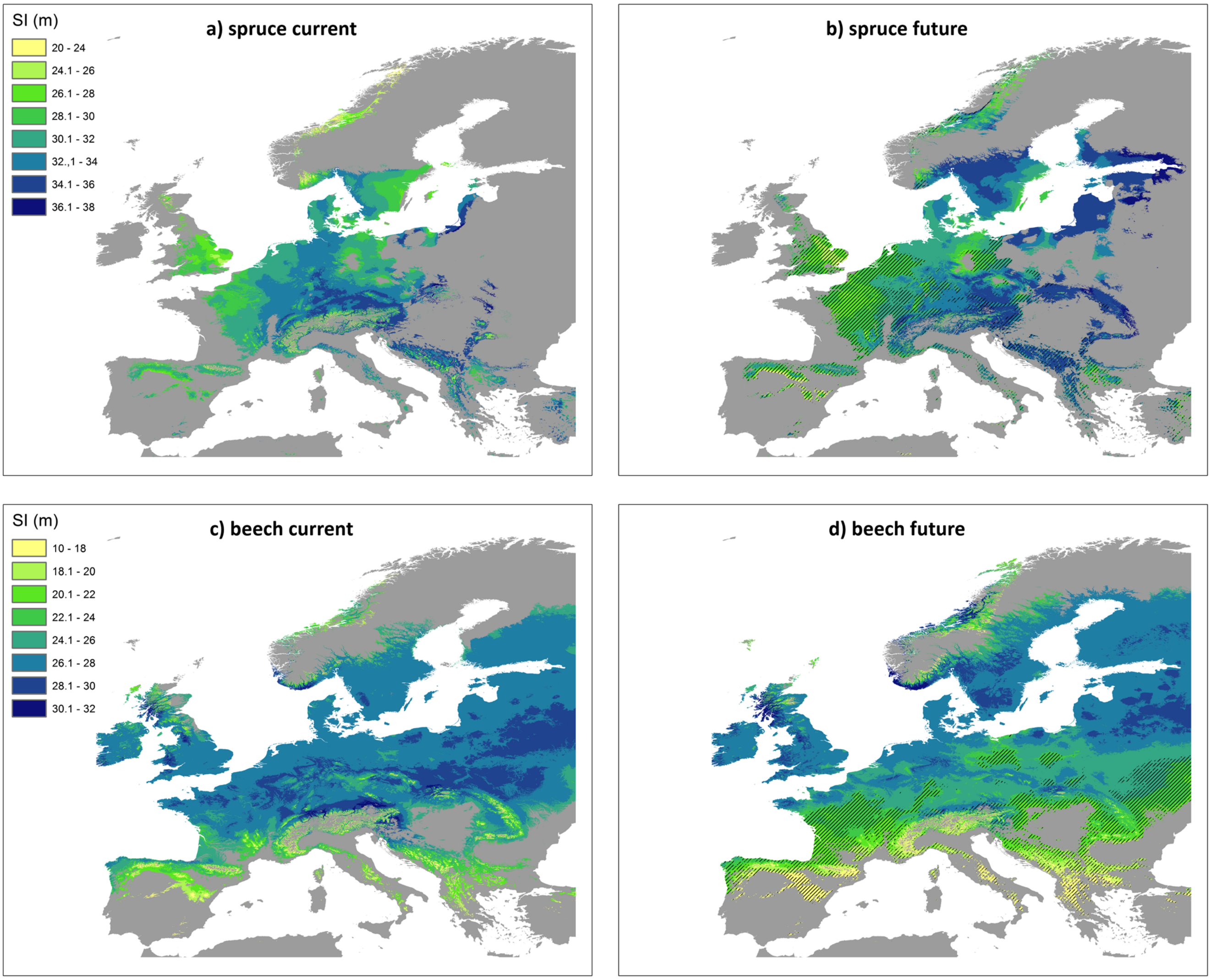

Fig. 7 Map of predicted SI of Norway spruce and European beech for present and future climatic conditions based on plots without extreme soil conditions, i.e., limitations due to soil conditions are not taken into account. The gray areas mask the extrapolation range of the models. Predictions for the future are hatched when current climatic conditions are present in the training data, but future climatic conditions fall into the extrapolation range

3.3.5 Spruce— future climate

As the chosen climate model (MPI-ESM RCP 4.5) predicts a clear increase in temperature but not much change in precipitation, changes in SI are mainly temperature-driven. SI increases in the mountains as T_5to9 increases and no longer limits height growth while T1 is still rather low. The same is true for Southern Finland, Norway, and the mountain areas in the Balkans. In Germany, the model predicts slightly lower SI mainly due to rising T1.

3.3.6 Beech— current climate

For beech, low SI are predicted for mountainous regions. In the non-masked regions of Southern Europe, low SI are predicted due to elevation and low precipitation. For current climate conditions, summer temperature mostly does not reach values that seriously limit height growth. In the South of Germany, environmental conditions are very favorable for beech and SI is high. Both at the Southern and Northern edge of the non-masked area, a decrease in SI is visible due to high or low T_wq, respectively.

The map of Europe shows the effects caused by the fit of the environmental variables as the country factor was set to zero. However, in the model for beech, the country factor has a strong impact. When taking this factor into account, predicted SI are approximately 14% higher in Germany than in France, a difference that could not be explained by any of the environmental variables available for selection.

3.3.7 Beech—future climate

In the predictions for the future, the strong effect of elevation in the model becomes apparent. Despite rising temperatures, SI remains low in the mountains. In comparison to the map for current conditions, there is a clear shift to the north for regions of high SI. For Southern Germany, a decrease in SI is predicted. These changes are temperature-driven.

4 Discussion

4.1 Harmonized site indices as a measure for potential productivity

We propose height of the 100 largest trees—recommended by Assmann (1961)—and corresponding age as stable and sensible measures that can be derived based on a common definition from various inventory sources. Data must allow for distinguishing the top 100 trees and assigning height and age estimates—requirements met by most single-tree-based sampling designs. In comparison to the mid height—the yield table standard for site classes—the top height is relatively robust also in uneven-aged stands, as it is most likely that the 100 largest diameters represent dominant upper canopy trees and it is not affected by thinning from below (Kramer and Akça 1995). Another option would be to choose the Weise height as top height. It is defined as the height corresponding to the root mean square diameter of the top 20% of diameters of a tree species on a site, which represent dominant trees well throughout the stand's development (Kramer and Akça 1995).

Once harmonized height and age measures have been derived from the inventory data, each plot can be assigned a species-specific static site index based on age and height in relation to lower and upper boundary age-height curves fitted to the data. We employed the Chapman-Richards function which is often used to model growth. It has three directly interpretable growth parameters and shows comparably fast height saturation. However, we did not use it as a growth function. We chose the Chapman-Richards function because it describes well the upper and lower boundary lines of the data which are required to derive static site indices. In this context, the curves fitted might only be interpreted as height growth development as far as cross-sectional data can be interpreted as longitudinal data. But curves fitted to cross-sectional data might be quite different from curves fitted to longitudinal data. Perin et al. (2013), for instance, assert non-saturating height growth for Norway spruce in Belgium from true time series (longitudinal data), while pseudo time series from inventories (cross-sectional data) support saturating height growth (Dagnelie et al. 1988). Besides the ecophysiological meaning (Ryan and Yoder 1997; Koch et al. 2004), the question of whether stand height saturates or not has a significant effect on the interpretation of data. While non-saturating functions can interpret continued height growth of older stands as an age effect, saturating functions must assume changes in the height asymptote as an effect of changing site conditions. In the end, the static site index does not intend to predict the true trajectory of a stand's top height through time and thus predict the true top height this stand will reach at age 100. In this sense, the decision to define the static site index by the height at a reference age of 100 years should not be misleading. The statement behind the static site index is NOT what height young stands are to be expected to reach at age 100, BUT what height stands at this site would have reached if they had been planted 100 years ago. As stated in the introduction, the aim of the static site index is to relate site condition data to a stand productivity measure free of age trends. However, changes in silvicultural prescriptions like earlier rotation of fast growing stands can introduce a bias into cross-sectional data, but on the other hand, longitudinal data integrate changing site conditions which surely affect height growth. Evidence for forests in Central Europe suggests accelerated growth over the last decades (Pretzsch et al. 2014; Charru et al. 2014; Spiecker 1999). A promising solution to the dilemma is the interpretation of longitudinal data with dynamic site conditions (Yue et al. 2016). Especially where large-scale inventories permit establishing time series—such as the German NFI 1987, 2002, and 2012—the consideration of changing site conditions offers a great potential for future analyses.

The concept of site index was developed for regular, even-aged stands, and the trend to structurally diverse mixed stands and thinning from above reduces the informative value of SI (Pretzsch 2009). We considered this as far as possible in the static site index formation by only including plots where the investigated species accounted for ≥ 70% of the plot basal area, a threshold that has been used in similar studies based on NFI data (e.g., Seynave et al. 2008; Charru et al. 2014), and by removing plots where the coefficient of variation of age was greater than 0.25. Apart from that, as the developed SI models predict SI independent of stand age and density, they allow comparing site productivity based on environmental conditions and can, for this purpose, be applied to forest systems differing from pure and even-aged stands (Bontemps and Bouriaud 2014).

More generally, the suitability of SI, i.e., the height at a certain age, as an indicator of site productivity can be discussed, as SI is merely an indicator of site productivity, but not a physiological measure and does not completely capture productivity (Skovsgaard and Vanclay 2013; Bontemps and Bouriaud 2014).

For now, we see the following advantages in our approach. In order to derive a static site index, no repeated measurements are necessary. Top height and static SI are simple measures traditionally used in forestry. Most large-scale inventories provide the required information. SI can then be related to environmental variables. Another option to capture the relationship between productivity and environmental conditions would be to model height in dependence on age and environmental variables in one step (Vallet and Perot 2016; Brandl et al. 2014). In our case, we preferred a two-step approach for two reasons: First, the approach presented in this study allows a mere descriptive site (index) assessment of a stand without the introduction of any modeled effects of environmental variables and all the uncertainty going with it. Thus, the harmonized site index represents the current height growth potential of NFI plots as closely as possible and enables comparisons of different stands without an attempt to explain these differences. In a model that predicts height in dependence on age and environmental variables, the resulting SI range is less similar to the real situation, if the available environmental variables only explain part of the variation in heights, which is often the case. Second, modeling the SI in dependence on environmental variables in a separate step has the advantage that the effect and explanatory power of environmental variables on SI is immediately clear and separated from the effect of age. Our approach also offers the possibility to derive changes in SI from model predictions for current and future conditions and add the modeled trend to the SI calculated at inventory points.

4.2 Site index dependency on environmental variables

In a wide temperature range, productivity strongly increases with rising temperatures. This would be expected due to longer growing seasons and higher enzyme activity. Beyond the temperature optimum, a negative effect of further rising temperatures is fitted. For beech, this is obvious in the effect of T_wq. But the effect of temperature is actually similar for spruce. The curve for T_5to9 still slightly increases at the high temperature margin. But as higher temperatures during the growing season usually go in line with higher temperatures in January, which have a negative effect in the spruce model, the overall effect of temperature on SI depends on whether T_5to9 or T1 increase more strongly in the future and thus the overall effect might be increasing, decreasing or compensatory. However, the predicted map for spruce productivity in 2061–2080 shows that the joint effect is that of an optimum relationship. Cold temperatures limit growth due to a shorter growing season and reduced enzyme activity. The temperature effect can also be interpreted in relation to the effect of water supply. At high temperatures, droughts are more likely and photosynthesis stops due to water shortage. Apart from the interconnection with the whole temperature regime, the effect of T1 in the spruce model might be explained with the necessity to put more resources in defense mechanisms (Matyssek et al. 2012). Different provenances might also play a role (Tollefsrud et al. 2008). The effect of precipitation is described by a saturation curve. Above a given amount of water, precipitation is no longer the limiting factor. In the spruce model, this effect is very stable and clear. It depends little on the chosen temperature variables and allows deriving a threshold value of about 750 mm of annual precipitation below which productivity is reduced. For beech, productivity strongly decreases when precipitation sum during growing season falls below 500 mm.

The effect of the country factor in the spruce model is negligible. In contrast, in the beech model, productivity in France is distinctly lower than that in Germany. We introduced this factor in order to take possible differences in inventory design into account. For instance, it might be an effect of the difference in age estimation. However, it does not seem likely that the difference is so strong for beech whereas it is very low for spruce. In addition, the filtering of the data (e.g., discarding plots with no defined forest structure or coppice plots) should prevent this. In the South of France, small, unproductive beeches can be found, as beech is quite sensitive to drought and well adapted to climates with high atmospheric humidity, which are more likely in Germany. However, the climate variables offered in variable selection did not capture these differences completely (neither did continentality or aridity indices). We had to include elevation in the beech model for a much better explanation of differences in productivity. Above 200 m, there is a strong negative effect of elevation. The downside is that such a model is less apt to predict productivity for future climate scenarios, as the effect of elevation partly absorbs the climate effect and is (apart from different soil conditions and wind speed) in fact a climate effect. This becomes obvious in the map for beech productivity in 2061–2080, where productivity remains low in mountain areas even with rising temperatures. Other possible explanations for the differences between the two countries could be differences in provenance, management, soil conditions, and nitrogen deposition. Nitrogen deposition, for instance, is higher in Germany than in France (Michel and Seidling 2017). As the factor country is not considered for predictions on the European scale, actual SI in Germany is higher than in the maps shown for Europe. Thus, if the focus is on Germany or France instead of the whole Europe, taking the country factor into account provides more accurate and realistic predictions. However, the climate trend, i.e., the magnitude and direction of the changes in SI, is not affected by the country factor.

Albert and Schmidt (2010) fit an effect similar to the effect of precipitation in our study for precipitation during the growing season in their SI model for Norway spruce and water balance in their model for European beech. Their results show an increasing SI with rising temperatures during growing season and a slow-down at high temperatures. In contrast, in our study not only a slow-down but even a decline in SI at the warm margin is suggested. Our database extends much further to the warm margin (T_5to9 for spruce: 97.5% = 16 °C and max. = 17.3 °C; T_5to9 for beech: 97.5% = 16.7 °C and max. = 18.3 °C) whereas the maximum in the data of Albert and Schmidt lies only at 15.4 °C for both spruce and beech. Nothdurft et al. (2012) fit an optimum relationship between temperature during growing season as well as a limitation of growth at low precipitation during growing season for both beech and spruce. In the spruce model containing climate variables of Seynave et al. (2005), SI decreases with a fall in spring temperature and with a summer climatic water deficit. For beech, Seynave et al. (2008) find that both cold temperatures at the beginning of the growing season as well as high July temperatures limit SI, which is expressed in the effect of T_wq in our beech model. On the whole, our findings are well in line with results from other studies carried out in Germany and France. Rising temperatures will first lead to an increase in productivity as long as water supply is not limiting. Above an optimum range, a further increase in temperature has no positive effect on productivity anymore and can even lead to a decline in SI as water shortage becomes more likely and respiration increases more strongly than assimilation (Schultz 2002).

Nineteen percent of the variation in SI of spruce and 40% of the variation of SI in beech can be explained by the SI models. At first glance, this seems small, but it is not surprising, as tree growth is a complex process and there are many influences that we could not take into account considering our database and method. For instance, even after having removed plots with extreme soil conditions, the influence of physical and chemical soil conditions on growth might be considerable (Mellert and Ewald 2014; Prietzel et al. 2008) and thus models including soil parameters—especially if these are not interpolated but measured at the plot—achieve higher explanatory power (e.g., Seynave et al. 2005). We only used easily available mean climate parameters, but of course, the influence of climate on growth is much more complex and growth is not only shaped by average conditions but also by extreme events like droughts (Bréda et al. 2006). Further reasons for a reduced goodness of fit might be found in an insufficient accuracy of climate data and in spatial genetic differentiations of a tree species (Bontemps and Bouriaud 2014). Nitrogen deposition, which has been identified as an important factor behind observed growth trends (Pretzsch et al. 2014; Yue et al. 2016), might partly account for unexplained differences in productivity. In addition, not only on the side of the explanatory variables, but also on the side of the response, there is uncertainty involved due to sampling design, errors in age estimation and height measurements, which we analyze and discuss in detail in Appendix 1.

Still, the models can explain a remarkable part of variation in SI (for beech, comparable to the model of Albert and Schmidt 2010, which includes soil parameters and spatial effects, and distinctly higher than the model of Nothdurft et al. 2012; for spruce, those of Albert and Schmidt 2010 achieve an R^2 of 0.39 and Nothdurft et al. an R^2 of 0.32, but these models include soil parameters, nitrogen deposition, and spatial effects or stand characteristics and elevation respectively). As the climate effects are ecologically plausible, the models can be used to assess changes in site productivity due to changes in climatic conditions. Even if SI prediction might be over- or underestimated due to regression to the mean, the differences between predicted SI for present conditions and future scenarios are clear and give an indication of the changes in productivity that might be expected for the species in the future. In the end, our approach is not intended to predict exact heights, but to compare stands and assess trends in productivity. Still, the maps have to be interpreted carefully, as they include both the uncertainty in the modeled effects as well as the uncertainty in the climate scenarios.

It also needs to be emphasized that the first step of our approach, the determination of a static site index as a measure for productive potential, is independent of the SI models presented here. The static site index can be used as a stand-alone method to assess and compare current stands. And of course, it can function as a response variable in models containing better explanatory variables and thus achieving higher predictive power.

5 Conclusion

Data from national forest inventories are becoming increasingly accessible for science and the public. They offer tremendous potential to enhance our understanding of tree species' distribution and growth potential. When combining different national forest inventories, a relatively simple measure for the growth potential is needed. A static site index can be calculated whenever data allow for distinguishing a top collective and assigning height and age estimates. Based on this, a harmonized site index could be derived from joint French and German NFI data. Virtual stands constituted a helpful tool in estimating height and age errors and their propagation in the site index. Explaining static site index from basic climate data resulted in simple and robust models that can be applied to climate change scenarios.

One premise to exploit the potential of NFI data to enhance our understanding of tree species' distribution and growth potential is the existence of reliable site data. Currently, data sets like WorldClim (Hijmans et al. 2005) or the European soil data base (JRC 2001-2016) provide harmonized site data with comparably high resolution of 1 km—approximately the resolution of the inventory coordinates. Still, neither the parameter set nor the spatial and temporal resolution, in the case of climate, appear satisfying, especially in mountainous terrain.

Efforts like the environmental data base to the German NFI "staoDB" (this virtual issue) or the "ecologie" files to the French NFI are necessary and at the same time still require harmonization.

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Compliance with ethical standards

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

Appendix 1: Error estimation from virtual data

The uncertainties afflicted with height, age, and site indices are assessed using a dataset of virtual stands based on yield table characteristics. Comparisons of samples, drawn from the virtual dataset according to different sampling designs, present a tool to check that the combination of different NFIs is justified.

Methods

To obtain an error estimate of the site index in terms of bias and variance, we simulated DBH-height distributions assuming a given DBH variance and a DBH-dependent height variance. We used the stand biometrics of yield tables for Norway spruce of Assmann and Franz (1963, medium yield level) to create virtual stands of 1 ha. These yield tables comprise stand parameters for six site classes over an age range of 20 to 120 years. To create the virtual stands the stem number N per hectare, the root mean square diameter d_q and the corresponding height h_q were needed. DBH distributions were generated by drawing N samples from d_q-dependent Weibull functions (Nagel and Biging 1995):

$$f(x) = \left(\frac{a}{b}\right)*\left(\frac{x}{b}\right)^{(a-1)}*exp\left(-\left(\frac{x}{b}\right)^{a}\right) \quad (1)$$

with $x = DBH - 7$ and the shape parameter $a = 3.4 + 0.35 * (d_q - 7) - 0.247 * d_q$ and the scale parameter $b = -2.5 + 1.1 * (d_q - 7)$. To fit the tabulated d_q, the resulting DBH distribution was corrected for the small offset. Heights were simulated based on diameters by using uniform height-diameter curves (Sloboda et al. 1993):

$$h_i = 1.3 + (h_q - 1.3) * \exp\left(-(b0 + b1^* d_q)*(1/DBH_i - 1/d_q)\right) + \varepsilon(0,\sigma) \quad (2)$$

where (0,σ) represents a normally distributed error with a mean of zero and a standard deviation $\sigma = bs0 + bs1 * \log(sd(DBH))$ with $bs0 = 0.14$ and $bs1 = 0.56$.

The effect of stand density on the site index determination was quantified by randomly setting stem number to 20, 40, 60, 80, or 100% of the original value from the yield table.

From the virtual stand, one sample according to the sampling method of the German NFI and one sample according to the sampling method of the French NFI were drawn. In the German NFI, the sampling probability p_G of each tree depends on its basal area and the basal area factor $zf = 4$:

$$p_G = \pi^* \frac{\mathrm{DBH}^2}{40000^* zf} \quad (3)$$

In the French NFI, the sampling probability p_F of each tree depends on the size of the concentric circle corresponding to its DBH:

$$p_F = \begin{cases} \pi^* \dfrac{6^2}{10000} & \text{for } 7.5\ \text{cm} \leq DBH < 22.5\ \text{cm} \\ \pi^* \dfrac{9^2}{10000} & \text{for } 22.5\ \text{cm} \leq DBH < 37.5\ \text{cm} \\ \pi^* \dfrac{15^2}{10000} & \text{for } 37.5\ \text{cm} \leq DBH \end{cases} \quad (4)$$

Now, the sampling design of the German and French NFI can be simply imitated by drawing random numbers from a uniform distribution between 0 and 1: if the sampling probability p of the tree is bigger than the number drawn, the tree is included in the sample. The heights of the sample trees were calculated from species-specific uniform height-diameter curves adding a random error term as in Albert (2000). From these heights, a maximum of three (if available) trees were chosen to represent the actually "measured height." The heights of the sample trees were calculated from species-specific uniform height-diameter curves based on the "measured" heights.

To estimate the error of d_{top} and h_{top} due to the sampling design, the procedure was repeated 1000 times whereby site classes and age spectrum of the yield table were sampled at random. This resulted in a dataset of 1000 virtual stands and 1000 samples according to the German NFI sampling method and 1000 samples according to the French NFI sampling method. The error, i.e., the difference in the d_{top} and h_{top} estimates from the inventory sampling and the true d_{top} and h_{top} of the entire stand, can be quantified in terms of root mean squared error (RMSE) and bias. Bias was determined by least squares regression without intercept of true d_{top} (or h_{top}) against d_{top} (or h_{top}) estimates from the inventory sampling.

In order to assess the influence of age errors on SI estimation, the Chapman-Richards-functions for the upper and the lower boundary line of Norway spruce were used. True SI between 20 and 40 m in 4 m-steps were assumed. Based on these true SI, true heights for each age in 5-year-steps from 20 and 120 years were derived. Measurements afflicted with age errors were simulated by subtracting/adding the absolute value of a random error from N(0, 5) from/to the trues ages, but maintaining the true heights. The difference between true SI and the SI estimation for the simulated measurement afflicted with age error was calculated and averaged over 1000 repetitions.

Results

Since height variance between the trees in a stand is typically lower than the diameter variance, the bias and variance of the determined top height h_{top} are smaller than for the d_{top}. The correlation between the measure calculated from the stand and the measure calculated from the sample is very high (NFI Germany: 0.991, NFI France: 0.996) and the bias is negligible (NFI Germany: 1.014, NFI France: 1.009) (Fig. 8a). This ensures that there are no systematic deviations resulting from the two sampling methods. Furthermore, h_{top} is relatively stable with respect to effects of density. Although SI is slightly underestimated at all densities, the difference is always lower than 0.8 m (Fig. 8a) and the standard deviation is less than 1.2 m. Figure 8b shows that there is no big or systematic deviation between French and German NFI samples at all.

As the second possible error source in the site index estimation, we investigated the effect made by under- or overestimating stand age. As Fig. 8c shows, an underestimation of age leads to an overestimation of the site index of about 2 m at age 40 which decreases to about 0.25 m at age 100. Likewise, an overestimation of age leads to a slightly lower underestimation of the site index of about 1.6 m at age 40 and 0.2 m at age 100.

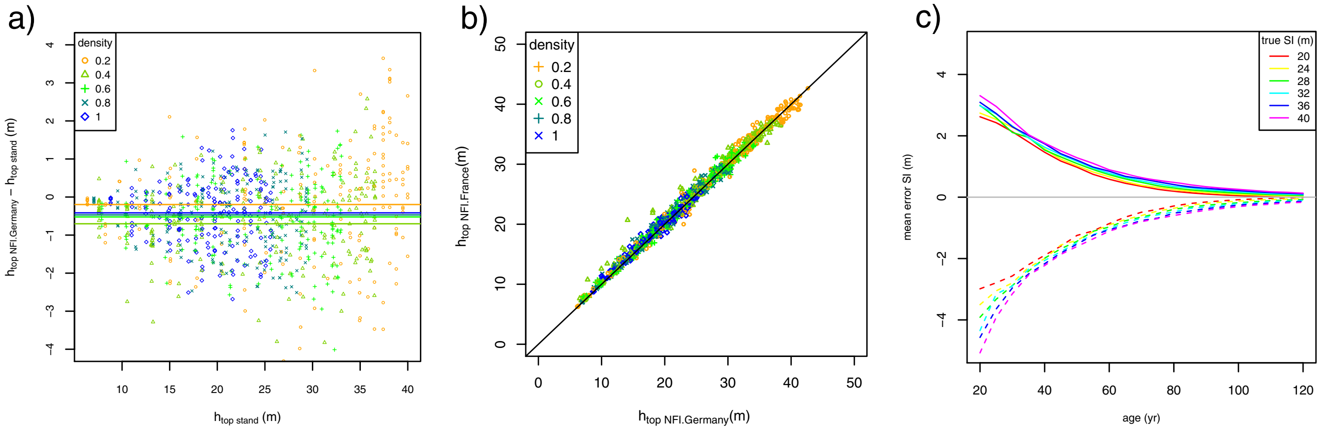

Fig. 8 **a** Difference between the true stand h_{top} and the calculated h_{top} from the German NFI sample in dependence on the true stand h_{top} for different relative stand densities. The lines mark the mean differences for each stand density. **b** Comparison between h_{top} calculated from the German NFI sample and h_{top} calculated from the French NFI sample. **c** Assuming a true SI the upper lines show the error in SI estimation for an assumed overestimation of age, the lower dashed lines show the error in SI estimation for an assumed underestimation of age using the Chapman-Richards functions for Norway spruce

Appendix 2: Static site indices for Norway spruce, European beech, Douglas-fir, Scots pine, sessile oak, and pedunculate oak

Besides Norway spruce and European beech, static site indices were derived for four other common species: Scots pine, Douglas-fir, sessile oak, and pedunculate oak. Thus, we show that the method is applicable to a wide range of species and are able to compare the species' growth potential.

Figure 9 displays age-height scatter plots and the fits of the Chapman-Richards function for the six investigated species from the joint data sets of the German and French NFI. For Douglas-fir, there are only few measurements available for ages > 70 years, and for the other species, ages up to at least 130 years are well represented. Table 5 summarizes the function parameters for the joint data set. As can be clearly seen in Fig. 9, the species with the highest growth potential is Douglas-fir, followed by Norway spruce. This is also

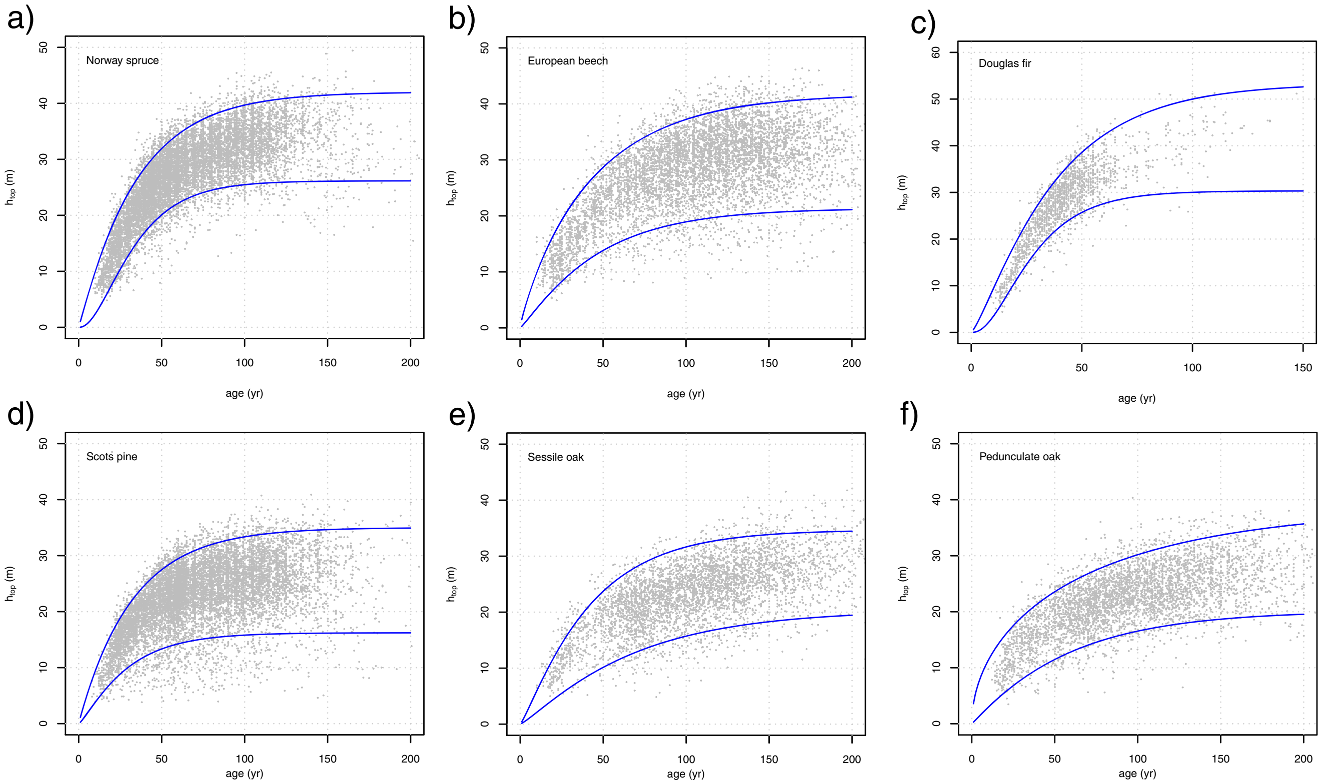

Fig. 9 Age-height scatter plots for the six investigated tree species in the German and French NFI data: **a** Norway spruce, **b** European beech, **c** Douglas-fir, **d** Scots pine, **e** sessile oak, and **f** pedunculate oak. Lines depict quantile regression for the 5% and 95% percentiles with the Chapman-Richards function

Table 5 Results of fitting the Chapman-Richards function to the lower 5% and the upper 95% percentiles of the age-height distribution for the joint German and French inventory data

Variable	Quantile curve	Parameter/function	Spruce	Beech	Pine	Douglas-fir	Sessile oak	Pedunculate oak
Sample size		*N* (Germany) =	10,552	5247	9693	1045	1929	1647
		N (France) =	914	1595	1372	768	2475	2844
Chapman-Richards (CR)	Lower	*A* =	26.16	21.35	16.22	30.33	20.37	20.18
		k =	0.0448	0.0232	0.0390	0.0553	0.0164	0.0176
		p =	2.35	1.15	1.28	2.54	1.2	1.05
	Upper	*A* =	42.01	41.79	35.01	53.37	34.69	38.80
		k =	0.0294	0.0208	0.0304	0.0301	0.0261	0.0095
		p =	1.05	0.86	0.98	1.29	1.2	0.51

represented by the fitted asymptotes (A) of the upper boundary line in Appendix Table 5.

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Publication III

Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany (under review)

Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany

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Abstract

Aim of study: (i) To estimate site productivity based on German national forest inventory (NFI) data using above-ground wood biomass growth (ΔB) of the stand and (ii) to develop a model that explains site productivity quantified by ΔB in dependence on climate and soil conditions as well as stand characteristics for Norway spruce (Picea abies (L.) Karst.).

Area of study: Germany, which ranges from the North Sea to the Bavarian Alps in the south encompassing lowlands in the north, uplands in central Germany and low mountain ranges mainly in southern Germany.

Material and methods: Biomass growth of the stand between the 2nd and 3rd NFI was calculated as measure for site productivity. Generalized additive models were fitted to explain biomass growth in dependence on stand age, stand density and environmental variables.

Main results: Great part of the variation in biomass growth was due to differences in stand age and stand density. Mean annual temperature and summer precipitation, temperature seasonality, base saturation, C/N ratio and soil texture explained further variation. External validation of the model using data from experimental plots showed good model performance.

Research highlights: The study outlines both the potential as well as the restrictions in using biomass growth as a measure for site productivity and as response variable in statistical site-productivity models: biomass growth of the stand is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. However, it entails the difficulty of how to deal with the influence of management on stand density.

Keywords

site index, site potential, biomass growth, statistical model, climate

Introduction

How to best summarize site productivity in one measure has been a crucial question in forestry (Skovsgaard & Vanclay, 2008; Bontemps & Bouriaud 2014). The most widely used measure is the height-age site index (SI), i.e. an expected or realized stand height at a given reference age (Assmann, 1961). Height has the advantages that it can be measured directly and that it is generally not much affected by management (Wenk *et al.*, 1990). In fact, SI is so well-established in forest research and practice, that it is often taken as the true productivity rather than simply an indicator that may or may not reflect the site potential (Skovsgaard & Vanclay, 2008). This belief is based on Gehrhardt's first refinement of Eichhorn's rule stating that the relationship between total volume production of a tree species and stand height is identical for all site indices known as general yield level. But later he refined this relationship by specifying different relationships between total volume production and stand height for each site index referred to as a special yield level. Evaluating experimental plots of Norway spruce in Southern Germany, Assmann found that the total volume production of stands of the same age and SI can still vary ± 15 % in dependence on site characteristics. This leads to the so-called subdivided special yield level (Pretzsch, 2009). These findings of Assmann, that SI does not completely capture site productivity, motivated us to use a measure for site productivity that comprises more aspects of productivity than mere height and to relate it to site conditions. As Assmann established the theory of the subdivided special yield level investigating experimental plots of Norway spruce (one of the most common and economically important tree species in Germany), we focus on this species as well. Our study is based on German national forest inventory (NFI) data.

Numerous studies model the relationship between site conditions and site productivity based on NFI data. Mostly SI is the measure of site productivity (e.g. Seynave *et al.*, 2005; Albert & Schmidt, 2010; Nothdurft *et al.*, 2012), but a variety of other measures has been used as well, e.g. stand basal area increment (Charru *et al.*, 2010; Charru *et al.*, 2014) or mean annual volume increment (Gustafson *et al.*, 2003; Condés & García-Robredo, 2012). Watt *et al.* (2010) compared two models for *Pinus radiata* productivity in dependence on site characteristics. In the first model SI is the response variable, in the second model productivity is expressed as the mean annual increment at a standard age for a standard density predicted from a stand basal area growth model and auxiliary relations for height and volume. Wang *et* *al.* (2005) estimated net primary productivity (NPP) of forest ecosystems in China from inventories and modelled it in dependence on site conditions.

NPP encompasses the entire production of organic substances (i.e. net biomass growth) as well as the turnover (of plant organs or entire individuals) in a given time period (Pretzsch, 2009). However, as root biomass, turnover of plant organs and investments in reproduction can only be approximate estimates using NFI data, including these components introduces a lot of uncertainty into NPP estimations. Therefore, in order to estimate site productivity we chose the physiological measure above-ground wood biomass growth (ΔB) of the stand. However, predictions of ΔB can easily be converted into approximate NPP estimates by using published scaling factors (e.g. Offenthaler & Hochbichler, 2006; Rötzer *et al.*, 2010). Using experimental plots the focus often is on total volume production. But as the history of stand development of NFI plots is not known, total volume (or biomass) production cannot be estimated. In contrast to total volume (or biomass) production, ΔB is strongly influenced by stand density and stand age. On the one hand ΔB can be limited by stand structure and density, on the other hand it can be limited by site conditions. Thus, actual ΔB and potential ΔB must be distinguished (Kahle, 2015). Actual ΔB is the realized ΔB under the current stand structure, density and age. Potential ΔB is the capability of the site to produce biomass, irrespective of how much of this potential is utilized under the current stand structure and density (Skovsgaard & Vanclay, 2008). It is determined by site conditions and thus reflects site potential. As most forests in Germany are managed, ΔB estimated from NFI data will generally not correspond to potential ΔB. Thus, a central aspect is how to take stand density into account (Bontemps & Bouriaud, 2014). Besides stand density, stand age has a strong influence on ΔB and has to be taken into account when assessing site potential.

Inspired by the idea that based on NFI data direct productivity-environment relationships can be established when taking stand density effects into account (Bontemps & Bouriaud, 2014), this study investigates whether the use of ΔB is a feasible way to do so and whether there is an additional benefit in using ΔB as a complementary measure to SI for site productivity. Main aim of the study was to estimate site productivity based on German NFI data and develop a model that explains site productivity in dependence on site conditions for Norway spruce. We validated the model using an independent dataset from experimental plots. Our research questions were: (1) What stand variables explain the variability in ΔB for a given site index? (2) How can the strong influence of stand density on ΔB best be dealt with? (3) Can actual and potential ΔB be differentiated based on NFI data? (4) How is the influence of site conditions on ΔB?

Material and Methods

Study area

Germany ranges from the North Sea to the Bavarian Alps in the south encompassing lowlands in the north, uplands in central Germany and low mountain ranges mainly in southern Germany. 30 % of the area is covered by temperate forests. In the northwest and the north the climate is oceanic, whereas in the east there is a strong continental influence. In central and southern Germany the climate varies from moderately oceanic to continental. The Alps and some low mountain ranges have a mountain climate with lower temperatures and higher precipitation.

Data

National Forest Inventory Data

To estimate biomass growth data of the second (2002) and third (2012) NFI were used. NFI in Germany is based on a permanent nationwide 4 km × 4 km grid. Each grid point in forest area is the center of an angle-count sampling (BMELV, 2011). There are trees that were included in the angle-count sampling (basal area factor 4) in NFI 3 but had not been thick enough to be included in NFI 2. Other trees were measured for the NFI 2 but were missing in the NFI 3. Diameter at breast height (dbh) and height of these trees were predicted for the middle of the period between NFI 2 and NFI 3 (Jenkins *et al.*, 2001; Dahm, 2006) using the function of Sloboda (Riedel *et al.*, 2017). Thus, plots where thinning occurred between the inventories are included in our dataset. However, plots where all trees that had been surveyed in NFI 2 were missing in NFI 3 due to harvest or mortality were excluded. For the study plots with a basal area proportion of spruces ≥ 70 % and stand age (calculated as mean of the age estimations of the sample trees weighted by the stem numbers per ha that they represent) between 30 and 150 years were selected. Plots where the climate signal is likely to be confounded by extreme soil characteristics (gley soils, pseudogley soils and moor soils) were discarded. Finally, 3830 plots remained for analysis.

Above-ground wood biomass was estimated using species-specific functions of dbh and height. We chose the functions of Zell (2008), as they were developed based on German NFI data. The functions estimate total above-ground wood biomass, i.e. comprise both stem wood biomass as well as branch biomass. The growth of above-ground wood biomass per year was determined for each tree as the difference between NFI 3 and NFI 2 divided by the period length. These values were extrapolated to 1 ha and summed up at plot-level resulting in one ΔB assigned to each plot (Jenkins *et al.*, 2001; Dahm, 2006). In summary, ΔB represents total above-ground wood biomass net growth of the stand, i.e. turnover of plant organs is not considered. A detailed description of how ΔB is derived based on the angle-count sample is presented in Appendix 1.

The stand density index of Reineke (SDI) (Reineke, 1933; Zeide, 2005) with an exponent of -1.605 was used as a measure of stand density. As tree species differ in their requirements of growing space, SDI values are species specific. In order to allow comparisons between different species or to use the SDI for mixed stands, it is necessary to weight the SDI. For each species the 95-percentile of the SDI distribution of pure stands was determined. Weighting factors were calculated dividing the 95-percentile value of spruce (used as reference species) by the 95-percentile value of the respective tree species. For each NFI plot species specific SDI values were multiplied by the weighting factors and then summed up to the overall SDI of the respective plot. A detailed description of the calculation of the SDI is presented in Appendix 2. Statistical values of the NFI data are summarized in Table 1.

Table 1. Characterization (minimum, maximum, mean, standard deviation) of the NFI plots (n = 3830) used for modelling.

Parameter	Min	Max	Mean	SD
Mean diameter (cm)	9.9	70.5	32.5	9.9
Dominant height (m)	4.9	48.9	29.9	5.3
Stand age (yr)	30	150	71	27
SDI	59	2325	984	350
Biomass (t ha^{-1})	16	862	292	109
ΔB (t ha^{-1} yr^{-1})	0.2	24.8	9.0	4.1

Environmental Data

Regionalized daily climate (Böhner *et al.*, 2018) and soil data (von Wilpert *et al.*, 2017) are available at the NFI plots. Based on the daily climate data, for each NFI plot annual values of the climate variables presented in Table 2 were calculated and then averaged over the measurement period between NFI 2 and NFI 3.

Table 2. Overview of environmental variables (abbreviation, unit, minimum, maximum, mean, standard deviation) for the NFI plots used in the study.

Parameter	Abbreviation	Unit	Min	Max	Mean	SD
Mean annual temperature	T_yr	°C	3.6	11.4	8.2	1.1
Mean temperature May to Sept.	T_5to9	°C	9.8	18.3	14.8	1.2
Mean temperature warmest quarter	T_wq	°C	11.9	20.1	16.5	1.2
Max. temperature warmest month	Tmax_wm	°C	17.6	27.7	23.5	1.5
Mean temperature coldest quarter	T_cq	°C	-5.1	3.3	-0.5	1.2
Min. temperature coldest month	Tmin_cm	°C	-9.5	-1.1	-5.1	1.4
Temperature seasonality (standard deviation *100)	T_sd	°C*100	598	788	693	39
Temperature annual range (Tmax_wm–Tmin_cm)	T_range	°C	23.6	32.3	28.6	1.6
Annual precipitation sum	P_yr	mm	504	2589	1036	301
Precipitation sum May to Sept.	P_5to9	mm	251	1364	490	151
Precipitation sum warmest quarter	P_wq	mm	165	886	315	99
Precipitation seasonality (coefficient of variation)	P_cv		43	65	52	4
Evapotranspiration (Penman-Monteith) May to Sept.	ETpm_5to9	mm	269	504	407	37
Available water capacity of the first 60 cm	AWC	mm	78	202	138	21
Base saturation of the first 60 cm	BS	%	1	100	30	26
Clay content of the first 60 cm	clay	%	1	53	19	9
Silt content of the first 60 cm	silt	%	1	74	40	12
Sand content of the first 60 cm	sand	%	1	96	41	19
C/N-ratio of the first 60 cm	CN		7	34	15	3

The relationship between the variability in ΔB and stand variables

In order to address the first research question (What stand variables explain the variability in ΔB for a given site index?), we explored the variation in ΔB not already explained by SI. We aimed at identifying the stand and tree characteristics that differ between plots of greater and lesser ΔB but of the same SI: Is greater productivity mainly due to greater stem numbers or do stem numbers not differ that much, but trees are thicker and radial growth of single trees is faster? First, for each plot SI was determined by estimating the top height and extrapolating it to age 100 applying the Chapman-Richards function (Brandl *et al.*, 2018). Second, a generalized additive model (GAM) was fitted explaining ΔB in dependence on SI (package mgcv (Wood, 2011) in R 3.3.2 (R Core Team, 2016)). Stand age was included as additional covariate in order to account for the influence of age on ΔB. The residuals of this model correspond to the variation in ΔB not explained by SI and age. Third, we divided the residuals in quartiles and tested if stand and tree parameters differed significantly between the quartiles using Kruskal Wallis and post-hoc Nemenyi-Test (significance level p = 0.01), as the data were not normally distributed. On plot level we considered SDI, stem number (N), standing above-ground wood biomass and quadratic mean diameter (dg), on single tree level we considered height, dbh and relative dbh increment, i.e. dbh increment between NFI 2 and NFI 3 divided by the dbh measured at NFI 2. Relative dbh increment was only assessed for trees measured at both inventories. In order to be able to compare height and dbh of trees of varying ages height and dbh had to be rescaled: A 95%-quantile regression was applied describing height or dbh respectively as a fourth order polynomial of age. Then, each tree's height or dbh respectively was divided by the predicted 95%-quantile of height or dbh respectively at the tree's age resulting in a relative measure independent of age.

Details on the methodology are given in Appendix 3.

Modelling site productivity from site conditions

We modelled ΔB in dependence on site and stand characteristics using generalized additive models with a gamma error distribution and log-link function. A variety of climate and soil variables was offered to variable selection (Table 2). Climate variables comprise annual precipitation sum (P_yr), summer precipitation (P_wq), precipitation during growing season (P_5to9), mean annual temperature (T_yr), summer temperature (T_wq, Tmax_wm), temperature during growing season (T_5to9), winter temperature (Tmin_cm, T_cq) as well as temperature variability (T_sd, T_range). Soil parameters include base saturation (BS), soil texture variables (clay, silt, sand), C/N-ratio (CN) and available water capacity (AWC) of the first 60 cm. We selected the best model of all possible combinations of explanatory variables using AIC as criterion. Combinations including highly correlated variables (Dormann *et al.*, 2013) had been discarded beforehand.

ΔB strongly depends on stand density. Stand density itself depends both on thinning regime and environmental conditions, since favorable sites allow a greater stand density than unfavorable sites (Pretzsch, 2002). We wanted to find a measure of site productivity that is independent of forest management and solely reflects differences in site quality. Stand density could be included as covariate into the model and set to a fixed value for predictions. But as stand density is not independent of site quality, it weakens the explanatory power of the environmental variables. Therefore, we tried to separate the effect of environmental conditions from the effect of forest management on stand density. Our approach follows the methodology applied to experimental plots when characterizing density on plots of varying thinning grades on the same site. Density of a given stand is expressed by the ratio of the basal area of the stand and the maximum basal area observed on the same site (Pretzsch, 2002). Regarding NFI plots as a huge experimental design we identified plots of similar site conditions using k-means clustering. The k-means method partitions the observations into a specified number of groups (i.e. clusters) so that the sum of squares from the observations to the assigned cluster centers is minimized. Based on a comprehensive set of climatic (P_yr, P_wq, P_cv, T_yr, T_wq, Tmin_cm, T_sd, ETpm_5to9) and soil variables (BS, AWC, silt, sand, CN) observations were assigned to 21 clusters using the algorithm of Hartigan & Wong (1979) and trying 1000 initial random sets of cluster centers. The optimal number of clusters had been determined according to the Bayesian information criterion for expectation-maximization, initialized by hierarchical clustering for parameterized Gaussian mixture models using the R package mclust (Scrucca *et al.*, 2016). For each cluster, interpreted as one experimental plot with a set of comparable site conditions but different thinning grades, the 95-percentile of the SDI distribution (SDI_{95}) was determined. Again we chose the 95-percentile instead of the maximum in order not to give potential outliers too much influence. Still, SDI_{95} is interpreted as the maximum SDI that can be reached under the corresponding site conditions. Then, for each NFI plot the ratio of its SDI and the SDI_{95} of the corresponding cluster was calculated resulting in a relative density (RD) that reflects the effect of thinning on density. ΔB can then be explained by RD, age and the environmental variables.

Validation

The model's predictive performance was evaluated by calculating root mean squared error (RMSE) based on a 10-fold cross validation (data splitting train data : test data = 9 : 1) (e.g. Mellert *et al.*, 2016). Besides, we checked for systematic errors by determining the slope of a least squares regression without intercept of observed ΔB against predicted ΔB both at the scale of the linear predictor, i.e. the log scale (e.g. Dolos *et al.*, 2015).

For external validation independent data of 78 long-term experimental plots on 14 locations in Bavaria were available. From these data the increment periods which were close to the inventory periods of the NFI were used. Table 3 comprises the stand characteristics of the experimental plots.

Table 3. Characterization of the experimental plots (n = 78) used for validation; stand age, mean height and mean diameter are obtained from the last survey.

Parameter	Min	Max	Mean	SD
Stand age (yr)	20	118	44	22
Mean height (m)	9.1	39.1	21.8	6.2
Mean diameter (cm)	11.5	52.7	26.8	9.0
Mean annual temperature (°C)	7.0	9.0	8.2	0.7
Temperature seasonality (°C*100)	706	754	726	15
Precipitation sum warmest quarter (mm)	245	427	338	66
Base saturation of the first 60 cm (%)	5	100	41	26
Sand content of the first 60 cm (%)	9	64	28	18
C/N-ratio of the first 60 cm	7	25	17	6

Results

The relationship between the variability in ΔB and stand variables

In the data there was a clear trend to larger quadratic mean diameter (dg), dbh, standing biomass and ΔB with increasing SI. Thus, in general greater ΔB coincided with higher SI. However, there was considerable variation in ΔB that was not explained by SI and stand age. This residual variation could be related to stand variables (Table 4): Differences in ΔB were largely due to differences in stand density (Figure 1a). Sites with greater ΔB generally had a higher stem number per ha, whereas there was no clear trend for quadratic mean diameter. Standing above-ground wood biomass significantly differed between the quartiles of the distribution of the residuals and showed an increasing trend. Trees on sites with greater ΔB but same SI did not have greater single tree diameters on average, but relative dbh increments were higher (Figure 1b). There was no clear trend in single tree heights. Thus, in general, at a given SI greater ΔB was mainly due to greater stand density: Production was higher, because stem number and standing biomass was higher. In addition, faster dbh-growth contributed to the greater ΔB.

Table 4. Detailed results of the comparison between the 4 quartiles of the distribution of the residuals; Larger residuals go in line with greater ΔB at a given site index and stand age; significance levels are p = 0.05 (*), p = 0.01 (**) and p = 0.001 (***); trend denotes whether there is an increasing (+) or decreasing (-) trend with greater ΔB or whether the data exhibit no clear trend (+-); same letters denote groups that do not differ significantly.

parameter	**significance**	**trend**	**1. quartile**	**2. quartile**	**3. quartile**	**4. quartile**
dbh	***	+-	a	a	b	b
height	***	+-	a	b	c	a
rel. dbh inc.	***	+	a	b	c	d
SDI	***	+	a	b	c	d
N	***	+	a	b	c	d
dg	***	-	a	ab	bc	c
biomass	***	+	a	b	c	d

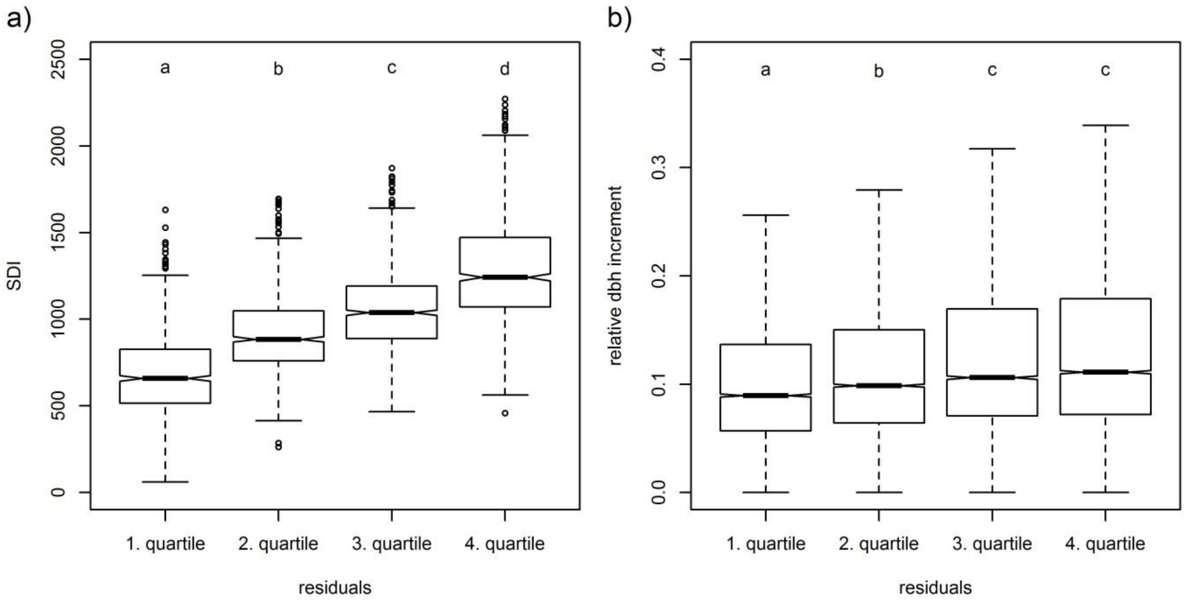

Figure 1. Comparison of SDI (a) and relative dbh increment (b) between the quartiles of the distribution of the residuals. Larger residuals go in line with greater ΔB at a given site index and stand age.

ΔB in dependence on site conditions

The final model can be described with:

[1] $$\Delta B_{act} = \exp(f(RD) + f(age) + f(T_{yr}) + f(P_{wq}) + f(T_{sd}) + f(BS) + f(sand) + f(CN) + \varepsilon)$$

where f denotes a regression spline (Table 5).

ΔB strongly depends on stand density and stand age, but plausible effects of site conditions can be fitted as well (Figure 2). Relative density (RD) has a strong, approximately linear positive effect. ΔB decreases with increasing stand age from 30 years onwards (for model fitting plots with stand ages between 30 and 150 years were used). ΔB increases with rising mean annual temperatures (T_yr). The increase is stronger in the low and medium temperature range, whereas the slope flattens at higher temperatures. The effect of precipitation is smaller. Low summer precipitation (P_wq) clearly limits ΔB. As above a value of about 800 mm confidence intervals become very wide, no conclusions should be drawn from the subsequent curve progression. ΔB is reduced at both extremes of temperature seasonality (T_sd). Optimum ΔB is reached at medium base saturation (BS), whereas high base saturation has a negative effect on ΔB. To a lesser extent low base saturation reduces ΔB as well. Low sand content (sand) has a positive effect on ΔB, whereas the effect of very high sand content is negative. ΔB decreases nearly linearly with rising C/N ratio.

Table 5. Detailed summary of the site productivity model (edf: estimated degrees of freedom).

	Estimate	Standard error	T statistics	p value
intercept	2.119	0.004	571.335	$< 2 \times 10^{-16}$
	edf	**Ref. df**	**F statistics**	**p value**
f(RD)	8.124	8.799	755.645	$< 2 \times 10^{-16}$
f(age)	3.188	3.993	684.052	$< 2 \times 10^{-16}$
f(T_yr)	4.533	5.651	15.338	2.69×10^{-16}
f(P_wq)	4.896	6.033	12.314	8.22×10^{-14}
f(T_sd)	3.139	3.944	11.509	4.03×10^{-9}
f(BS)	2.669	3.335	8.364	8.12×10^{-6}
f(sand)	7.302	8.314	5.328	6.79×10^{-7}
f(CN)	1.256	1.474	15.427	6.65×10^{-6}
Adjusted R^2		0.758		
RMSE		1.996 ($t\ ha^{-1}\ yr^{-1}$)		
slope (observed against predicted ΔB)		0.988		

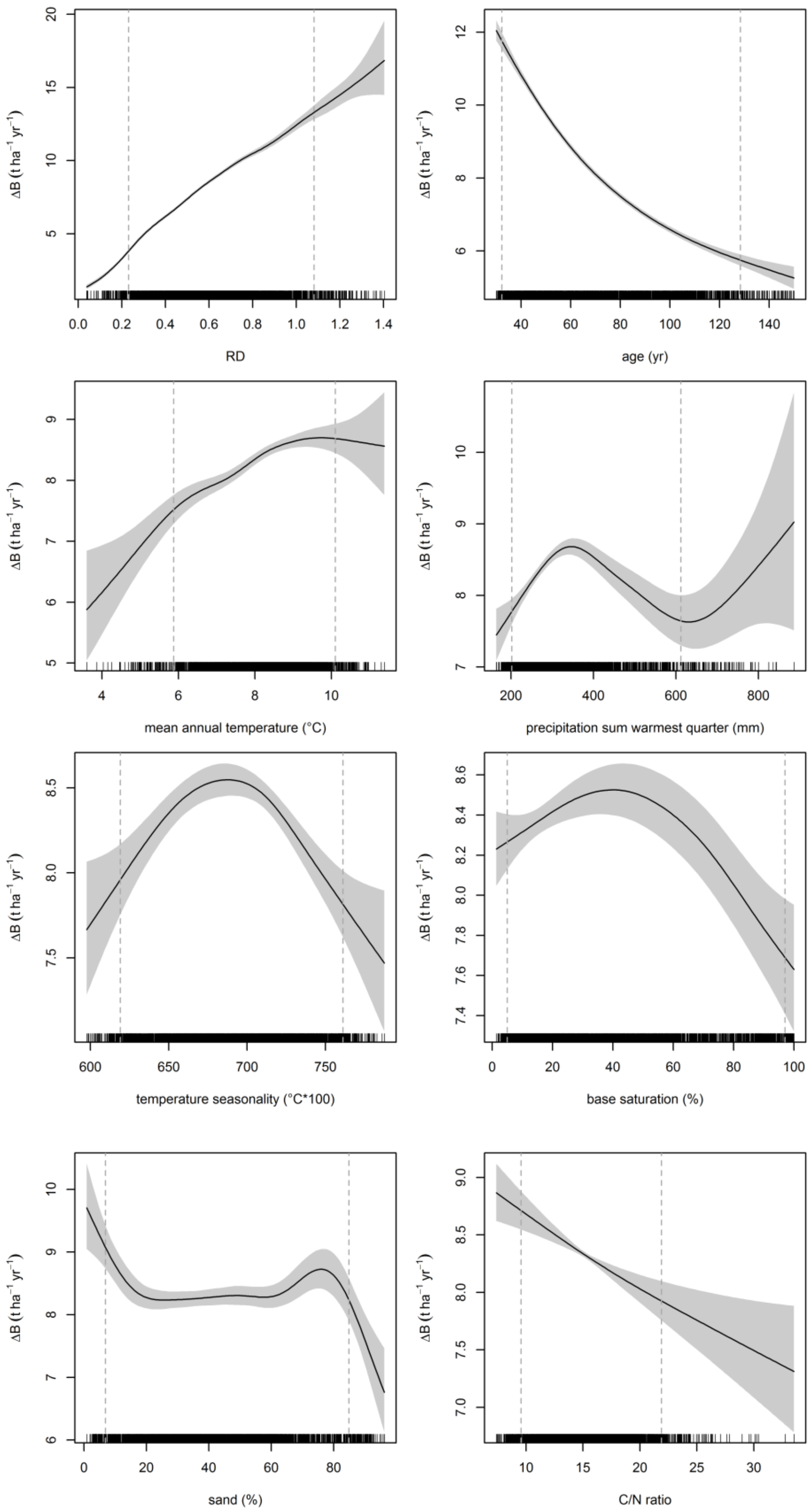

Figure 2. Effects of explanatory variables (RD, age, mean annual temperature, precipitation sum warmest quarter, temperature seasonality, base saturation, sand content and C/N ratio) on ΔB when the other variables are set to their means (table 1 and table 2). Grey areas comprise 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate; the vertical dashed lines mark the 2.5 and 97.5% quantiles of the covariate's distribution.

Validation

Cross-validation resulted in a RMSE of 1.996 t ha^{-1} yr^{-1}. The slope of the regression of observed against predicted ΔB was nearly 1 (0.988). External validation of the model with an independent data set revealed that differences in ΔB can be predicted quite reliably (Figure 3). The R² of the linear relationship is 0.753. RMSE was 1.652 t ha^{-1} yr^{-1}.

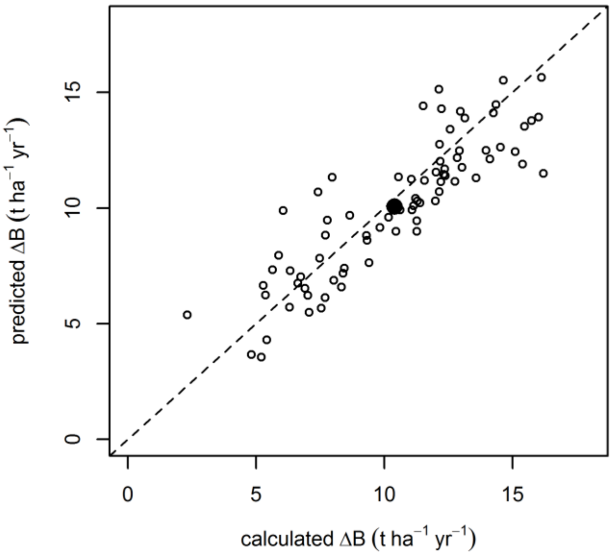

Figure 3. Predicted ΔB values plotted against calculated ΔB values for the experimental plots. The solid black dot represents the mean values of the validation dataset. The dashed line marks the 1:1 relation.

Discussion

ΔB as a measure for site productivity

As the trend to structurally diverse mixed stands and thinning from above reduces the informative value of SI (Pretzsch, 2009), it makes sense to look for complementary measures of site productivity (Bontemps & Bouriaud, 2014). We chose above-ground wood biomass growth (ΔB): On the one hand, ΔB encompasses height and dbh increment as well as stand density, and on the other hand it is feasible to estimate ΔB based on NFI data. We preferred ΔB to volume increment for two reasons: First, it constitutes a physiological measure closer to net primary productivity than volume increment. Second, wood density is taken into account which facilitates the comparison between different species.

ΔB serves as an indicator or proxy of site productivity. Therefore, when interpreting our results, we relate them to productivity. However, it has to be kept in mind that there are more aspects to productivity like below-ground biomass growth and turnover of plant organs that are not taken into account.

Sites with similar SI and stand age showed noticeable variation in biomass growth: Greater ΔB was mainly due to higher stem numbers, reinforced by larger relative dbh increments. If more productive sites at similar SI and age differ more in stem number and only to a lesser degree in diameters from less productive ones, site productivity is better captured looking at ΔB of the stand than at the increment of single trees alone or mere stand height. It has to be kept in mind that this effect was found for sites of similar SI and is not a general principle. When looking at the entire data set i.e. the whole range of site indices and ages there is a clear trend to larger dg with increasing SI. The differences in productivity at same SI cannot immediately be traced back to differences in site conditions and thus be interpreted as subdivided specific yield levels, as most forests in Germany are managed and therefore differences in stand density leading to differences in productivity are mainly due to thinning. Still, maximum stand density i.e. carrying capacity on a given site depends on site conditions (Pretzsch, 2002). Favorable sites would show greater dbh increment than unfavorable sites given the same stand density. But as forest owners might tend to keep higher stem numbers at favorable sites, better site conditions are sometimes not expressed as much in greater dbh increment but in higher stand density. Thus, exploring the relationship between the variability in ΔB and stand variables at a given SI and stand age emphasized the importance of adequately dealing with stand density when modelling ΔB. Therefore, we differentiated between management effects and environmental effects on stand density by calculating a relative density in the modelling approach. This allowed us to develop a model that separates the effects of thinning from the effects of site conditions on productivity. Of course, this is an idealization as the effects of thinning regime and site quality can never be separated completely and there are many influences on stand density not encompassed by the explanatory variables used in this study. We modelled ΔB in dependence on age, relative stand density and environmental variables in one step and can predict potential ΔB by setting the relative density and age to reference values, just as height can be modelled in dependence on age and environmental variables in one step and SI can be predicted by setting age to a reference age (e.g. Brandl *et al.*, 2014; Vallet & Perot, 2016). Actual ΔB can be predicted by setting the relative density and age to the current values of the given plot. An alternative approach would be to first estimate a productivity measure detrended from age and density effects and in a second step model this detrended productivity index in dependence on environmental variables (e.g. Watt *et al.*, 2010; Charru *et al.*, 2014), which is in analogy with the approach of first deriving the SI of a stand, i.e. detrending height of the age effect, and then modelling SI in dependence on environmental variables (e.g. Albert & Schmidt, 2010).

ΔB in dependence on site conditions

Overall the model shows a high goodness of fit and validation on an independent data set showed that it reliably predicts differences in ΔB. The effects of age and relative density on ΔB in the model are clear and ecologically plausible: Since stand density is directly connected to leaf biomass (Pretzsch *et al.*, 2014b), dense stands reach maximum leaf area and thus maximum light interception (Zeide, 2001). Therefore, it makes sense that productivity increases with increasing stand density. This result is in contrast to Pretzsch (2006) who found a unimodal optimum relationship between stand density and growth. This contradiction might be due to our use of NFI data instead of data of experimental plots. As most German forests are managed the proportion of unthinned NFI plots with such high stand densities as to cause reductions in growth is too small to influence the model effect.

One would expect net primary productivity for a given stand to increase until an age of about 50 years and then decline again due to the changing balance between gross primary productivity and respiration during stand development (Barnes *et al.*, 1998). But in this study ΔB declines monotonously with stand age within the age range considered (30 until 150 years). On the one hand, this might indicate that the age dependence of above-ground wood biomass growth differs from the age dependence of NPP. On the other hand, it can be explained by our use of cross-sectional data instead of time series, i.e. we did not follow the trajectory of one stand through time. Plots of the same age can differ in their developmental stage (Mehtätalo, 2004). Replacing age by dominant height as an indicator for developmental stage reveals the expected pattern with an increase in ΔB at low dominant heights followed by a slow decline at greater heights (not shown). Still, in order to compare and predict site productivity it is preferable to use stand age in the model (Mehtätalo, 2004).

Adding climate and soil parameters as explanatory variables renders plausible effects on ΔB. On a global scale aboveground NPP is relatively low in cold and dry climates and rapidly rises as both temperatures and water availability increase (Barnes *et al.*, 1998). This global-scale pattern can also be observed on a German scale, although we are looking at ΔB here. Temperature regime and water supply clearly are limiting factors, and as both increase, productivity rises. The most influential environmental factor in our study is mean annual temperature. This is consistent with other current studies. For instance, Pretzsch *et al.* (2014a) concluded that mainly rising temperatures and extended growing seasons increase growth.

Kauppi *et al.* (2014) identified the spatial and temporal variation of growing degree days as the main causal factor affecting variations in forest growth. At the high end of the temperature range the increase of ΔB with rising temperatures slows down and approximates a more or less constant level. One might expect a decline at very high temperatures due to drought stress (Dolos *et al.*, 2015). However, due to high risks and adapted forest management spruce dominated stands in Germany simply do not occur in sufficient numbers at very high temperatures in order to clearly detect such an effect. On a global scale water supply is a crucial variable constraining biomass (Stegen *et al.*, 2011). The effect of precipitation in our study is rather weak, as water is, except in extreme drought years, not generally the growth limiting factor in our data set (spruce dominated NFI plots in Germany): Annual precipitation of 92 % of the plots exceeds the threshold value of 800 mm given by Mayer (1992) for the optimum growth range. Still, ΔB decreases when summer precipitation is low. Within the same climate ΔB differs, since it is influenced by soil properties, species composition and the stage of ecosystem development (Barnes *et al.*, 1998). The effect of base saturation on ΔB follows an optimum relationship. On acidic soils the supply of basic cations reduces growth, whereas on calcareous sites Ca-K-antagonism (Rehfuess, 1990) and immobilization of phosphor (Mellert & Ewald, 2014) can occur. Low sand content has a positive effect on ΔB, whereas high sand contents affect ΔB negatively. The effect of sand content might both reflect effects of nutrient and water supply. Soils with high sand content often have a low available water capacity and are poor in nutrients.

The proportion of explained variance by environmental variables is small, but therein comparable with other studies (e.g. Condés & García-Robredo, 2012; Charru *et al.*, 2014). If we could look at total volume production the effect of site conditions on productivity would be accumulated over the whole life of the stand. The same applies to stand height. Differences in site conditions cannot be reflected as distinctly in ΔB between a time span of 10 years. For instance, when looking at a rather short time span, it is more likely that weather variability between the years does not reflect average climate conditions and thus blurs the effect of climate on growth. However, this time span in combination with corresponding climate data allows to assess short-term growth response, which can also be perceived as an advantage of this approach. Environmental data are regionalized and thus introduce uncertainty into the analysis. Environmental influences on forest growth must be summarized into a few quantifiable factors. It is no wonder that their effect is small considering the complexity of tree growth. Complex interactions between site conditions and forest management, extreme events as well as genetic variability may greatly affect productivity.

Comparisons with studies about site factors influencing biomass (e.g. Chave *et al.*, 2003; Keith *et al.*, 2009; Stegen *et al.*, 2011) are only possible to a certain degree, as biomass and biomass growth may react differently to environmental influences. For instance, an extension of the growing season will increase biomass growth as long as water supply is not limiting. Forest biomass may stay the same, since trees only move faster along their life's trajectory and die at a younger age, but self-thinning lines remain constant (Pretzsch *et al.*, 2014a).

Benefit of using ΔB

Productivity is often estimated based on height information alone (e.g. Seynave *et al.*, 2005; Albert & Schmidt, 2010; Nothdurft *et al.*, 2012), thus taking only the vertical aspect of productivity, i.e. height growth, into account. The results of this study illustrate the importance of the horizontal aspect of productivity, i.e. density and radial growth, as sites that do not differ significantly in SI and age can still differ in productivity. Recent analyses of Norway spruce stands in Bavaria (Southern Germany) based on NFI data could be interpreted in the light of these findings: Based on NFI data similar site indices are estimated for the two Bavarian forest eco-regions Swabia and Spessart. A SI-model based on Bavarian NFI data also predicts similar site indices for these two regions (Brandl *et al.*, 2014). However, in forestry practice Swabia is generally considered the better site for spruce. Looking at our data we found that sites of similar stand age (Spessart 80 years, Swabia 76 years) and SI (Spessart 36.7 m, Swabia 36.4 m) in Swabia indeed have greater above-ground wood biomass (Spessart 296 t ha^{-1}, Swabia 403 t ha^{-1}) and show greater above-ground wood biomass growth (ΔB) (Spessart 7.8 t ha^{-1} yr^{-1}, Swabia 9.9 t ha^{-1} yr^{-1}). In contrast to the mentioned SI-model our model predicts significant differences in productivity. Actual ΔB can be predicted using actual stand density and age (Spessart 8.4 t ha^{-1} yr^{-1}, Swabia 10.4 t ha^{-1} yr^{-1}). Setting a fixed age (e.g. 80 years) and a fixed relative stand density (e.g. 0.7) potential ΔB can be predicted (Spessart 8.7 t ha^{-1} yr^{-1}, Swabia 9.5 t ha^{-1} yr^{-1}) resulting in a difference of 9.2 % due to climate and soil. Potential ΔB cannot be compared to the measured values, but reveals differences in site potential. This example illustrates the benefit of not only looking at SI but also at ΔB when assessing site productivity. Differences like these are important when estimating C-balances or assessing economic values.

Conclusion

As the use of SI as an indicator for site productivity is not unquestioned, we looked for a more direct measure of productivity that can be estimated based on NFI data. ΔB of the stand is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. ΔB entails the difficulty of how to deal with the influence of stand density and stand age which we explored in the study. However, there is the advantage of encompassing at once a stand's productivity in the response variable with no need to consider the question of different yield levels later on. We conclude that the stand-alone use of ΔB as a measure for site potential is not recommendable, because many assumptions are needed when dealing with the effect of stand density. Still, considering both traditional SI and ΔB might result in a more accurate picture of site potential as there are sites that do not differ significantly in SI, but still differ in productivity. Using ΔB as response it was possible to fit plausible effects of site conditions. These effects are small in comparison to the effects of stand structure. Still, connecting ΔB with climatic variables allows predictions of productivity for future climatic scenarios.

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Appendix 1: Calculation of ΔB of the stand based on single tree measurements of the 2nd and the 3rd NFI in Germany

1) Obtaining diameter at breast height (dbh) and height for all sample trees on a NFI plot

In German NFI sampling, dbh of all trees in the angle-count sampling with basal area factor 4 (ACS_4) is measured, whereas height is only measured for a subsample of trees (main storey: two trees of the dominant species group and one tree of each remaining species group, under storey and top storey: one tree of each species group) (BMELV, 2011). Heights that are not measured are derived from species-specific uniform height-diameter curves (Riedel *et al.*, 2017).

There are trees that were included in ACS_4 in NFI 3 but had not been thick enough to be included in NFI 2. Other trees were measured for the NFI 2 but were missing in the NFI 3 due to harvest, thinning or mortality. Diameter at breast height and height of these trees were predicted for the middle of the period between NFI 2 and NFI 3 (e.g. Jenkins *et al.*, 2001; Dahm, 2006) using the function of Sloboda (Riedel *et al.*, 2017).

2) Estimation of single tree above-ground wood biomass

Species-specific functions by Zell (2008) were used for the calculation of total single tree above-ground wood biomass (kg) based on dbh (cm) and height (m) measurements or estimations respectively:

$$biomass = a * dbh^{b} * height^{c}$$

Coefficients a, b and c for each species present in the NFI data are detailed in Table S1.

Table S3. Coefficients (a, b and c) for each species group in the biomass functions developed by Zell (2008). Species were assigned to the species groups according to Klein & Schulz (2012).

species group	**a**	**b**	**c**	**species**
spruce	0.0673	1.9378	0.6382	*Picea abies, Picea spec.*, all other conifers not specified in NFI data
pine	0.058	2.034	0.637	*Pinus sylvestris, Pinus mugo, Pinus nigra, Pinus strobus, Pinus spec.*
fir	0.04	2.06631	0.67061	*Abies alba, Abies grandis, Abies spec., Pseudotsuga menziesii, Taxus baccata*
larch	0.079	1.857	0.736	*Larix decidua, Larix kaempferi*
beech	0.0365	2.1082	0.7696	*Fagus sylvatica, Acer platanoides, Acer campestre, Acer pseudoplatanus, Aesculus hippocastanum, Carpinus betulus, Castanea sativa, Juglans spec., Prunus avium, Prunus padus, Prunus serotina, Sorbus spec., Tilia spec.,* other deciduous trees with high life expectancy
oak	0.04428151	2.096	0.712	*Quercus petraea , Quercus robur, Quercus rubra, Fraxinus excelsior, Robinia pseudoacacia, Ulmus spec.*
alder	0.018	2.069	0.9	*Alnus glutinosa, Alnus incana, Alnus spec.*
birch	0.060	1.971	0.7	*Betula pendula, Betula pubescens, Malus sylvestris, Populus alba, Populus nigra, Populus tremula, Populus x canescens, Populus trichocarpa x maximoviczii, Pyrus communis, Salix spec., Sorbus aria, Sorbus aucuparia, Sorbus torminalis,* other deciduous trees with low life expectancy

3) Calculation of the biomass increment of single trees

The biomass increment in kg yr^{-1} of each tree was calculated:

$$biomass\ increment\ per\ year = \frac{biomass_{NFI3} - biomass_{NFI2}}{year_{NFI3} - year_{NFI2}}$$

In general:

$year_{NFI3} = 2012$

$year_{NFI2} = 2002$

Special case: ingrowth (trees that were included in the ACS_4 in NFI 3 but had not been thick enough to be included in NFI 2)

$year_{NFI3} = 2012$

$year_{NFI2} = 2007$

Special case: missing trees due to harvest, thinning or mortality (trees that were measured for the NFI 2 but were missing in the NFI 3)

$year_{NFI3} = 2007$

$year_{NFI2} = 2002$

4) Estimation of the biomass increment of the stand in kg ha^{-1} yr^{-1}

One NFI plot represents a stand of one ha. Each sample tree in ACS_4 represents a certain number of trees per ha (N_{ha}) according to its basal area (BA):

$$N_{ha} = \frac{4}{BA}$$

In order to obtain growth per ha the growth of the individual tree is multiplied by its N_{ha}. N_{ha} depends on the basal area of the tree, i.e. N_{ha} is higher at the first measurement than at the second measurement as the basal area of the trees increases. Therefore, for scaling up to one ha we used the mean of the stem number per ha of the 2nd and 3rd NFI. (Standard evaluation of the German NFI uses N_{ha} of the second measurement to estimate growth values on ha basis (Dahm, 2006). For consistency with the general NFI evaluation we had used N_{ha} of the 3rd NFI (i.e. the second measurement) at first. However, our validation on an independent dataset of experimental plots showed that this would result in a systematic underestimation of ΔB

(see also Eastaugh & Hasenauer, 2013). Therefore, we decided to use the mean of the stem number per ha of the 2nd and 3rd NFI.)

$$biomass\ increment\ per\ year\ and\ ha = biomass\ increment\ per\ year * N_{ha}$$

Biomass growth of the stand in kg ha^{-1} yr^{-1} is then derived by summing up biomass increment per year and ha of all trees on the NFI plot:

$$\Delta B = \sum_{1}^{n} biomass\ increment\ per\ year\ and\ ha$$

with n being the number of sample trees on the plot.

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Appendix 2: Estimation of the stand density index (SDI) for each NFI plot

The estimation of stand density is based on the stand density index of Reineke (Reineke, 1933; Zeide, 2005):

$$SDI = N * \left(\frac{25}{dg}\right)^{-1.605}$$

N: stem number per ha
dg: quadratic mean diameter (cm)

(1) The 95th percentile of the SDI distribution (SDI_95) of pure stands for each species was determined.

(2) Weighting factors were calculated by dividing the 95-percentile value of spruce (used as reference species) by the 95-percentile value of the respective tree species (Table S2):

$$weighting\ factor = \frac{SDI\_95_{spruce}}{SDI\_95_{species}}$$

Table S2. 95th percentile of SDI distribution and weighting factor for each species.

species	95th percentile of SDI distribution (SDI_95)	Weighting factor
spruce	1674.457	1.000
pine	1483.888	1.128
fir	1330.258	1.259
larch	1314.548	1.274
Japanese larch	1260.751	1.328
Douglas fir	1536.864	1.090
beech	1188.593	1.409
oak	1171.272	1.430
alder	1514.525	1.106
birch	1030.464	1.625
ash	1413.660	1.184
poplar	1180.323	1.419
red oak	1207.188	1.387

(3) For each NFI plot SDI was calculated separately for each species:

$$SDI_{species} = N_{species} * \left(\frac{25}{dg_{species}}\right)^{-1.605}$$

(4) The species-specific $\mathrm{SDI}_{\mathrm{species}}$ was corrected by multiplying with the weighting factor:

$$SDI_{species\_corr} = weighting\ factor * SDI_{species}$$

(5) Species-specific $\mathrm{SDI}_{\mathrm{species\_corr}}$ for all species at a plot were summarized resulting in one SDI for each NFI plot:

$$SDI = \sum_{1}^{n_{species}} SDI_{species\_corr}$$

$\mathrm{n}_{\mathrm{species}}$: number of different species at the plot

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Appendix 3: Detailed information on the methods used for investigating the relationship between the variability in ΔB and stand variables

(1) Site index (SI) estimation for each NFI plot

For each plot SI was determined based on the method presented in Brandl *et al.* (2018): First, top height h_{top} (defined as the height corresponding to the root mean square diameter d_{top} of the top 100 diameters of a tree species on a site) was determined. Second, SI was determined by scaling the position of $h_{top}(i)$ between a lower and upper boundary height at age i with the ratio of the span between lower and upper boundary height at age 100 and the span between lower and upper boundary height at age i (Figure S1):

$$\widehat{SI} = h_{top\ l(100)} + \left(h_{top\ (i)} - h_{top\ l(i)}\right) \cdot \frac{h_{top\ u(100)} - h_{top\ l(100)}}{h_{top\ u(i)} - h_{top\ l(i)}}$$

with $h_{top\ l}$ and $h_{top\ u}$ as the lower and upper boundary height at the respective age.

Lower and upper boundary lines had been adopted from Brandl *et al.* (2018) and are described by the Chapman-Richards functions (Richards, 1959):

$$h_{top\ (i)} = A * (1 - e^{-k*age_i})^p$$

with A = 42.014, k = 0.029 and p = 1.048 for the upper boundary line and with A = 26.159, k = 0.045 and p = 2.346 for the lower boundary line.

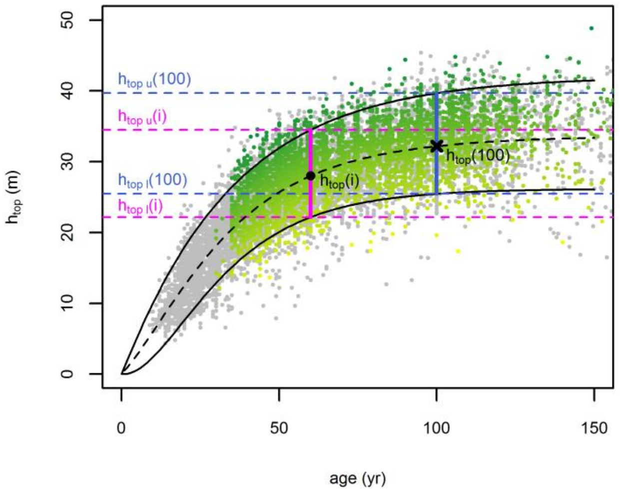

Figure S1. Illustration of translating the top height $h_{top}(i)$ of a NFI plot of age i to the corresponding height $h_{top}(100)$ at the reference age of 100 years i.e. the SI; green points mark heights and ages of NFI plots used in the study; grey points correspond to the data used for the determination of the boundary lines (solid black curves); the black dot marks an example stand at age 60 with a top height of 28 m. The black cross marks its translation to h_{top} at age 100, resulting in a SI of about 32 m.

(2) Generalized additive model (GAM): ΔB in dependence on SI and stand age

A GAM was fitted explaining ΔB in dependence on SI and stand age using the package mgcv (Wood, 2011) in R 3.3.2 (R Core Team, 2016) (Table S3, Figure S2):

$$\Delta B = \exp(f(SI) + f(age) + \varepsilon)$$

The residuals of this model can be interpreted as the variation in ΔB not explained by SI and age.

Table S3. Detailed model summary for the GAM.

	Estimate	Standard error	T statistics	p value
Intercept	9.0736	0.0054	1680	$< 2 \times 10^{-16}$
	edf	df residuals	F statistics	p value
f(SI)	4.150	5.171	131.5	$< 2 \times 10^{-16}$
f(stand age)	6.533	7.671	332.9	$< 2 \times 10^{-16}$
Adjusted R²		0.474		

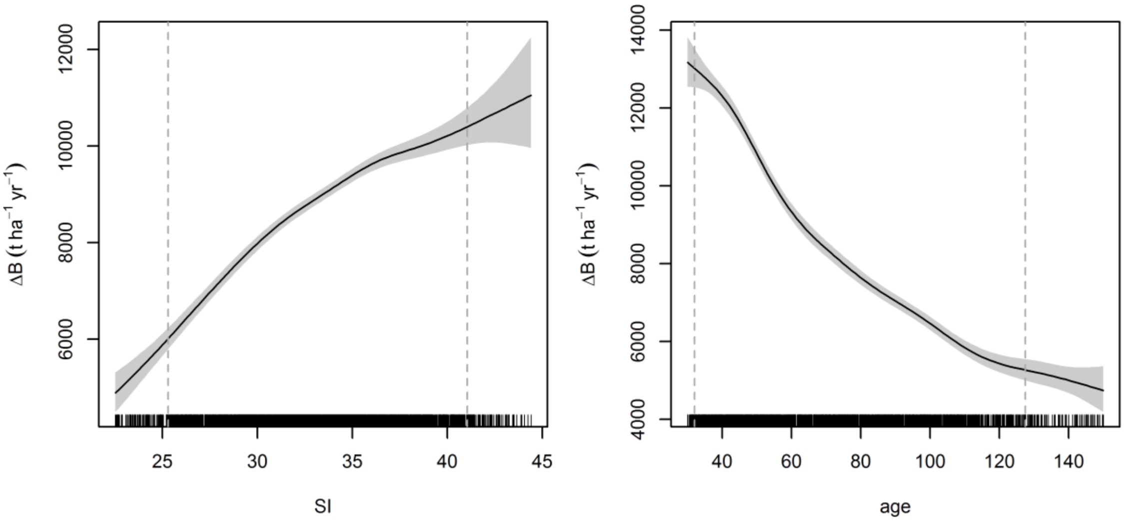

Figure S2. Effects of SI and stand age respectively on ΔB when the other variable is set to its mean. Grey areas comprise 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate; the vertical dashed lines mark the 2.5 and 97.5% quantiles of the covariate's distribution.

(2) Quantile regression for rescaling single tree height and dbh

In order to be able to compare trees of varying ages height and dbh had to be rescaled: A 95%-quantile regression was fitted to the respective variable (height or dbh) as a fourth order polynomial of age (Table S4, Figure S3).

$$variable = \alpha + \beta_1 age + \beta_2 age^2 + \beta_3 age^3 + \beta_4 age^4$$

The result can be interpreted as the maximum height or dbh that can be reached at a certain age. In order not to give outliers too much influence a 95%-quantile regression was used instead of simply drawing an envelope curve.

In the next step, each tree's height or dbh respectively was divided by the predicted 95%-quantile of height or dbh respectively at the tree's age. The resulting value is independent of age and can be interpreted as the percentage of the maximum height or dbh a tree can reach.

Table S4. Estimates of coefficients and statistical characteristics of the quantile regressions on height and dbh.

	coefficient	Estimate	Standard error	T Statistics	p value
height	α	7.50790	1.83909	4.08240	0.00004
	β_1	0.83118	0.10557	7.87308	0.00000
	β_2	-0.00939	0.00213	-4.41139	0.00001
	β_3	0.00005	0.00002	3.04934	0.00230
	β_4	0.00000	0.00000	-2.32715	0.01996
dbh	α	-17.64376	7.33892	-2.40414	0.01622
	β_1	2.55928	0.42098	6.07933	0.00000
	β_2	-0.03399	0.00852	-3.98666	0.00007
	β_3	0.00022	0.00007	3.01045	0.00261
	β_4	0.00000	0.00000	-2.33020	0.01980

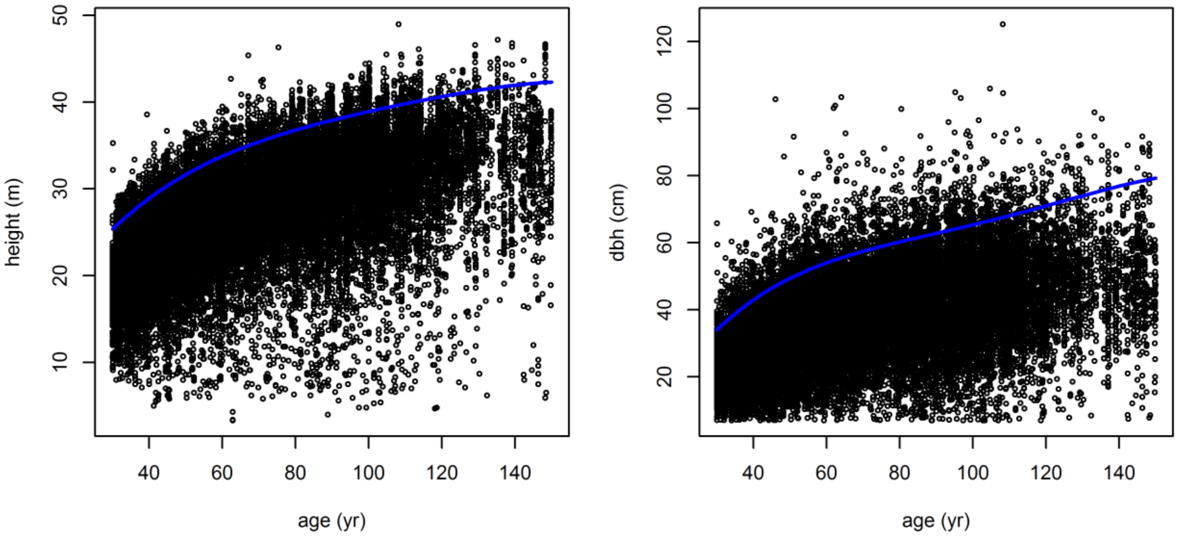

Figure S3. Height or dbh respectively plotted against age of single trees on NFI plots used in the study. The blue line marks the fit of the quantile regression.

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Publication IV

Positive biodiversity-productivity relationship predominant in global forests

RESEARCH ARTICLE SUMMARY

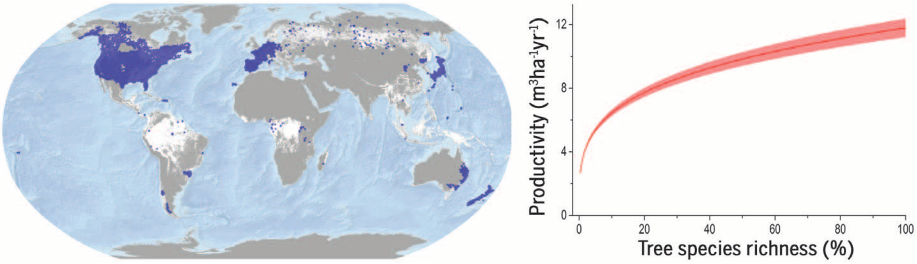
FOREST ECOLOGY

Positive biodiversity-productivity relationship predominant in global forests

Jingjing Liang,* Thomas W. Crowther, Nicolas Picard, Susan Wiser, Mo Zhou, Giorgio Alberti, Ernst-Detlef Schulze, A. David McGuire, Fabio Bozzato, Hans Pretzsch, Sergio de-Miguel, Alain Paquette, Bruno Hérault, Michael Scherer-Lorenzen, Christopher B. Barrett, Henry B. Glick, Geerten M. Hengeveld, Gert-Jan Nabuurs, Sebastian Pfautsch, Helder Viana, Alexander C. Vibrans, Christian Ammer, Peter Schall, David Verbyla, Nadja Tchebakova, Markus Fischer, James V. Watson, Han Y. H. Chen, Xiangdong Lei, Mart-Jan Schelhaas, Huicui Lu, Damiano Gianelle, Elena I. Parfenova, Christian Salas, Eungul Lee, Boknam Lee, Hyun Seok Kim, Helge Bruelheide, David A. Coomes, Daniel Piotto, Terry Sunderland, Bernhard Schmid, Sylvie Gourlet-Fleury, Bonaventure Sonké, Rebecca Tavani, Jun Zhu, Susanne Brandl, Jordi Vayreda, Fumiaki Kitahara, Eric B. Searle, Victor J. Neldner, Michael R. Ngugi, Christopher Baraloto, Lorenzo Frizzera, Radomir Bałazy, Jacek Oleksyn, Tomasz Zawiła-Niedźwiecki, Olivier Bouriaud, Filippo Bussotti, Leena Finér, Bogdan Jaroszewicz, Tommaso Jucker, Fernando Valladares, Andrzej M. Jagodzinski, Pablo L. Peri, Christelle Gonmadje, William Marthy, Timothy O'Brien, Emanuel H. Martin, Andrew R. Marshall, Francesco Rovero, Robert Bitariho, Pascal A. Niklaus, Patricia Alvarez-Loayza, Nurdin Chamuya, Renato Valencia, Frédéric Mortier, Verginia Wortel, Nestor L. Engone-Obiang, Leandro V. Ferreira, David E. Odeke, Rodolfo M. Vasquez, Simon L. Lewis, Peter B. Reich

INTRODUCTION: The biodiversity-productivity relationship (BPR; the effect of biodiversity on ecosystem productivity) is foundational to our understanding of the global extinction crisis and its impacts on the functioning of natural ecosystems. The BPR has been a prominent research topic within ecology in recent decades, but it is only recently that we have begun to develop a global perspective.

RATIONALE: Forests are the most important global repositories of terrestrial biodiversity, but deforestation, forest degradation, climate change, and other factors are threatening approximately one half of tree species worldwide. Although there have been substantial efforts to strengthen the preservation and sustainable use of forest biodiversity throughout the globe, the consequences of this diversity loss pose a major uncertainty for ongoing international forest management and conservation efforts. The forest BPR represents a critical missing link for accurate valuation of global biodiversity and successful integration of biological conservation and socioeconomic development. Until now, there have been limited tree-based diversity experiments, and the forest BPR has only been explored within regional-scale observational studies. Thus, the strength and spatial variability of this relationship remains unexplored at a global scale.



Global effect of tree species diversity on forest productivity. Ground-sourced data from 777,126 global forest biodiversity permanent sample plots (dark blue dots, left), which cover a substantial portion of the global forest extent (white), reveal a consistent positive and concave-down biodiversity-productivity relationship across forests worldwide (red line with pink bands representing 95% confidence interval, right).

RESULTS: We explored the effect of tree species richness on tree volume productivity at the global scale using repeated forest inventories from 777,126 permanent sample plots in 44 countries containing more than 30 million trees from 8737 species spanning most of the global terrestrial biomes. Our findings reveal a consistent positive concave-down effect of biodiversity on forest productivity across the world, showing that a continued biodiversity loss would result in an accelerating decline in forest productivity worldwide.

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The BPR shows considerable geospatial variation across the world. The same percentage of biodiversity loss would lead to a greater relative (that is, percentage) productivity decline in the boreal forests of North America, Northeastern Europe, Central Siberia, East Asia, and scattered regions of South-central Africa and South-central Asia. In the Amazon, West and Southeastern Africa, Southern China, Myanmar, Nepal, and the Malay Archipelago, however, the same percentage of biodiversity loss would lead to greater absolute productivity decline.

CONCLUSION: Our findings highlight the negative effect of biodiversity loss on forest productivity and the potential benefits from the transition of monocultures to mixed-species stands in forestry practices. The BPR we discover across forest ecosystems worldwide corresponds well with recent theoretical advances, as well as with experimental and observational studies on forest and nonforest ecosystems. On the basis of this relationship, the ongoing species loss in forest ecosystems worldwide could substantially reduce forest productivity and thereby forest carbon absorption rate to compromise the global forest carbon sink. We further estimate that the economic value of biodiversity in maintaining commercial forest productivity alone is $166 billion to $490 billion per year. Although representing only a small percentage of the total value of biodiversity, this value is two to six times as much as it would cost to effectively implement conservation globally. These results highlight the necessity to reassess biodiversity valuation and the potential benefits of integrating and promoting biological conservation in forest resource management and forestry practices worldwide. ■

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RESEARCH ARTICLE

FOREST ECOLOGY

Positive biodiversity-productivity relationship predominant in global forests

Jingjing Liang,[1]* Thomas W. Crowther,[2,3]† Nicolas Picard,[4] Susan Wiser,[5] Mo Zhou,[1] Giorgio Alberti,[6] Ernst-Detlef Schulze,[7] A. David McGuire,[8] Fabio Bozzato,[9] Hans Pretzsch,[10] Sergio de-Miguel,[11,12] Alain Paquette,[13] Bruno Hérault,[14] Michael Scherer-Lorenzen,[15] Christopher B. Barrett,[16] Henry B. Glick,[3] Geerten M. Hengeveld,[17,18] Gert-Jan Nabuurs,[17,19] Sebastian Pfautsch,[20] Helder Viana,[21,22] Alexander C. Vibrans,[23] Christian Ammer,[24] Peter Schall,[24] David Verbyla,[25] Nadja Tchebakova,[26] Markus Fischer,[27,28] James V. Watson,[1] Han Y. H. Chen,[29] Xiangdong Lei,[30] Mart-Jan Schelhaas,[17] Huicui Lu,[19] Damiano Gianelle,[31,32] Elena I. Parfenova,[26] Christian Salas,[33] Eungul Lee,[34] Boknam Lee,[35] Hyun Seok Kim,[35,36,37,38] Helge Bruelheide,[39,40] David A. Coomes,[41] Daniel Piotto,[42] Terry Sunderland,[43,44] Bernhard Schmid,[45] Sylvie Gourlet-Fleury,[46] Bonaventure Sonké,[47] Rebecca Tavani,[48] Jun Zhu,[49,50] Susanne Brandl,[10,51] Jordi Vayreda,[52,53] Fumiaki Kitahara,[54] Eric B. Searle,[29] Victor J. Neldner,[55] Michael R. Ngugi,[55] Christopher Baraloto,[56,57] Lorenzo Frizzera,[31] Radomir Bałazy,[58] Jacek Oleksyn,[59,60] Tomasz Zawiła-Niedźwiecki,[61,62] Olivier Bouriaud,[63,64] Filippo Bussotti,[65] Leena Finér,[66] Bogdan Jaroszewicz,[67] Tommaso Jucker,[41] Fernando Valladares,[68,69] Andrzej M. Jagodzinski,[59,70] Pablo L. Peri,[71,72,73] Christelle Gonmadje,[74,75] William Marthy,[76] Timothy O'Brien,[76] Emanuel H. Martin,[77] Andrew R. Marshall,[78,79] Francesco Rovero,[80] Robert Bitariho,[81] Pascal A. Niklaus,[45] Patricia Alvarez-Loayza,[82] Nurdin Chamuya,[83] Renato Valencia,[84] Frédéric Mortier,[46] Verginia Wortel,[85] Nestor L. Engone-Obiang,[86] Leandro V. Ferreira,[87] David E. Odeke,[88] Rodolfo M. Vasquez,[89] Simon L. Lewis,[90,91] Peter B. Reich[20,60]

The biodiversity-productivity relationship (BPR) is foundational to our understanding of the global extinction crisis and its impacts on ecosystem functioning. Understanding BPR is critical for the accurate valuation and effective conservation of biodiversity. Using ground-sourced data from 777,126 permanent plots, spanning 44 countries and most terrestrial biomes, we reveal a globally consistent positive concave-down BPR, showing that continued biodiversity loss would result in an accelerating decline in forest productivity worldwide. The value of biodiversity in maintaining commercial forest productivity alone—US$166 billion to 490 billion per year according to our estimation—is more than twice what it would cost to implement effective global conservation. This highlights the need for a worldwide reassessment of biodiversity values, forest management strategies, and conservation priorities.

The biodiversity-productivity relationship (BPR) has been a major ecological research focus over recent decades. The need to understand this relationship is becoming increasingly urgent in light of the global extinction crisis because species loss affects the functioning and services of natural ecosystems (1, 2). In response to an emerging body of evidence that suggests that the functioning of natural ecosystems may be substantially impaired by reductions in species richness (3–10), global environmental authorities, including the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) and United Nations Environment Programme (UNEP), have made substantial efforts to strengthen the preservation and sustainable use of biodiversity (2, 11). Successful international collaboration, however, requires a systematic assessment of the value of biodiversity (11). Quantification of the global BPR is thus urgently needed to facilitate the accurate valuation of biodiversity (12), the forecast of future changes in ecosystem services worldwide (11), and the integration of biological conservation into international socioeconomic development strategies (13).

The evidence of a positive BPR stems primarily from studies of herbaceous plant communities (14). In contrast, the forest BPR has only been explored at the regional scale [(3, 4, 7, 15) and references therein] or within a limited number of tree-based experiments [(16, 17) and references therein], and it remains unclear whether these relationships hold across forest types. Forests are the most important global repositories of terrestrial biodiversity (18), but deforestation, climate change, and other factors are threatening a considerable proportion (up to 50%) of tree species worldwide (19–21). The consequences of this diversity loss pose a critical uncertainty for ongoing international forest management and conservation efforts. Conversely, forest management that converts monocultures to mixed-species stands has often seen a substantial positive effect on productivity with other benefits (22–24). Although forest plantations are predicted to meet 50 to 75% of the demand for lumber by 2050 (25, 26), nearly all are still planted as monocultures, highlighting the potential of forest management in strengthening the conservation and sustainable use of biodiversity worldwide.

Here, we compiled in situ remeasurement data, most of which were taken at two consecutive inventories from the same localities, from 777,126 permanent sample plots [hereafter, global forest biodiversity (GFB) plots] across 44 countries and territories and 13 ecoregions to explore the forest BPR at a global scale (Fig. 1). GFB plots encompass forests of various origins (from naturally regenerated to planted) and successional stages (from stand initiation to old-growth). A total of more than 30 million trees across 8737 species were tallied and measured on two or more consecutive inventories from the GFB plots. Sampling intensity was greater in developed countries, where nationwide forest inventories have been fully or partially funded by governments. In most other countries, national forest inventories were lacking, and most ground-sourced data were collected by individuals and organizations (table S1).

On the basis of ground-sourced GFB data, we quantified BPR at the global scale using a data-driven ensemble learning approach (Materials and methods, Geospatial random forest). Our quantification of BPR involved characterizing the shape and strength of the dependency function through the elasticity of substitution (θ), which represents the degree to which species can substitute for each other in contributing to forest productivity; θ measures the marginal productivity—the change in productivity resulting from one unit decline of species richness—and reflects the strength of the effect of tree diversity on forest productivity, after accounting for climatic, soil, and plot-specific covariates. A higher θ corresponds to a greater decline in productivity due to one unit loss in biodiversity. The niche-efficiency (N-E) model (3) and several preceding studies (27–30) provide a framework for interpreting the elasticity of substitution and approximating BPR with a power function model:

$$P = \alpha \cdot f(\mathbf{X}) \cdot S^{\theta} \tag{1}$$

where P and S signify primary site productivity and tree species richness (observed on a 900-m^2 area basis on average) (Materials and methods), respectively; $f(\mathbf{X})$ is a function of a vector of control variables $\mathbf{X}$ (selected from stand basal area and 14 climatic, soil, and topographic covariates); and α is a constant. This model is capable of representing a variety of potential patterns of

BPR. $0 < \theta < 1$ represents a positive and concave down pattern (a degressively increasing curve), which is consistent with the N-E model and preceding studies (3, 27–30), whereas other θ values can represent alternative BPR patterns, including decreasing ($\theta < 0$), linear ($\theta = 1$), convex ($\theta > 1$), or no effect ($\theta = 0$) (Fig. 2) (14, 31). The model (Eq. 1) was estimated by using the geospatial random forest technique based on GFB data and covariates acquired from ground-measured and remote-sensing data (Materials and methods).

We found that a positive BPR predominated in forests worldwide. Out of 10,000 randomly selected subsamples (each consisting of 500 GFB plots), 99.87% had a positive concave-down relationship with relative species richness ($0 < \theta < 1$), whereas only 0.13% show negative trends, and none was equal to zero or greater than or equal to 1 (Fig. 2). Overall, the global forest productivity increased with a declining rate from 2.7 to 11.8 $m^3\ ha^{-1}\ year^{-1}$ as relative tree species richness increased from the minimum to the maximum value, which corresponds to a θ value of 0.26 (Fig. 3A).

At the global scale, we mapped the magnitude of BPR (as expressed by θ) using geospatial random forest and universal kriging. By plotting values of θ onto a global map, we revealed considerable geospatial variation across the world (Fig. 3B). The highest θ (0.29 to 0.30) occurred in the boreal forests of North America, Northeastern Europe, Central Siberia, and East Asia and the sporadic tropical and subtropical forests of South-central Africa, South-central Asia, and the Malay Archipelago. In these areas of the highest elasticity of substitution (32), the same percentage of biodiversity loss would lead to a greater percentage of reduction in forest productivity (Fig. 4A). In terms of absolute productivity, the same percentage of biodiversity loss would lead to the greatest productivity decline in the Amazon; West Africa's Gulf of Guinea; Southeastern Africa, including Madagascar; Southern China; Myanmar; Nepal; and the Malay Archipelago (Fig. 4B). Because of a relatively narrow range of the elasticity of substitution (32) estimated from the global-level analysis (0.2 to 0.3), the regions of the greatest productivity decline under the same percentage of biodiversity loss largely matched the regions of the greatest productivity (fig. S1). Globally, a 10% decrease in tree species richness (from 100 to 90%) would cause a 2 to 3% decline in productivity, and with a decrease in tree species richness to one (Materials and methods, Economic analysis), this decline in forest productivity would be 26 to 66% even if other things, such as the total number of trees and forest stocking, remained the same (fig. S4).

Discussion

Our global analysis provides strong and consistent evidence that productivity of forests would decrease at an accelerating rate with the loss of biodiversity. The positive concave-down pattern we discovered across forest ecosystems worldwide corresponds well with recent theoretical advances

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in BPR (3, 28–30), as well as with experimental (27) and observational (14) studies on forest and nonforest ecosystems. The elasticity of substitution (32) estimated in this study (ranged between 0.2 and 0.3) largely overlaps the range of values of the same exponent term (0.1 to 0.5) from previous theoretical and experimental studies [(10) and references therein]. Furthermore, our findings are consistent with the global estimates of the biodiversity-dependent ecosystem service debt under distinct assumptions (10) and with recent reports of the diminishing marginal benefits of adding a species as species richness increases, based on long-term forest experiments dating back to 1870 [(15, 33) and references therein].

Our analysis relied on stands ranging from unmanaged to extensively managed forests—managed forests with low operating and investment costs per unit area. Conditions of natural forests would not be comparable with intensively managed forests, because timber production in the latter systems often focuses on a single or limited number of highly productive tree species. Intensively managed forests, where saturated resources can weaken the effects of niche efficiency (3), are shown in some studies (34, 35) to have higher productivity than that of natural diverse forests of the same climate and site conditions (fig. S3). In contrast, other studies (6, 22–24) compared diverse stands with monocultures at the same level of management intensity and found that the positive effects of species diversity on tree productivity and other ecosystem services are applicable to intensively managed forests. As such, there is still an unresolved debate on the BPR of intensively managed forests. Nevertheless, because intensively managed forests only account for a minor (<7%) portion of global forests (18), our estimated BPR would be minimally affected by such manipulations and thus should reflect the inherent processes governing the vast majority of global forest ecosystems.

We focused on the effect of biodiversity on ecosystem productivity. Recent studies on the opposite causal direction [productivity-biodiversity relationship (14, 36, 37)] suggest that there may be a potential two-way causality between biodiversity and productivity. It is admittedly difficult to use correlative data to detect and attribute causal effects. Fortunately, substantial progress has been made to tease the BPR causal relationship from other potentially confounding environmental variables (14, 38, 39), and this study made considerable efforts to account for these otherwise

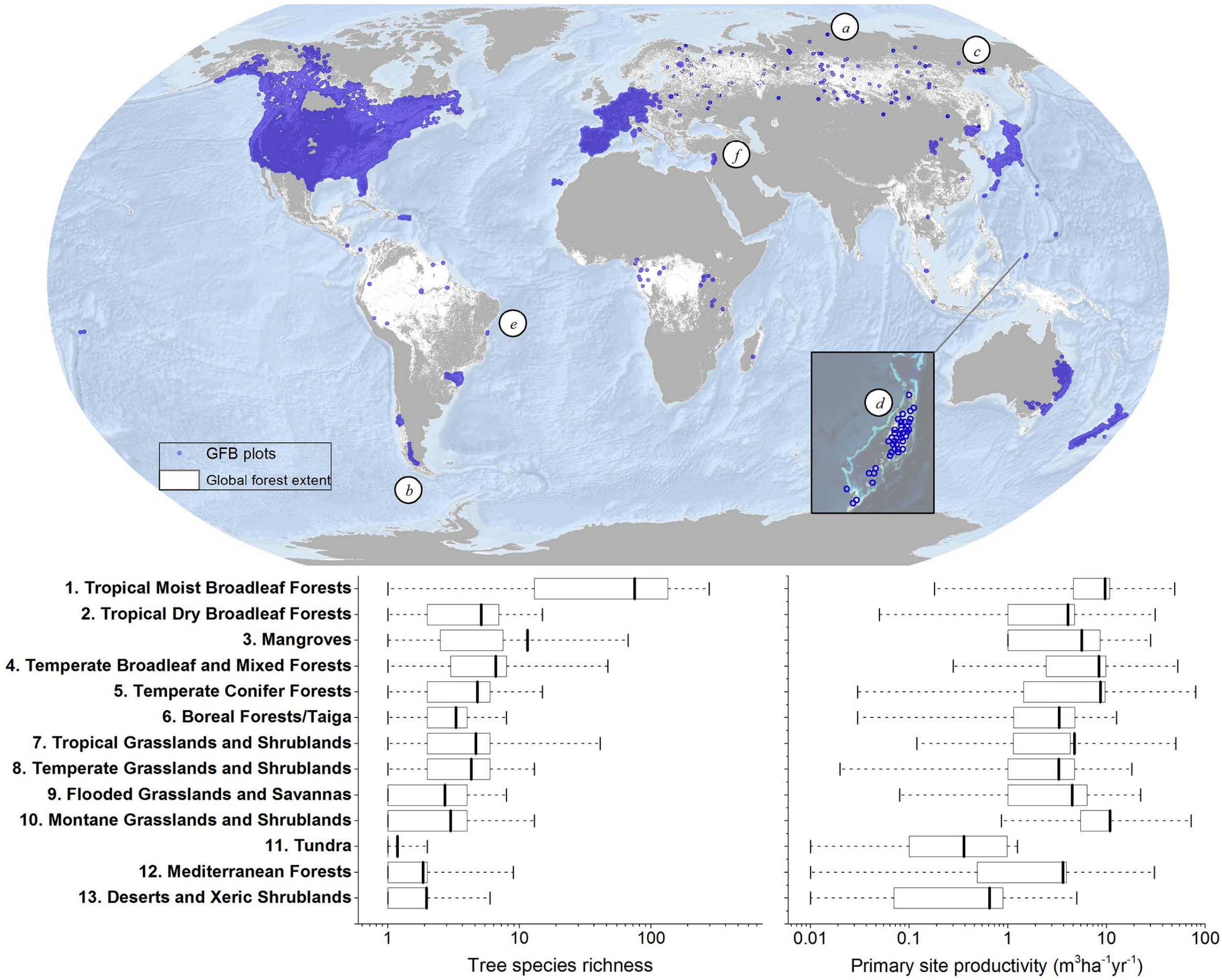

Fig. 1. GFB ground-sourced data were collected from in situ remeasurement of 777,126 permanent sample plots consisting of more than 30 million trees across 8737 species. GFB plots extend across 13 ecoregions [vertical axis, delineated by the World Wildlife Fund where extensive forests occur within all the ecoregions (72)], and 44 countries and territories. Ecoregions are named for their dominant vegetation types, but all contain some forested areas. GFB plots cover a substantial portion of the global forest extent (white), including some of the most distinct forest conditions: (*a*) the northernmost (73°N, Central Siberia, Russia), (*b*) southernmost (52°S, Patagonia, Argentina), (*c*) coldest (–17°C annual mean temperature, Oimyakon, Russia), (*d*) warmest (28°C annual mean temperature, Palau, United States), and (*e*) most diverse (405 tree species on the 1-ha plot, Bahia, Brazil). Plots in war-torn regions [such as (*f*)] were assigned fuzzed coordinates to protect the identity of the plots and collaborators. The box plots show the mean and interquartile range of tree species richness and primary site productivity (both on a common logarithmic scale) derived from ground-measured tree- and plot-level records. The complete list of species is presented in table S2.

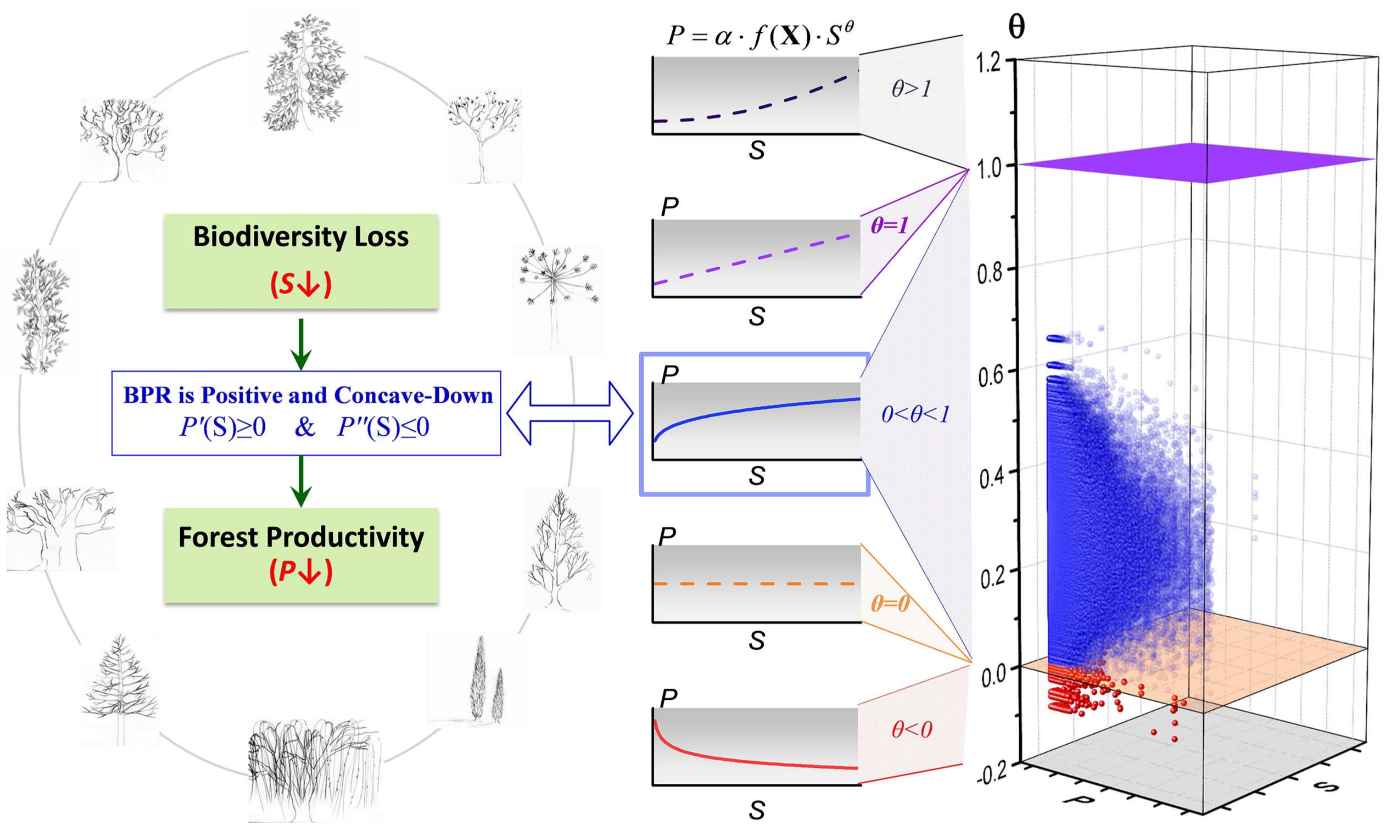

Fig. 2. Theoretical positive and concave-down biodiversity–productivity relationship supported by empirical evidence drawn from the GFB data. (**Left**) The diagram demonstrates that under the theoretical positive and concave-down (monotonically and degressively increasing) BPR (*3*, *27*, *28*), loss in tree species richness may reduce forest productivity (*73*). (**Middle**) Functional curves represent different BPR under different values of elasticity of substitution (θ). θ values between 0 and 1 correspond to the positive and concave-down BPR (blue curve). (**Right**) The three-dimensional scatter plot shows θ values we estimated from observed productivity (*P*), species richness (*S*), and other covariates. Out of 5,000,000 estimates of θ (mean = 0.26, SD = 0.09), 4,993,500 fell between 0 and 1 (blue), whereas only 6500 were negative (red), and none was equal to zero or greater than or equal to 1; the positive and concave-down BPR was supported by 99.9% of our estimates.

potentially confounding environmental covariates in assessing likely causal effects of biodiversity on productivity.

Because taxonomic diversity indirectly incorporates functional, phylogenetic, and genomic diversity, our results that focus on tree species richness are likely applicable to these other elements of biodiversity, all of which have been found to influence plant productivity (*1*). Our straightforward analysis makes clear the taxonomic contribution to forest ecosystem productivity and functioning, and the importance of preserving species diversity to biological conservation and forest management.

Our findings highlight the necessity to reassess biodiversity valuation and reevaluate forest management strategies and conservation priorities in forests worldwide. In terms of global carbon cycle and climate change, the value of biodiversity may be considerable. On the basis of our global-scale analyses (Fig. 4), the ongoing species loss in forest ecosystems worldwide (*1*, *21*) could substantially reduce forest productivity and thereby forest carbon absorption rate, which would in turn compromise the global forest carbon sink (*40*). We further estimate that the economic value of biodiversity in maintaining commercial forest productivity is $166 billion to $490 billion per year ($1.66 \times 10^{11}$ to 4.90×10^{11} year^{-1} in 2015 US$) (Materials and methods, Economics analysis). By itself, this estimate does not account for other values of forest biodiversity (including potential values for climate regulation, habitat, water flow regulation, and genetic resources), and represents only a small percentage of the total value of biodiversity (*41*, *42*). However, this value is already between two to six times the total estimated cost that would be necessary if we were to effectively conserve all terrestrial ecosystems at a global scale [$76.1 billion per year (*43*)]. The high benefit-to-cost ratio underlines the importance of conserving biodiversity for forestry and forest resource management.

Amid the struggle to combat biodiversity loss, the relationship between biological conservation and poverty is gaining increasing global attention (*13*, *44*), especially with respect to rural areas where livelihoods depend most directly on ecosystem products. Given the substantial geographic overlaps between severe, multifaceted poverty and key areas of global biodiversity (*45*), the loss of species in these areas has the potential to exacerbate local poverty by diminishing forest productivity and related ecosystem services (*44*). For example, in tropical and subtropical regions, many areas of high elasticity of substitution (*32*) overlapped with biodiversity hotspots (*46*), including Eastern Himalaya and Nepal, Mountains of Southwest China, Eastern Afromontane, Madrean pine-oak woodlands, Tropical Andes, and Cerrado. For these areas, only a few species of commercial value are targeted by logging. As such, the risk of losing species through deforestation would far exceed the risk through harvesting (*47*). Deforestation and other anthropogenic drivers of biodiversity loss in these biodiversity hotspots are likely to have considerable impacts on the productivity of forest ecosystems, with the potential to exacerbate local poverty. Furthermore, the greater uncertainty in our results for the developing countries (Fig. 5) reflects the well-documented geographic bias in forest sampling, including repeated measurements, and reiterates the need for strong commitments toward improving sampling in the poorest regions of the world.

Our findings reflect the combined strength of large-scale integration and synthesis of ecological data and modern machine learning methods to increase our understanding of the global forest system. Such approaches are essential for generating global insights into the consequences of biodiversity loss and the potential benefits of

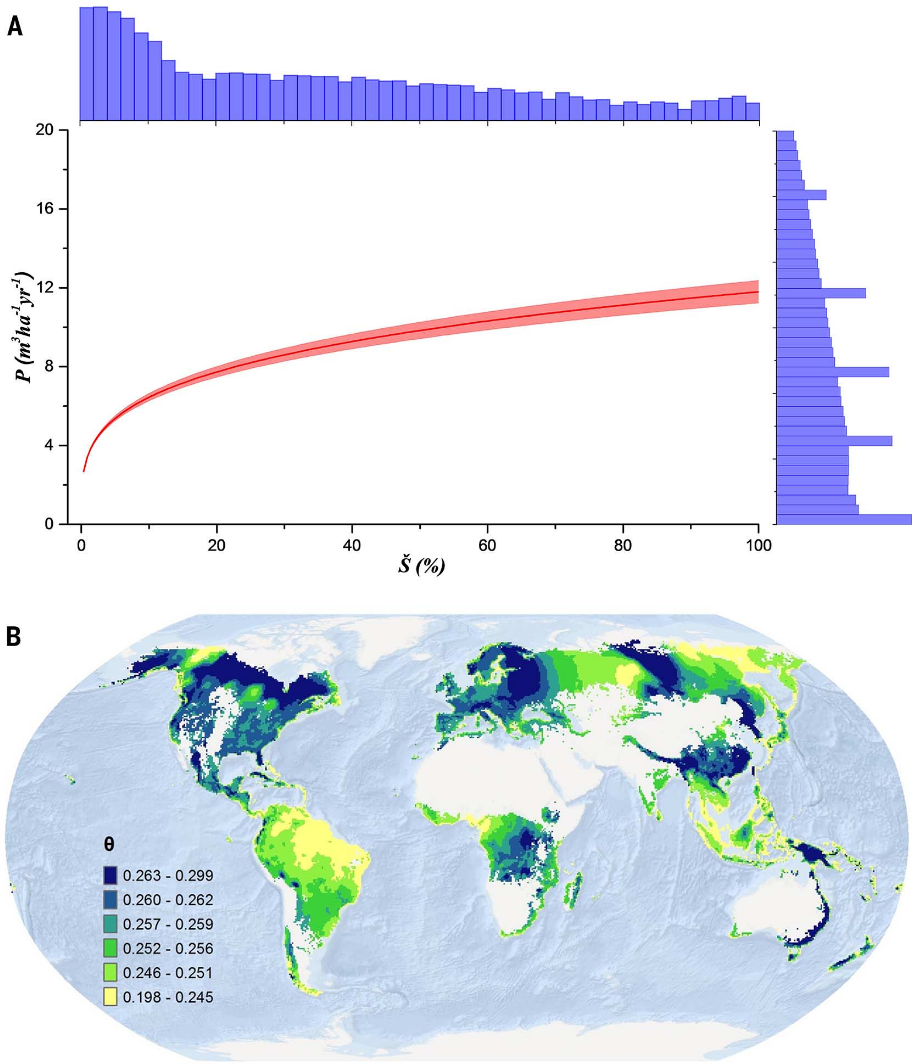

Fig. 3. The estimated global effect of biodiversity on forest productivity was positive and concave-down, and revealed considerable geospatial variation across forest ecosystems worldwide. (**A**) Global effect of biodiversity on forest productivity (red line with pink bands representing 95% confidence interval) corresponds to a global average elasticity of substitution (θ) value of 0.26, with climatic, soil, and other plot covariates being accounted for and kept constant at sample mean. Relative species richness (Š) is in the horizontal axis, and productivity (P, m^3 ha^{-1} year^{-1}) is in the vertical axis (histograms of the two variables on top and right in the logarithm scale). (**B**) θ represents the strength of the effect of tree diversity on forest productivity. Spatially explicit values of θ were estimated by using universal kriging (Materials and methods) across the current global forest extent (effect sizes of the estimates are shown in Fig. 5), whereas blank terrestrial areas were nonforested.

integrating and promoting biological conservation in forest resource management and forestry practices—a common goal already shared by intergovernmental organizations such as the Montréal and Helsinki Process Working Groups. These findings should facilitate efforts to accurately forecast future changes in ecosystem services worldwide, which is a primary goal of IPBES (*11*), and provide baseline information necessary to establish international conservation objectives, including the United Nations Convention on Biological Diversity Aichi targets, the United Nations Framework Convention on Climate Change REDD+ goal, and the United Nations Convention to Combat Desertification land degradation neutrality goal. The success of these goals relies on the understanding of the intrinsic link between biodiversity and forest productivity.

Materials and methods

Data collection and standardization

Our current study used ground-sourced forest measurement data from 45 forest inventories collected from 44 countries and territories (Fig. 1 and table S1). The measurements were collected in the field from predesignated sample area units, i.e., Global Forest Biodiversity permanent sample plots (hereafter, GFB plots). For the calculation of primary site productivity, GFB plots can be categorized into two tiers. Plots designated as “Tier 1” have been measured at two or more points in time with a minimum time interval between measurements of two years or more (global mean time interval is 9 years, see Table 1). “Tier 2” plots were only measured once, and primary site productivity can be estimated from known stand age or dendrochronological records. Overall, our study was based on 777,126 GFB plots, of which 597,179 (77%) were Tier 1, and 179,798 (23%) were Tier 2. GFB plots primarily measured natural forests ranging from unmanaged to extensively managed forests, i.e., managed forests with low operating and investment costs per unit area. Intensively managed forests with harvests exceeding 50 percent of the stocking volume were excluded from this study. GFB plots represent forests of various origins (from naturally regenerated to planted) and successional stages (from stand initiation to old-growth).

Table 1. Definition, unit, and summary statistics of key variables.

Variable	Definition	Unit	Mean	Standard deviation	Source	Nominal resolution
Response variables						
P	Primary forest productivity measured in periodic annual increment in stem volume (PAI)	$m^3\ ha^{-1}\ year^{-1}$	7.57	14.52	Author-generated from ground-measured data	
Plot attributes						
S	Tree species richness, the number of live tree species observed on the plot	unitless	5.79	8.64	ground-measured	
A	Plot size, area of the sample plot	ha	0.04	0.12	ground-measured	
Y	Elapsed time between two consecutive inventories	year	8.63	11.62	ground-measured	
G	Basal area, total cross-sectional area of live trees measured at 1.3 to 1.4 m above ground	$m^2\ ha^{-1}$	19.00	18.94	Author-generated from ground-measured data	
E	Plot elevation	m	469.30	565.92	G/SRTM (74)	
I_1	Indicator of plot tier $I_1 = 1$ if a plot was Tier-2, $I_1 = 0$ if otherwise	unitless	0.23	0.42	Author-generated from ground-measured data	
I_2	Indicator of plot size $I_2 = 1$ when $0.01 \le ps < 0.05$, $I_2 = 2$ when $0.05 \le ps < 0.15$, $I_2 = 3$ when $0.15 \le ps < 0.50$, $I_2 = 4$ when $0.50 \le ps < 1.00$, where ps was plot size (hectares)	unitless	1.43	0.80	Author-generated from ground-measured data	
Climatic covariates						
T_1	Annual mean temperature	0.1°C	108.4	55.92	WorldClim v.1 (75)	1 km^2
T_2	Isothermality	unitless index*100	35.43	7.05	WorldClim v.1	1 km^2
T_3	Temperature seasonality	Std.(0.001°C)	7786.00	2092.39	WorldClim v.1	1 km^2
C_1	Annual precipitation	mm	1020.00	388.35	WorldClim v.1	1 km^2
C_2	Precipitation seasonality (coefficient of variation)	unitless%	27.54	16.38	WorldClim v.1	1 km^2
C_3	Precipitation of warmest quarter	mm	282.00	120.88	WorldClim v.1	1 km^2
PET	Global Potential Evapotranspiration	$mm\ year^{-1}$	1063.43	271.80	CGIAR-CSI (76)	1 km^2
IAA	Indexed Annual Aridity	unitless index*10^{-4}	9915.09	4512.99	CGIAR-CSI	1 km^2
Soil covariates						
O_1	Bulk density	$g\ cm^{-3}$	0.70	0.57	WISE30sec v.1 (77)	1 km^2
O_2	pH measured in water	unitless	3.72	2.80	WISE30sec v.1	1 km^2
O_3	Electrical conductivity	$dS\ m^{-1}$	0.44	0.76	WISE30sec v.1	1 km^2
O_4	C/N ratio	unitless	9.64	7.78	WISE30sec v.1	1 km^2
O_5	Total nitrogen	$g\ kg^{-1}$	2.71	4.62	WISE30sec v.1	1 km^2
Geographic coordinates and classification						
x	Longitude in WGS84 datum	degree				
y	Latitude in WGS84 datum	degree				
Ecoregion	Ecoregion defined by World Wildlife Fund (78)					

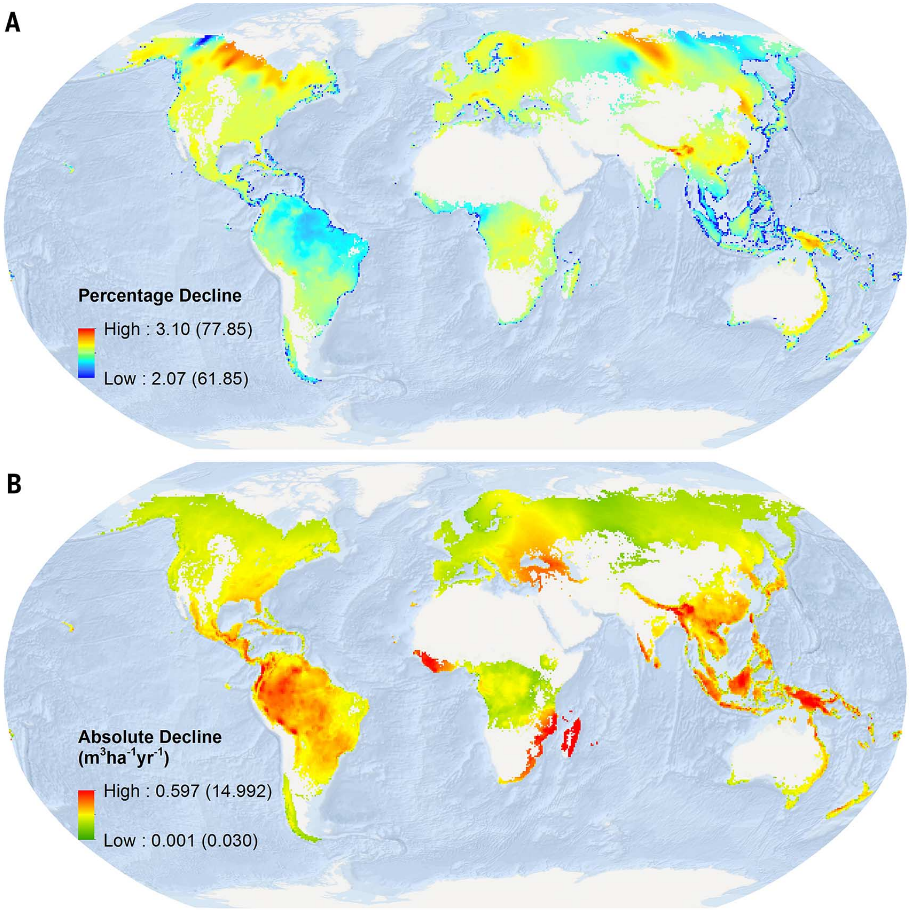

Fig. 4. Estimated percentage and absolute decline in forest productivity under 10 and 99% decline in current tree species richness (values in parentheses correspond to 99%), holding all the other terms constant. (**A**) Percent decline in productivity was calculated according to the general BPR model (Eq. 1) and estimated worldwide spatially explicit values of the elasticity of substitution (Fig. 3B). (**B**) Absolute decline in productivity was derived from the estimated elasticity of substitution (Fig. 3B) and estimates of global forest productivity (fig. S1). The first 10% reduction in tree species richness would lead to a 0.001 to 0.597 m^3 ha^{-1} $year^{-1}$ decline in periodic annual increment, which accounts for 2 to 3% of current forest productivity. The raster data are displayed in 50-km resolution with a 3 SD stretch.

For each GFB plot, we derived three key attributes from measurements of individual trees—tree species richness (S), stand basal area (G), and primary site productivity (P). Because for each of all the GFB plot samples, S and P were derived from the measurements of the same trees, the sampling issues commonly associated with biodiversity estimation (48) had little influence on the S–P relationship (i.e., BPR) in this study.

Species richness, S, represents the number of different tree species alive at the time of inventory within the perimeter of a GFB plot with an average size of approximately 900 m^2. Ninety-five percent of all plots fall between 100 and 1,100 m^2 in size. To minimize the species-area effect (49), we studied the BPR here using a geospatial random forest model in which observations from nearby GFB plots would be more influential than plots that are farther apart (see §Geospatial random forest). Because nearby plots are most likely from the same forest inventory data set, and there was no or little variation of plot area within each data set, the BPR derived from this model largely reflected patterns under the same plot area basis. To investigate the potential effects of plot size on our results, we plotted the estimated elasticity of substitution (θ) against plot size, and found that the scatter plot was normally distributed with no discernible pattern (fig. S2). In addition, the fact that the plot size indicator I_2 had the second lowest (0.8%) importance score (50) among all the covariates (Fig. 6) further supports that the influence of plot size variation in this study was negligible.

Across all the GFB plots, there were 8,737 species in 1,862 genera and 231 families, and S values ranged from 1 to 405 per plot. We verified all the species names against 60 taxonomic databases, including NCBI, GRIN Taxonomy for Plants, Tropicos–Missouri Botanical Garden, and the International Plant Names Index, using the 'taxize' package in R (51). Out of 8737 species recorded in the GFB database, 7425 had verified taxonomic information with a matching score (51) of 0.988 or higher, whereas 1312 species names partially matched existing taxonomic databases with a matching score between 0.50 and 0.75, indicating that these species may have not been documented in the 60 taxonomic databases. To facilitate inter-biome comparison, we further developed relative species richness ($\breve{S}$), a continuous percentage score converted from species richness (S) and the maximal species richness of a set of sample plots (S^*) using

$$\breve{S} = \frac{S}{S^*} \tag{2}$$

Stand basal area (G, in m^2 ha^{-1}) represents the total cross-sectional area of live trees per unit sample area. G was calculated from individual tree diameter-at-breast-height (dbh, in cm):

$$G = 0.000079 \cdot \sum_i dbh_i^2 \cdot \kappa_i \tag{3}$$

where κ_i denotes the conversion factor (ha^{-1}) of the ith tree, *viz.* the number of trees per ha represented by that individual. G is a key biotic factor of forest productivity as it represents stand density—often used as a surrogate for resource acquisition (through leaf area) and stand

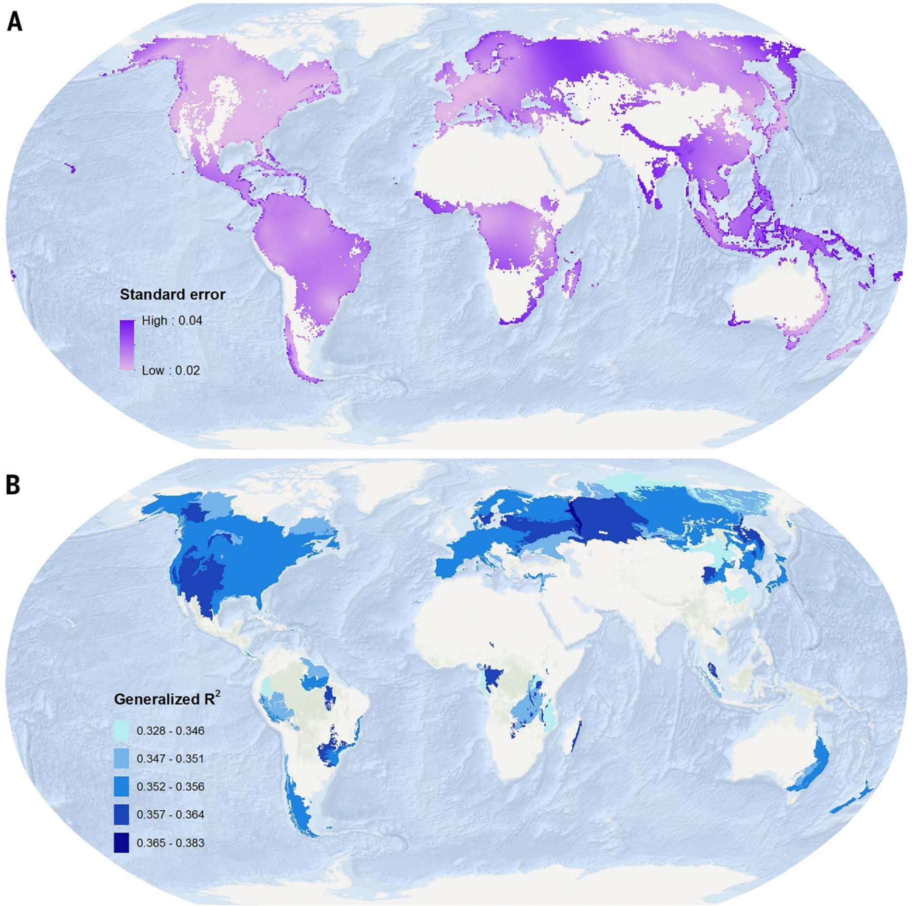

Fig. 5. Standard error and generalized R^2 of the spatially explicit estimates of elasticity of substitution (θ) across the current global forest extent in relation to Š. (**A**) Standard error increased as a location was farther from those sampled. (**B**) The generalized R^2 values were derived with a geostatistical nonlinear mixed-effects model for GFB sample locations, and thus (B) only covers a subset of the current global forest extent.

competition (52). Accounting for basal area as a covariate mitigated the artifact of different minimum dbh across inventories, and the artifact of different plot sizes.

Primary site productivity (P, in m^3 ha^{-1} yr^{-1}) was measured as tree volume productivity in terms of periodic annual increment (PAI) calculated from the sum of individual tree stem volume (V, in m^3)

$$P = \frac{\sum_{i,2} V_{i,2} \cdot \kappa_i - \sum_{i,1} V_{i,1} \cdot \kappa_i + M}{Y} \qquad (4)$$

where $V_{i,1}$ and $V_{i,2}$ (in m^3) represent total stem volume of the ith tree at the time of the first inventory and the second inventory, respectively. M denotes total removal of trees (including mortality, harvest, and thinning) in stem volume (in m^3 ha^{-1}). Y represents the time interval (in years) between two consecutive inventories. P accounted for mortality, ingrowth (i.e., recruitment between two inventories), and volume growth. Stem volume values were predominantly calculated using region- and species-specific allometric equations based on dbh and other tree- and plot-level attributes (Table 1). For the regions lacking an allometric equation, we approximated stem volume at the stand level from basal area, total tree height, and stand form factors (53). In case of missing tree height values from the ground measurement, we acquired alternative measures from a global 1-km forest canopy height database (54). For Tier 2 plots that lacked remeasurement, P was measured in mean annual increment (MAI) based on total stand volume and stand age (52), or tree radial growth measured from increment cores. Since the traditional MAI metric does not account for mortality, we calculated P by adding to MAI the annual mortality based on regional-specific forest turnover rates (55). The small and insignificant correlation coefficient between P and the indicator of plot tier (I_1), together with the negligible variable importance of I_1 (1.8%, Fig. 6), indicate that PAI and MAI were generally consistent, such that MAI could be a good proxy of PAI in our study. Although MAI and PAI have considerable uncertainty in any given stand, it is difficult to see how systematic bias across diversity gradients could occur on a scale sufficient to influence the results shown here.

P, although only representing a fraction of total forest net primary production, has been an important and widely used measure of forest productivity, because it reflects the dominant aboveground biomass component and the long-lived biomass pool in most forest ecosystems (56). Additionally, although other measures of productivity (e.g., net ecosystem exchange processed to derive gross and net primary production; direct measures of aboveground net primary production including all components; and remotely sensed estimates of LAI and greenness coupled with models) all have their advantages and disadvantages, none would be feasible at a similar scale and resolution as in this study.

To account for abiotic factors that may influence primary site productivity, we compiled 14 geospatial covariates based on biological relevance and spatial resolution (Fig. 6). These covariates, derived from satellite-based remote sensing and ground-based survey data, can be grouped into three categories: climatic, soil, and topographic (Table 1). We preprocessed all geospatial covariates using ArcMap 10.3 (57) and R 2.15.3 (58). All covariates were extracted to point locations of GFB plots, with a nominal resolution of 1 km^2.

Geospatial random forest

We developed geospatial random forest—a data-driven ensemble learning approach—to characterize the biodiversity–productivity relationship (BPR), and to map BPR in terms of elasticity of substitution ([31]) on all sample sites across the world. This approach was developed to overcome two major challenges that arose from the size and complexity of GFB data without assuming any underlying BPR patterns or data distribution. First, we need to account for broad-scale differences in vegetation types, but global classification and mapping of homogeneous vegetation types is lacking ([59]); and secondly, correlations and trends that naturally occur through space ([60]) can be significant and influential in forest ecosystems ([61]). Geostatistical models ([62]) have been developed to address the spatial autocorrelation, but the size of the GFB data set far exceeds the computational constraints of most geostatistical software.

Geospatial random forest integrated conventional random forest ([50]) and a geostatistical nonlinear mixed-effects model ([63]) to estimate BPR across the world based on GFB plot data and their spatial dependence. The underlying model had the following form

$$\log P_{ij}(\mathbf{u}) = \theta_i \cdot \log \breve{S}_{ij}(\mathbf{u}) + \boldsymbol{\alpha}_\mathbf{i} \cdot \mathbf{X}_{\mathrm{ij}}(\mathbf{u}) + e_{ij}(\mathbf{u}), \mathbf{u} \in \mathfrak{D} \subset \Re^2, \qquad (5)$$

where $\log P_{ij}(\mathbf{u})$ and $\log \breve{S}_{ij}(\mathbf{u})$ represent natural logarithm of productivity and relative species richness (calculated from actual species richness and the maximal species richness of the training set) of plot i in the jth training set at point locations $\mathbf{u}$, respectively. The model was derived from the niche–efficiency model, and θ corresponds to the elasticity of substitution ([31]). $\boldsymbol{\alpha}_\mathbf{i} \cdot \mathbf{X}_{\mathrm{ij}}(\mathbf{u}) = \alpha_{i0} + \alpha_{i1} \cdot x_{ij1} + \ldots + \alpha_{in} \cdot x_{ijn}$ represents n covariates and their coefficients (Fig. 6 and Table 1).

To account for potential spatial autocorrelation, which can bias tests of significance due to the violation of independence assumption and is especially problematic in large-scale forest ecosystem studies ([60], [61]), we incorporated a spherical variogram model ([62]) into the residual term $e_{ij}(\mathbf{u})$. The underlying geostatistical assumption was that across the world BPR is a second-order stationary process—a common geographical phenomenon in which neighboring points are more similar to each other than they are to points that are more distant ([64]). In our study, we found strong evidence for this gradient (Fig. 7), indicating that observations from nearby GFB plots would be more influential than plots that are farther away. The positive spherical semivariance curves estimated from a large number of bootstrapping iterations indicated that spatial dependence increased as plots became closer together.

The aforementioned geostatistical nonlinear mixed-effects model was integrated into random forest analysis ([50]) by means of model selection and estimation. In the model selection process, random forest was employed to assess the contribution of each of the candidate variables to the dependent variable $\log P_{ij}(\mathbf{u})$, in terms of the amount of increase in prediction error as one variable is permuted while all the others are kept constant. We used the randomForest package ([65]) in R to obtain importance measures for all the covariates to guide our selection of the final variables in the geostatistical nonlinear mixed-effects model, $\mathbf{X}_{\mathrm{ij}}(\mathbf{u})$. We selected stand basal area (G), temperature seasonality (T_3), annual precipitation (C_1), precipitation of the warmest quarter (C_3), potential evapotranspiration (PET), indexed annual aridity (IAA), and plot elevation (E) as control variables since their importance measures were greater than the 9 percent threshold (Fig. 6) preset to ensure that the final variables accounted for over 60 percent of the total variable importance measures.

For geospatial random forest analysis of BPR, we first selected control variables based on the variable importance measures derived from random forests ([50]). We then evaluated the values of elasticity of substitution ([32]), which are expected to be real numbers greater than 0 and less than 1, against the alternatives, i.e., negative BPR (H_{01}: θ < 0), no effect (H_{02}: θ = 0), linear (H_{03}: θ = 1), and convex positive BPR (H_{04}: θ > 1). We

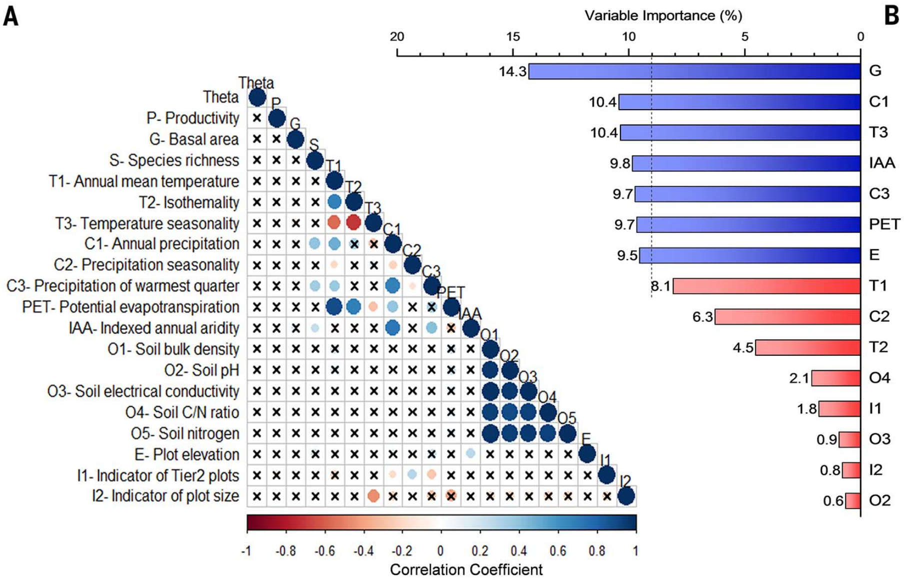

Fig. 6. Correlation matrix and importance values of potential variables for the geospatial random forest analysis. (**A**)There were a total of 15 candidate variables from three categories, namely plot attributes, climatic variables, and soil factors (a detailed description is provided in Table 1). Correlation coefficients between these variables were represented by sizes and colors of circles, and "×" marks coefficients not significant at α = 0.05 level. (**B**) Variable importance (%) values were determined by the geospatial random forest (Materials and methods). Variables with importance values exceeding the 9% threshold line (blue) were selected as control variables in the final geospatial random forest models. Elasticity of substitution (coefficient), productivity (dependent variable), and species richness (key explanatory variable) were not ranked in the variable importance chart because they were not potential covariates.

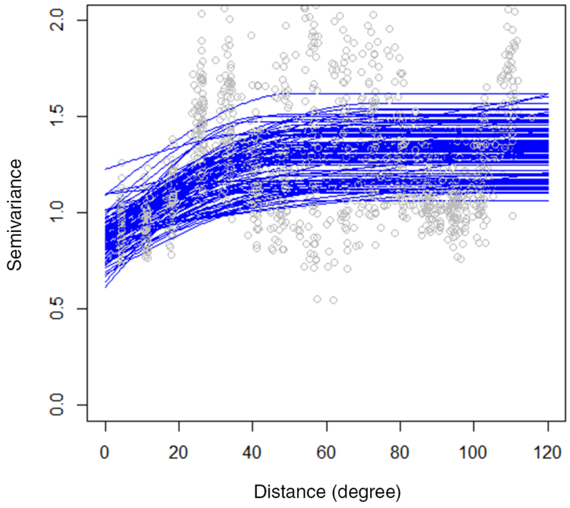

Fig. 7. Semivariance and estimated spherical variogram models (blue curves) obtained from geospatial random forest in relation to Š. Gray circles, semivariance; blue curves, estimated spherical variogram models. There was a general trend that semivariance increased with distance; spatial dependence of θ weakened as the distance between any two GFB plots increased. The final spherical models had nugget = 0.8, range = 50 degrees, and sill = 1.3. To avoid identical distances, all plot coordinates were jittered by adding normally distributed random noises.

Table 2. Parameters of the *global* geospatial random forest model in 10,000 iterations of 500 randomly selected (with replacement) GFB plots. Mean and SE of all the parameters were estimated by using bootstrapping. Effect sizes were represented by the Akaike information criterion (AIC), Bayesian information criterion (BIC), and generalized R^2 (*G-R*^{2}). Const, constant.

				Coefficients									
	Loglik	*AIC*	*BIC*	*G-R*^{2}	*const*	θ	*G*	*T3*	*C1*	*C3*	*PET*	*IAA*	*E*
Mean	−761.41	1546.71	1597.08	0.354	3.816	0.2625243	0.014607	−0.000106	0.001604	0.001739	−0.002566	−0.000134	−0.000809
SE	0.54	1.10	1.13	0.001	0.011	0.0009512	0.000039	0.000001	0.000008	0.000008	0.000009	0.000001	0.000002
Iteration													
1	−756.89	1537.78	1588.35	0.259	4.299	0.067965	0.014971	−0.000100	0.002335	0.001528	−0.003019	−0.000185	−0.000639
2	−801.46	1626.91	1677.49	0.281	3.043	0.167478	0.018232	−0.000061	0.000982	0.002491	−0.001916	−0.000103	−0.000904
3	−768.71	1561.41	1611.99	0.357	5.266	0.299411	0.008571	−0.000145	0.002786	0.002798	−0.003775	−0.000258	−0.000728
4	−775.19	1574.37	1624.95	0.354	4.273	0.236135	0.016808	−0.000126	0.001837	0.003755	−0.003075	−0.000182	−0.000768
5	−767.66	1559.32	1609.89	0.248	2.258	0.166024	0.018491	−0.000051	0.000822	0.002707	−0.001575	−0.000078	−0.000553
6	−773.76	1571.52	1622.10	0.342	3.983	0.266962	0.018675	−0.000113	0.001372	0.001855	−0.002824	−0.000101	−0.000953
7	−770.26	1564.53	1615.10	0.421	4.691	0.353071	0.009602	−0.000127	0.002390	−0.001151	−0.003337	−0.000172	−0.000441
2911	−778.21	1580.43	1631.00	0.393	3.476	0.187229	0.020798	−0.000069	0.001826	0.001828	−0.002695	−0.000135	−0.000943
2912	−755.35	1534.71	1585.28	0.370	2.463	0.333485	0.013165	−0.000005	0.001749	0.000303	−0.002447	−0.000119	−0.000223
2913	−800.52	1625.03	1675.61	0.360	4.526	0.302214	0.021163	−0.000105	0.001860	0.001382	−0.003207	−0.000166	−0.000974
2914	−725.89	1475.78	1526.36	0.327	2.639	0.324987	0.013195	−0.000057	0.001322	0.000778	−0.001902	−0.000080	−0.000582
2915	−753.64	1531.28	1581.85	0.324	4.362	0.202992	0.014003	−0.000146	0.001746	0.002229	−0.002844	−0.000143	−0.000750
2916	−796.75	1617.50	1668.08	0.307	3.544	0.244332	0.010373	−0.000118	0.002086	0.002510	−0.002667	−0.000152	−0.000650
2917	−746.88	1517.77	1568.34	0.348	4.427	0.290416	0.008630	−0.000107	0.002203	−0.000314	−0.002770	−0.000155	−0.000945
9997	−775.08	1574.17	1624.74	0.313	1.589	0.193865	0.012525	−0.000056	−0.000589	0.000550	−0.000066	−0.000155	−0.000839
9998	−781.20	1586.40	1636.98	0.438	5.453	0.412750	0.014459	−0.000169	0.002346	0.002175	−0.003973	−0.000117	−0.000705
9999	−734.72	1493.43	1544.01	0.387	4.238	0.211103	0.013415	−0.000118	0.001896	0.002450	−0.002927	−0.000076	−0.000648
10000	−776.14	1576.28	1626.86	0.355	2.622	0.468073	0.015632	−0.000150	−0.000093	0.001151	−0.000756	−0.000019	−0.000842

examined all the coefficients by their statistical significance and effect sizes, using Akaike information criterion (AIC), Bayesian information criterion (BIC), and the generalized coefficient of determination (66).

Global analysis

For the global-scale analysis, we calibrated the nonlinear mixed-effects model parameters (θ and α's) using training sets of 500 plots randomly selected (with replacement) from the GFB global dataset according to the bootstrap aggregating (bagging) algorithm. We calibrated a total of 10,000 models based on the bagging samples, using our own bootstrapping program and the nonlinear package nlme (63) of R, to calculate the means and standard errors of final model estimates (Table 2). This approach overcame computational limits by partitioning the GFB sample into smaller subsamples to enable the nonlinear estimation. The size of training sets was selected based on the convergence and effect size of the geospatial random forest models. In pilot simulations with increasing sizes of training sets (Fig. 8), the value of elasticity of substitution (32) fluctuated at the start until the convergence point at 500 plots. Generalized R^2 values declined as the size of training sets increased from 0 to 350 plots, and stabilized at around 0.35 as training set size increased further. Accordingly, we selected 500 as the size of the training sets for the final geospatial random forest analysis. Based on the estimated parameters of the global model (Table 2), we analyzed the effect of relative species richness on global forest productivity with a sensitivity analysis by keeping all the other variables constant at their sample means for each ecoregion.

Mapping BPR across global forest ecosystems

For mapping purposes, we first estimated the current extent of global forests in several steps. We aggregated the "treecover2000" and "loss" data (67) from 30 m pixels to 30 arc-second pixels (~1 km) by calculating the respective means. The result was ~1 km pixels showing the percentage forest cover for the year 2000 and the percentage of this forest cover lost between 2000 and 2013, respectively. The aggregated forest cover loss was multiplied by the aggregated forest cover to produce a single raster value for each ~1 km pixel representing a percentage forest lost between 2000 and 2013. This multiplication was necessary since the initial loss values were relative to initial forest cover. Similarly, we estimated the percentage forest cover gain by aggregating the forest "gain" data (67) from 30 m to 30 arc-seconds while taking a mean. Then, this gain layer was multiplied by 1 minus the aggregated forest cover from the first step to produce a single value for each ~1 km pixel that signifies percentage forest gain from 2000–2013. This multiplication ensured that the gain could only occur in areas that were not already forested. Finally, the percentage forest cover for 2013 was computed by taking the aggregated data from the first step (year 2000) and subtracting the computed loss and adding the computed gain.

We mapped productivity *P* and elasticity of substitution (32) across the estimated current extent of global forests, here defined as areas with 50 percent or more forest cover. Because GFB ground plots represent approximately 40 percent of the forested areas, we used universal kriging (62) to estimate *P* and θ for the areas with no GFB sample coverage. The universal kriging models consisted of covariates specified in Fig. 6B and a spherical variogram model with parameters (i.e., nugget, range, and sill) specified in Fig. 7. We obtained the best linear unbiased estimators of *P* and θ and their standard error in relation to Š across the current global forest extent with the *gstat* package of R (68). By combining θ estimated from geospatial random forest and universal kriging, we produced the spatially continuous maps of the elasticity of substitution (Fig. 3B) and forest productivity (fig. S1) at a global scale. The effect sizes of the best linear unbiased estimator of θ (in terms of standard error and generalized R^2) are shown in Fig. 5. We further estimated percentage and absolute decline in worldwide forest productivity under two scenarios of loss in tree species richness— low (10% loss) and high (99% loss). These levels represent the productivity decline (in both percentage and absolute terms) if local species richness across the global forest extent would decrease to 90 and 1 percent of the current values, respectively. The percentage decline was calculated based on the general BPR model (Eq. 1) and estimated worldwide spatially explicit values of the elasticity of substitution (Fig. 3B).

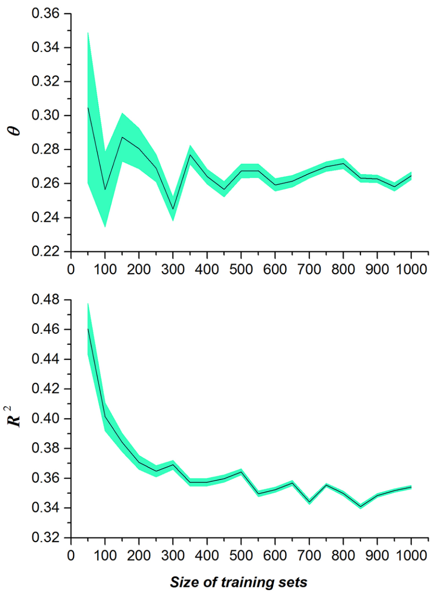

Fig. 8. Effect of the size of training sets used in the geospatial random forest on estimated elasticity of substitution (θ) and generalized R^2 in relation to Š. Mean (solid line) and SE band (green area) were estimated with 100 randomly selected (with replacement) training sets for each of the 20 size values (between 50 and 1000 GFB plots, with an increment of 50).

The absolute decline was the product of the worldwide estimates of primary forest productivity (fig. S1) and the standardized percentage decline at the two levels of biodiversity loss (Fig. 4A).

Economic analysis

Estimates of the economic value-added from forests employ a range of methods. One prominent recent global valuation of ecosystem services (*69*) valued global forest production [in terms of 'raw materials' (including timber, fiber, biomass fuels, and fuelwood and charcoal] provided by forests (table S1) (*69*) in 2011 at US$ 649 billion (6.49×10^{11}, in constant 2007 dollars). Using an alternative method, the UN FAO (*25*, *26*) estimates gross value-added in the formal forestry sector, a measure of the contribution of forestry, wood industry, and pulp and paper industry to the world's economy, at US$606 billion ($6.06 \times 10^{11}$, in constant 2011 dollars). Because these two reasonably comparable values are directly impacted by and proportional to forest productivity, we used them as bounds on our coarse estimate of the global economic value of commercial forest productivity, converted to constant 2015 US$ based on the US consumer price indices (*70*, *71*). As indicated by our global-scale analyses (Fig. 4A), a 10 percent decrease of tree species richness distributed evenly across the world (from 100% to 90%) would cause a 2.1 to 3.1 percent decline in productivity, which would equate to US$13–23 billion per year (constant 2015 US$). For the assessment of the value of biodiversity in maintaining forest productivity, a drop in species richness from the current level to one species would lead to 26–66% reduction in commercial forest productivity in the biomes that contribute substantially to global commercial forestry (fig. S4), equivalent to 166–490 billion US$ per year (1.66×10^{11} to 4.90×10^{11}, constant 2015 US$, calculated by multiplying the foregoing economic value-added from FAO and the other study by 26 and 66%, respectively.) Therefore, we estimated that the economic value of biodiversity in maintaining commercial forest productivity worldwide would be 166 billion to 490 billion US$ per year.

We held the total number of trees, global forest area and stocking, and other factors constant to estimate the value of productivity loss solely due to a decline in tree species richness. As such, these estimates did not include the value of land converted from forest and losses due to associated fauna and flora decline or forest habitat reduction. This estimate only reflects the value of biodiversity in maintaining commercial forest productivity that contributes directly to forestry, wood industry, and pulp and paper industry, and does not account for other values of biodiversity, including potential values for climate regulation, habitat, water flow regulation, genetic resources, etc. The total global value of biodiversity could exceed this estimate by orders of magnitudes (*41*, *42*).

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SUPPLEMENTARY MATERIALS

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Publication V

Climate change and mixed forests: how do altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech?

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RESEARCH PAPER

Climate change and mixed forests: how do altered survival probabilities impact economically desirable species proportions of Norway spruce and European beech?

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Abstract

· ***Key message*** **Economic consequences of altered survival probabilities under climate change should be considered for regeneration planning in Southeast Germany. Findings suggest that species compositions of mixed stands obtained from continuous optimization may buffer but not completely mitigate economic consequences. Mixed stands of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) (considering biophysical interactions between tree species) were found to be more robust, against both perturbations in survival probabilities and economic input variables, compared to block mixtures (excluding biophysical interactions).**

· ***Context*** Climate change is expected to increase natural hazards in European forests. Uncertainty in expected tree mortality and resulting potential economic consequences complicate regeneration decisions.

· ***Aims*** This study aims to analyze the economic consequences of altered survival probabilities for mixing Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) under different climate change scenarios. We investigate whether management strategies such as species selection and type of mixture (mixed stands vs. block mixture) could mitigate adverse financial effects of climate change.

· ***Methods*** The bio-economic modelling approach combines a parametric survival model with modern portfolio theory. We estimate the economically optimal species mix under climate change, accounting for the biophysical and economic effects of tree mixtures. The approach is demonstrated using an example from Southeast Germany.

· ***Results*** The optimal tree species mixtures under simulated climate change effects could buffer but not completely mitigate undesirable economic consequences. Even under optimally mixed forest stands, the risk-adjusted economic value decreased by 28%. Mixed stands economically outperform block mixtures for all climate scenarios.

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Contribution of the co-authors C.P., W.F., and T.K. conceived the original concept. S.B. carried out the statistical analysis of tree mortality data. S.F. and F.H. supported with preparation of climate and economic data. C.P. applied statistical analysis to study site and carried out economic analyses. C.P. wrote the manuscript. All others jointly discussed and revised the text of the manuscript.

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This article is part of the topical collection on Forest Adaptation and Restoration under Global Change

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• ***Conclusion*** Our results underline the importance of mixed stands to mitigate the economic consequences of climate change. Mechanistic bio-economic models help to understand consequences of uncertain input variables and to design purposeful adaptation strategies.

Keywords Survival analysis · Value at risk · Climate change · Species mixture · Forest restoration · Portfolio theory

1 Introduction

Tree species selection is a key strategic decision in forest management planning (Cubbage et al. 2007). Regeneration decisions generally depend on silvicultural considerations but will ultimately also be driven by economic considerations. Climate change is expected to change both, silvicultural suitability and expected returns, thus affecting regeneration decisions (Albert et al. 2017; Pukkala 2018; Schou et al. 2015; Yousefpour and Hanewinkel 2016). For Central Europe, models anticipate an increase in the frequency and severity of extreme weather events and resulting forest disturbances, such as wind throws, forest fires, or drought and related pathogen outbreaks (Gardiner et al. 2011; Jandl et al. 2015; Seidl et al. 2017). These developments may particularly affect the economically important Norway spruce (*Picea abies* (L.) Karst., further referred to as spruce), due to its higher susceptibility to hazards, such as drought (Albert et al. 2017), storm, and bark beetle outbreaks (Thiele et al. 2017) compared to broad-leaved species such as the European beech (*Fagus sylvatica* L., further referred to as beech) (Hanewinkel et al. 2011; Neuner et al. 2015). The planting of spruce into mixed stands has been suggested to increase stand resistance (Griess et al. 2012; Pretzsch et al. 2013). Therefore, the need for converting spruce-dominated forests towards less susceptible broad-leaved species is often accentuated (e.g., Teuffel et al. (2005)), while the reduction of spruce stands to extend the area of beech may lead to severe economic losses (Hanewinkel et al. 2010).

In order to quantify and compare the susceptibility of different species or forest types to natural hazards, empiric survival functions have increasingly been used (Griess et al. 2012; Neumann et al. 2017; Neuner et al. 2015; Nothdurft 2013; Staupendahl 2011; Thiele et al. 2017). In Southwest Germany, Neuner et al. (2015) demonstrated that tree survival of spruce under climate change may be increased through species admixture. Using a European-wide data set, and semiparametric survival functions, Neumann et al. (2017) showed the effects of climate variables and variability on disturbance patterns at the European level. While this study is valid for a large range of environmental conditions, it aggregates species to groups. Other, more species-specific studies have been limited to datasets in Southwest Germany (Griess et al. 2012; Neuner et al. 2015; Staupendahl and Zucchini 2011). The derived survival probabilities therefore only cover a limited range of climate conditions which restrict the application of future climate scenarios and potential effects on survival time of different species. The majority of climate change-related studies in forestry focus on silvicultural or yield science aspects, while economic consequences are assessed much less frequently (Thiele et al. 2017; Zubizarreta-Gerendiain et al. 2016). Neuner and Knoke (2017) are among the rare examples assessing the economic consequences of climate change for predefined mixed forest stand types. However, the survival functions used for this study only cover a limited environmental gradient.

Empiric survival functions of tree species have a particular appeal for integration into bio-economic decision models, to account for probability of stand failure (Burkhardt et al. 2014; Deegen and Matolepszy 2015; Staupendahl and Möhring 2011) and to estimate risk costs (Möllmann and Möhring 2017). These studies have mostly focused on adaptation strategies related to optimal rotation periods of single species. However, analyzing regeneration decisions in face of climate change requires the comparison of different species, as well as potential diversification strategies between them.

Portfolio theory following Markowitz (1952, 2010) has been used in forest economics to reflect consequences of tree species diversification, which may reduce risks (usually quantified as the standard deviation of returns) and aid species selection (Brunette et al. 2017; Dragicevic et al. 2016; Knoke et al. 2017). Empiric survival functions have so far occasionally been integrated in such bio-economic models (Griess and Knoke 2013; Neuner and Knoke 2017; Roessiger et al. 2013). Neuner and Knoke (2017) showed that climate change effects were economically less important in changing risks and returns compared to diversification and management strategies such as planting and pruning. This study could, however, only use a small set of predefined tree species mixtures. Investigating desirable species portfolios for different climate scenarios would need to go beyond predefined species mixtures, requiring information on survival probabilities for continuously changing tree species proportions under different climate conditions.

The use of empirical survival probabilities in bio-economic models has great relevance for risk-averse forest owners (Griess and Knoke 2013; Roessiger et al. 2013). Although forest owners consider risks in their decisions (Blennow and Sallnäs 2002; Seidl et al. 2016), the adaptation threshold for changing forest management strategies is still high (Eriksson 2014). This may be attributed to the uncertainty in expected consequences of climate change, which may delay adaptation strategies in regeneration decisions (Schou et al. 2015). A better understanding of the economic effects of altered survival probabilities has the potential of aiding regeneration decisions under climate change, thus avoiding adverse economic consequences for forest owners. Our objective was therefore to analyze the impact of altered survival probabilities on economically driven regeneration decisions, while accounting for economic and biophysical effects of tree species diversification.

In contrast to approaches used in the real options' theory (Schou et al. 2015; Yemshanov et al. 2015) and Bayesian updating (Yousefpour et al. 2014), which build on adaptation through updating information, here, we refer to adaptation in terms of changing tree species composition at the beginning of a forest's production. Once established, species mixtures may not immediately be changed for long periods without the need of carrying out harvesting operations in premature stands. Thus, the regeneration decision, investigated in this study, is a static decision at a defined point in time and based on information currently available. To illustrate the bio-economic approach, we used an example study site from Southeast Germany, focusing on spruce and beech. With this example, we refer to the challenge of supporting regeneration decisions following large-scale wind throw. This question is of high relevance for forest owners and political decision-makers in order to reduce the economic consequences of climate change and to design supportive policies.

For our study site, we investigate the overarching research hypothesis: *Under the adverse effects of climate change on tree survival, mixed forests dominated by beech are economically superior to spruce-dominated forests.* In this context, we also hypothesize that *the type of mixture in which these forests are established, in terms of mixed stands (allowing for interactions between tree species) or block mixture (mixed at forest level, excluding interactions between tree species), does not influence the optimal species composition.*

In order to contribute to this research hypothesis, we combined two key model components, which can be broadly applied to other sites, with a focus on Central Europe: First, we developed a model for analyzing climate effects on tree survival probabilities in Germany. The tree species-specific empiric survival model uses a European dataset and allows for model parametrization with a wide set of climate conditions, thus mimicking potential future climate conditions. This approach goes beyond existing survival modelling so far used in bio-economic models (e.g., Möllmann and Möhring 2017; Neuner and Knoke 2017). This is not only in terms of the extended data base. We also incorporated substantial methodological improvements in variable selection and model fitting using left-truncated and right-censored data—a situation often found in forest inventory. Second, we integrated this novel empiric model into a bio-economic simulation and optimization model, which builds on Monte Carlo Simulation and Portfolio Theory (Griess and Knoke 2013; Neuner and Knoke 2017). Our new and extended bio-economic modelling approach allows us to compare a principally unlimited set of different species proportions (as continuous decision variables) between two different diversification approaches: one excluding and one including biophysical interactions between tree species. The effects of mixture refer to tree survival based on our empiric model. We also account for potential effects on growth and timber quality of stands, while these are not the focus of our study. In summary, we can therefore investigate the influence of future climate scenarios to (1) the economically ideal species proportions and (2) the optimal type of mixture. This simulation-optimization approach also allowed us to (3) investigate the sensitivity of tree species selection on altered survival probabilities compared to other model assumptions, such as planting costs, discount rate, risk attitude, and coefficient of correlation between returns of the two species.

2 Materials and methods

2.1 Deriving survival probabilities under current and future climate

2.1.1 Modelling tree survival

In this study, we build on the parametric survival model for assessing tree survival developed and applied by Staupendahl (2011), Staupendahl and Zucchini (2011), Griess et al. (2012), and Neuner et al. (2015) for Germany. Survival time is assumed to follow the Weibull distribution. The parameters of the distribution and the impact of covariates on survival time are estimated by an Accelerated Failure Time (AFT) model. The probability of survival S at a certain time t, reflecting tree age, can be described by:

$$S(t) = \exp\left[-\left(\frac{t}{\beta}\right)^{\alpha}\right] \text{ with } t \geq 0 \qquad (1)$$

with α being the shape and β being the scale parameter. The shape parameter α represents the development of the hazards over time. According to Staupendahl (2011), values of one express a constant risk over time. Smaller or larger values express a decreasing or increasing hazard rate over time, respectively. Covariates are assumed to increase or decrease survival time and act on the scale parameter β. A detailed description accompanies the results in Table 1 (Appendix). Staupendahl and Möhring (2011) have outlined the advantages of this approach for supporting decision-making in forest management. First, age-dependent survival probability can be directly transferred into the conditional dropout probability of a stand, which has survived until a certain age class. This information is needed for appropriate discounting in discrete time. Second, the function is described by only two parameters compared to, for example, polynomial equations as used by Knoke and Wurm (2006) and Knoke and Seifert (2008).

2.1.2 Data used for parametrization and variable selection

Compared to earlier studies (Griess et al. 2012; Neuner et al. 2015), we use a further extended pan-European dataset on crown condition from Level I (systematic 16 × 16 km grid) and Level II (intensive monitoring sites) plots provided by ICP Forests[1] (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) (ICP Forests 2018). In general, the crown condition of sample trees is recorded annually. In order to identify mortality events, the cause of removal of a tree is an essential information (Eichhorn et al. 2016). Level I data provide this information since 2011. Details on the survey design and methods can be found in UNECE ICP Forests (2016). The dataset was complemented by data from the German Crown Condition Survey provided by the Thünen Institute of Forest Ecosystems (see footnote[1] for data availability and Wellbrock et al. 2018 for description of the dataset), which is available at a denser grid and provides a longer time series as well as more exact information on tree age (see Electronic Supplementary Material (ESM) Tables S1 and S2 and Fig. S1). The dataset is available from the Thünen Institute upon request. Using the pan-European dataset, the model can be fitted based on a wider range of temperature and precipitation factors, which improves the prediction of potential effects of future climate change on tree species survival and its applicability as a "space for time" approach (see also Neumann et al. (2017)). While earlier studies have mostly focused on spruce, here, we also incorporate the effect of climate variables and tree mixture on the survival time of beech.

The set of potential explanatory variables consisted of mixture proportions of the respective species as well as different climate variables taken from the BioClim variables available from the WorldClim database. The freely available dataset (see WorldClim 2018b) provides interpolations of observed climate data, which is representative for the time period 1960–1990 (see Hijmans et al. 2005 for details). We used the highest available resolution of 30 arc-seconds. The available bioclimatic (BioClim) variables were grouped into variables characterizing mean annual temperature or summer temperature, winter temperature, and precipitation (ESM Table S3). In order to prevent high collinearity between explanatory variables (Dormann et al. 2013), only one variable could be selected from each group. The variables could enter the model either as linear effect or as spline, thus accounting for potentially non-linear effects. The models' predictive performance was evaluated with 10-fold cross-validation (relation of data splitting train data: test data = 9: 1). The Brier score (Gerds and Schumacher 2006) was used as a determinant of prediction accuracy and model improvement. Left truncation of data was accounted for, as observation of a tree does not start at germination. In addition, we used a start age of 20 years, since very young trees are underrepresented in the data; this could lead to unrealistic survival probabilities at these ages (Moore 2016). We thus exclude risks in young stands and assume that through appropriate establishment and management techniques, stand establishment is successful.

To the best of our knowledge, this is the first study investigating the effects of tree mixture on both tree species and for a continuous set of mixtures. All analyses were carried out using the R programming language and environment (R Core Team 2017) using the packages "survival" (Therneau and Grambsch 2001) and "eha" (Broström 2015).

2.2 Economic analysis

2.2.1 Definition of alternatives

The aim of our study was not only to compare two mutually exclusive alternatives, made up by either planting tree species A or B (in our case spruce or beech), but also to allow for a mix of species. Consequently, the percentages forming the actual tree species mixture have not been predefined. We contrasted the following two types of mixtures: (1) *block mixture:* Following Knoke and Seifert (2008), we assumed that tree species were planted in large blocks, which may be mixed at the enterprise level. Biophysical interactions between tree species were excluded. Growth and survival thus correspond to that of monospecies stands. (2) *Mixed stands:* Here, we assumed a mixture of small species cohorts (groups of ~ 1000 m^2) to be within the stand, following Knoke and Seifert (2008). Biophysical interactions between tree species in mixed stands were assumed to affect stand resistance in accordance with results of our survival model (results will be described in "Plausible ranges of survival probabilities"). Mixing the two species within a stand was furthermore assumed to affect volume growth and wood quality. Here, we used the assumptions derived from Knoke and Seifert (2008) as applied in Griess and Knoke (2013) and Neuner and Knoke (2017). While spruce benefits from admixture with beech, beech suffers from a slight decrease in quality (ESM Table S8). Taken together, the effects on volume growth and wood quality lead to an increase in (nominal) returns from wood harvesting by up to + 15% for spruce and a decrease for beech of up to − 10% (ESM Table S8).

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[1] Data is provided upon request via the Programme Co-ordinating Centre at the Thünen Institute of Forest Ecosystems in Eberswalde, Germany (see icp-forests.net/data-requests).

2.2.2 Modern portfolio theory for deriving economically optimal species compositions

Here, we built on the general mean-variance analysis, which compares not only expected returns but also risks of different investments, based on statistical considerations (Markowitz 1952; Markowitz and Blay 2014). Given that expected returns of assets (e.g., investment in different tree species) are not perfectly correlated, diversification will reduce the standard deviation of the portfolio's return. Diversification can be achieved by assigning different weights to individual asset returns. In the context of silvicultural and land-use decisions, this translates into an allocation of forest area (or shares of area of the forest enterprise) for different tree species (Brunette et al. 2017; Dragicevic et al. 2016; Macmillan 1992). Following portfolio theory, the decision-maker would exclusively select "efficient" tree species portfolios. These are defined as combinations of assets which give the highest return for a given level of risk. The accepted level of risk, in terms of standard deviation of return, has to be estimated and depends on the individual risk attitude. Among a range of options in portfolio selection (Elton et al. 2014), the Value at Risk (VaR) (Jorion 2009) has frequently been used in forest management decisions, to illustrate risk aversion of forest (Couture et al. 2016; Hahn et al. 2014; Härtl et al. 2016) and land owners (Estrada et al. 2011; Wan et al. 2015) and to select a specific "optimal forest composition." Following the original ideas of Kataoka (1963), the VaR is a downside risk measure, which calculates the expected portfolio return at a specified quantile (we used 5%) at the undesirable (here left) tail of the return distribution. It can be interpreted as the return, which is exceeded with a probability of 95%. We used the maximization of this criterion to identify economically optimal tree species compositions for block mixtures and mixed stands under current and expected future climate conditions.

Following the notation by Elton et al. (2014), the $\mathrm{VaR_p}$ is estimated as

$$\mathrm{VaR_p} = E(\mathrm{R_p}) - z_\varphi \times s_\mathrm{p} \tag{2}$$

subject to $E(R_\mathrm{p}) \sim N(\mu; \sigma^2)$

With $E(R_\mathrm{p})$ being the expected portfolio return, z_φ is a constant derived from the Gaussian normal distribution ($N(\mu; \sigma^2)$), depending on the quantile of the distribution to be considered. We used z_φ of 1.65 for a 5% shortfall probability φ (corresponding to the 95% quantile). For block mixtures, $E(R_\mathrm{p})$ can be calculated as the weighted mean of individual returns of the assets i and j (in our example returns of tree species A and B) and their standard deviation s_p is estimated by:

$$\begin{aligned} s_\mathrm{P} &= \sqrt{\sum_i \sum_j w_i w_j \mathrm{cov}_{ij}} \\ &= \sqrt{w_\mathrm{A}^2\, s_\mathrm{A}^2 + w_\mathrm{B}^2\, s_\mathrm{B}^2 + 2\, w_\mathrm{A} w_\mathrm{B} \mathrm{cov}_\mathrm{A,B}} \end{aligned} \tag{3}$$

subject to

$$\begin{aligned} & w_\mathrm{A} + w_\mathrm{B} = 1; w_\mathrm{A}, w_\mathrm{B} \geq 0 \\ & \mathrm{cov}_\mathrm{A,B} = k_\mathrm{A,B} s_\mathrm{A} s_\mathrm{B} \end{aligned}$$

with w_A and w_B being the weight (i.e., area) assigned to tree species and $k_\mathrm{A,B}$ being the coefficients of correlation between returns of the two tree species. For mixed stands, returns and risks were directly simulated (see below) for a range of mixtures between spruce proportions (in terms of stand area) of 10 to 90% in 10 percentage point increments.

2.2.3 Deriving return distributions

Frequency distributions of return ($E(R)$) were estimated by means of Monte Carlo simulation (MCS) and 10,000 iterations, incorporating tree and mixture specific survival probabilities and timber price fluctuations. This approach follows the study by Neuner and Knoke (2017). Production period was divided into age classes with a width of 10 years. Simulation began at age 0, assuming bare land, reflecting the assumed situation at the example site and following the basic assumptions of Faustmann for the Land Expectation Value (LEV) (Faustmann 1849). The respective survival probability derived from the statistical model was translated into conditional dropout probability (according to Staupendahl and Möhring (2011)), which was then implemented into the simulation through a binomial distribution of failure or no failure at the end of each age class (Griess and Knoke 2013). In the case of undamaged stands, returns from regular thinning and regular harvest (at end of rotation period T) were simulated for each point in time t. In case of a simulated hazard, return from timber sales was reduced by 50% according to Dieter et al. (2001). Immediate replanting of stands was simulated and age was set to 0, which meant that the simulation run stopped and a new simulation run (i.e., rotation) started. Wood price fluctuations were integrated via bootstrapping using historical timber prices (described in more detail below).

In our analysis, expected portfolio return $E(R_\mathrm{p})$ is represented by the LEV, which corresponds to a net present value (NPV) accumulated over an infinite time horizon. Following Griess and Knoke (2013) and Clasen et al. (2011), the LEV of the simulation run i (LEV_i) was calculated as the sum of the NPV of the simulated individual rotation (NPV_i) and the appropriately discounted mean LEV of the future rotations ($\overline{\mathrm{LEV}}$) (Eq. 4).

$$\mathrm{LEV}_i \ = \mathrm{NPV}_i \ \overline{+\mathrm{LEV}}\cdot \mathrm{q}^{-T_i} \tag{4}$$

with

$$\overline{\mathrm{LEV}} = \overline{\mathrm{NPV}}\cdot \frac{q^{\overline{T}}}{q^{\overline{T}}-1}$$

$$q = (1+r); \overset{\hat{E}}{r}\,0$$

NPV_i is calculated as the sum of the discounted net cash flows in each year over the simulated rotation length T_i. T_i corresponds to the planned rotation time T or the time when the simulation is stopped, due to failure. To account for the fact that replanting of the subsequent forest generation is carried out earlier in case of failure, an average expected LEV of future generations (i.e., $\overline{\mathrm{LEV}}$) was calculated. For deriving $\overline{\mathrm{LEV}}$, the average $\overline{\mathrm{NPV}}$ for 10,000 simulated rotations and the corresponding average rotation lengths $\overline{T}$ until hazard occurred was estimated. $\overline{\mathrm{LEV}}$ was added to NPV_i and discounted according to the elapsed time period when simulation stopped, using discount rate r. In accordance with Deegen and Matolepszy (2015), we used a constant discount rate of 1.5% for the baseline assumption. To allow for a simpler interpretation, results are presented as yearly land rent (annuity) estimated through multiplying LEV_i by the discount rate r.

2.3 Example study site and data

We selected the district of Freyung in the Bavarian forest, located in the Southeast of Germany as an example site for our analysis. On August 18 of 2017, the region experienced an extreme storm event ("Kolle"). Local authorities estimated an amount of 2.3 Mio m^3 of storm-damaged timber and offered 60 Mio € of financial help to affected forest owners (BayStMELF 2017). The crucial question arising in such situations pertains to which tree species to incentivize and recommend to affected forest owners. The application example represents a typical situation of forest restoration in Central Europe, whereas developed methods are transferable to other regions.

2.3.1 Climate data

We used our statistical survival model to simulate economic consequences and silvicultural adaptation strategies for a range of climate scenarios. We used climate data from the freely accessible WorldClim database (version 1.4). Today's climate is characterized as average of the time period 1960–1990 (Hijmans et al. 2005; WorldClim 2018b). Future climate scenarios are based on the Max-Planck-Institute Earth System Model at base resolution (MPI-ESM-LR). For this climate model, the Representative Concentration Pathway (RCP) scenarios 2.6, 4.5, and 8.5 are available for the period 2061–2080 (ESM Table S4) (WorldClim 2018a).The climate projections are downscaled and bias corrected using WorldClim 1.4 as baseline "current" climate and also provided in the WorldClim database. We used the highest available spatial resolution of 30 s (~ 1 km).

2.3.2 Forest data

We used growth simulation and cost estimates for spruce and beech available from Clasen et al. (2011) in the Bavarian Forest region (ESM Tables S5 and S6). Tree growth was originally simulated by Clasen et al. (2011) using the single-tree-based stand simulator SILVA (version 2.2) (Pretzsch et al. 2002) (see ESM Table S5). Thinning was carried out at a fixed amount in each decade according to results from the growth simulator (Table S5). Hence, in accordance with the survival model, when referring to "mortality," we only refer to those trees, which would not have regularly been harvested during thinning or at the end of the planned rotation period. We used updated planting costs by data from Roessiger et al. (2013) and Messerer et al. (2017) reporting moderate values of 2000 € ha^{-1} for spruce and 3000 € ha^{-1} for beech. The use of potential natural regeneration in future generations, when rotation period reaches adequate tree age, was taken into account by using decreasing planting costs for the following rotation cycle (ESM Table S7). Planned rotation length was set at 120 years for beech and 90 for spruce according to the optimal rotation age of a risk-free consideration of annualized LEV at a constant discount rate of 1.5% (ESM Fig. S2). Resulting nominal net returns (excluding price fluctuations) for the planned rotation and in case of stand failure are summarized in the ESM Table S6. Timber price fluctuations were updated using the price quotients published by Messerer et al. (2017) for the period of 1975 to 2014.

2.4 Sensitivity analysis

While climate change is hypothesized to affect economic tree species selection, we also aimed to compare the magnitude of change in the optimized species composition to other important economic drivers. These include investment costs, Pearson correlation between returns, discount rate, and the assumed attitude towards risks. We carried out a sensitivity analysis by varying the input variables by up to ± 75% compared to the "baseline assumption," which refers to current (constant) climate conditions and assumptions described above. Please note that for alterations in the correlation coefficient, we tested absolute values of $k_{\mathrm{A,B}}$ between ± 0.75 rather than relative changes.

3 Results

3.1 Plausible ranges of survival probabilities

Based on the European dataset, survival probabilities of spruce were best described by the climate variables "sum of precipitation in the warmest quarter" and "mean temperature of warmest quarter," as well as the share of spruce in the stand (see Table 1 for coefficients). For beech, the explanatory variables "maximum temperature of the warmest month" and the "minimum temperature of the coldest month" were chosen according to the selection procedure. Since the effect of tree mixtures on tree survival is one of the key questions of our research, we also included the share of beech in the stand as an explanatory variable. The inclusion of this variable only marginally increased the Brier score by a value of 0.001.

Both species showed a positive effect of admixture on tree survival (Table 1). The shape parameter α of the Weibull distribution was similar for both tree species with 1.27 for beech and 1.30 for spruce (ESM Table S9), both indicating an increase in hazard rate with age. Being rather close to 1.0, the shape parameter reflects that hazard increases on a diminishing scale. Given the climate variables of our study site, we found that the survival probability of beech remained considerably higher than that of spruce. The probability of a tree in pure stands to still being alive at age 100 ($S(100)$) was 0.49 for spruce and 0.80 for beech, under a current climate at the study site (see lowest lines in Fig. 1 and ESM Table S9).

Climate change affected both species at a similar magnitude. Yet, due to the higher survival of beech under current climate, its absolute survival rates still remained at a much higher level compared to spruce. For example, under the most pessimistic climate change scenario (RCP 8.5), $S(100)$ dropped down to 0.37 and 0.69 for pure spruce and beech stands, respectively (Fig. 1 and ESM Table S9). Given the stabilizing effect of species mixtures, our model suggests that the survival probability of spruce trees could still be maintained at today's level when admixing pure spruce stands with 40% beech. The level of uncertainty in predicting the effect of climate variables on tree survival was much higher for beech than for spruce, particularly for temperature-related variables (Table 1). This might be because events (i.e., occurrence of death) in the data set of beech are not so closely related to temperature (e.g., storm), whereas most dominant disturbance agents of spruce such as bark beetle show a stronger relation with temperature (Seidl et al. 2014).

3.2 Effect of climate change on economically optimal block mixtures

For our example site and applying the average expected survival rates under today's conditions, we obtained expected annuities of 117 (± 44) € ha^{-1} year^{-1} for pure spruce and 39 (± 22) € ha^{-1} year^{-1} for pure beech stands, respectively. Despite its higher survival probabilities, beech had a much lower return and higher coefficient of variation (67%) compared to spruce (38%). This may be attributed to the much higher growth volume of spruce (ESM Table S8), its shorter rotation cycle, and lower planting costs compared to beech. Consequently, pure spruce stands would also give a much higher VaR (43 € ha^{-1} year^{-1}) compared to pure beech stands (2 € ha^{-1} year^{-1}) (see gray solid line in Fig. 2). Even when allowing the model to mix pure spruce and beech stands, it would still choose to dedicate the entire regeneration area to pure spruce stands. Hence, economic benefits of diversification from selling to various timber markets could not compensate for the high VaR of pure spruce stands (see gray circle in Fig. 2 and ESM Table S10).

The consideration of the effect of climate change through altered survival probabilities only slightly reduced the economically optimal spruce proportion for a risk-averse forest owner (see black solid line and black circle in Fig. 2 for RCP 8.5 scenario). For the moderate RCP 2.5 scenario, the highest VaR was achieved by planting pure spruce stands, while excluding biophysical interactions. Only under the RCP 4.5 scenario, would the economically optimal spruce proportion in a block mixture be reduced to 95% and further down to 81% under the RCP 8.5 scenario (Figs. 2 and 3a). The respective maximum VaR, represented here by the assumed objective function of the forest owner, was reduced by 18, 27, and 46% for the RCP scenarios 2.5, 4.5, and 8.5, respectively (circles in Fig. 3b). Expected portfolio return of the optimized species portfolios would decrease by up to 26% (circles in Fig. 3c).

This result reveals that even if the forest owner followed economically optimal adaptation measures to climate change by adjusting species composition, he would most likely still experience financial losses. We also found that for a block mixture design, the economically optimized regeneration planning would still be clearly dominated by spruce. This finding holds even under the most extreme climate scenario.

3.3 Stabilizing effect of mixed tree stands

The increased survival probabilities found for both species when grown in mixed stands (cf. Fig. 1) resulted in a considerably higher VaR compared to block-wise mixtures (dashed lines in Fig. 2 and triangles in Fig. 3b). Under a constant climate, the VaR of the economically optimal species proportion in the mixed stand design was 19% higher compared to the highest VaR attainable in block mixture (compare dashed gray lines to solid gray lines in Fig. 2). This advantage even increased to up to 57% under the climate change scenarios (Figs. 2 and 3b).

However, despite the stabilizing effect of horizontal heterogeneity, climate change would still affect the forest owner. For

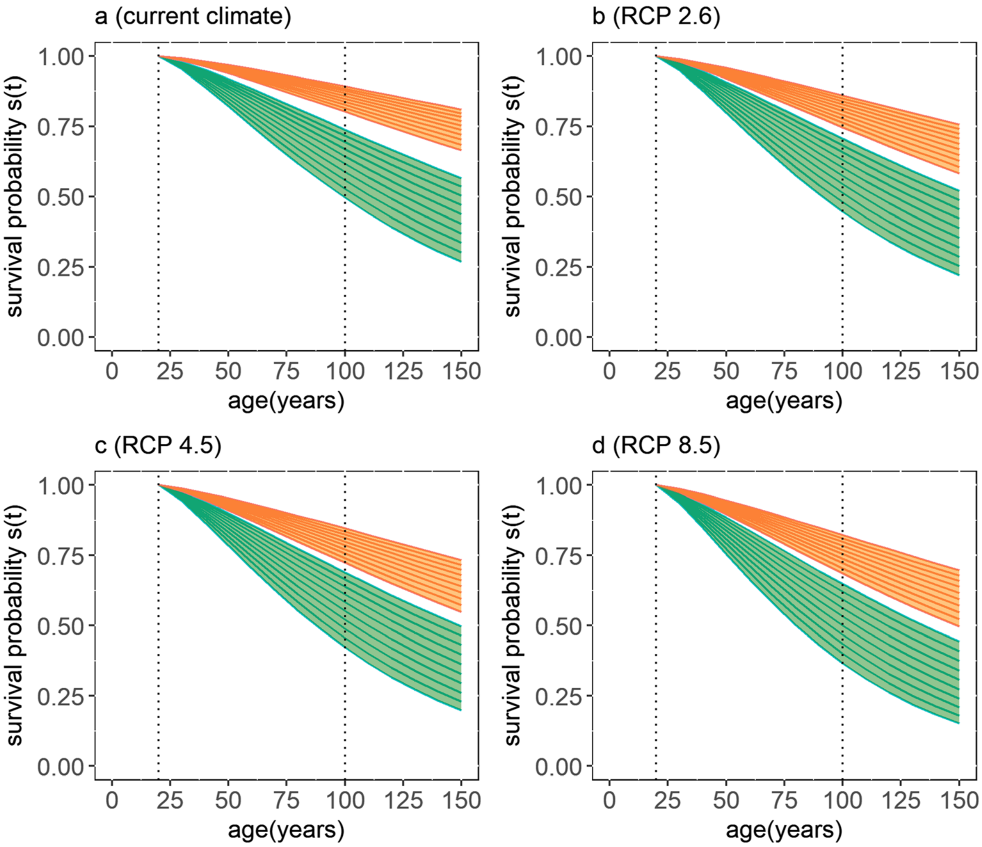

Fig. 1 Survival probabilities of beech (orange) and spruce (green) for the study site under current (**a**) and potential future climate, reflected by RCP 2.6 (**b**), RPC 4.5 (**c**), and RCP 8.5 (**d**) climate scenarios. Lines and shaded areas represent different species compositions in mixed stands, ranging from pure stands (lowest lines) to 10% of the respective species (upper lines) (see also ESM Table S9). Dashed vertical lines display the starting age of our model of 20 years (left line) and the reference age of 100 years, to which we refer as *s*(100) (see also ESM Table S9)

example, here the assumed objective function of the risk-averse forest owner (VaR) would still be reduced by up to 28% (for RCP 8.5) (Fig. 3b). Yet, compared to block mixtures and pure stands, economic consequences could be buffered considerably. The difference in absolute portfolio return between the optimized block mixture and mixed stands also declined with increasing severity of the climate scenario (Fig. 3c and ESM Table S11 for data on all mixtures).

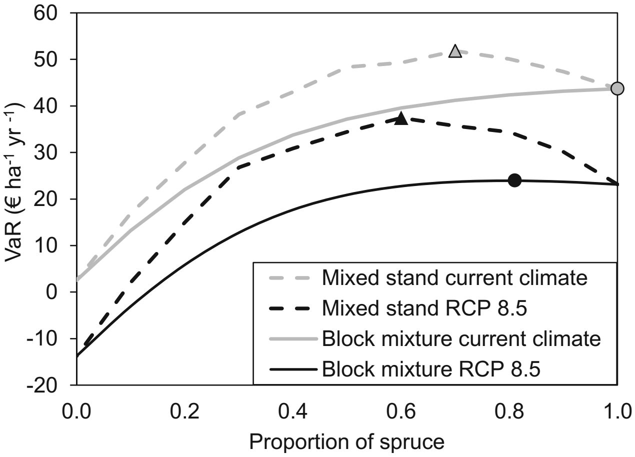

Fig. 2 Value at risk (VaR) under constant (current) climate (gray) and the most severe climate change scenario (RCP 8.5, black) for pure stands of spruce (proportion of spruce = 1) and beech (proportion of spruce = 0), compared to mixtures in blocks (solid lines) and mixed stands (dashed lines). Optimal stand compositions are given by triangles for mixed stands and circles for block mixtures and refer to respective symbols in Fig. 3 (see also ESM Tables S10 and S11)

The economically optimal spruce proportion in mixed tree stands was with 60–70% generally lower compared to the ideal block mixtures (Fig. 2). The effect was consistent for all climate scenarios studied (Fig. 3a). In our model, individual returns of spruce increase with an increasing admixture of beech. This is due to the higher stand resistance associated with lower hazard-induced losses and the shortening of rotation periods. The same effect was found for beech but was less pronounced, due to the various effects of admixture on tree growth and wood quality (see Knoke and Seifert (2008)). Consequently, given the overall higher return of spruce, this species still dominates the species portfolio of mixed stands. Even those mixed stands with spruce proportions larger than that of the optimal portfolio still outcompeted block mixtures. For instance, the VaR of a mixed stand with a share of 90% spruce, under the RCP 8.5 scenario, still gave a 26% higher VaR compared to the optimal block mixture with a lower spruce proportion of 81% (Fig. 2). Thus, if the forest owner seeks to maintain high spruce proportions, establishing mixed stands may be favorable to increase returns, while buffering economic risks. It should also be noted that pure spruce stands still

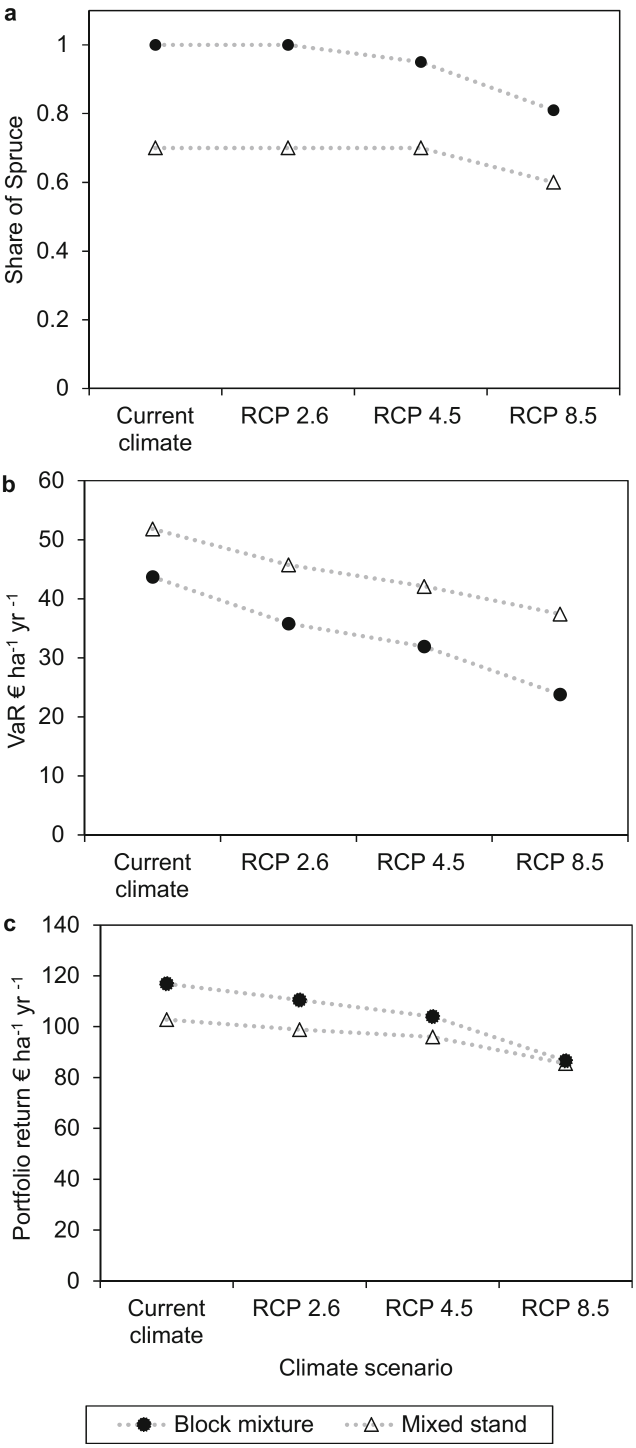

Fig. 3 Effects of climate change on economically optimal species portfolio (**a**), its respective maximized value at risk (VaR) (**b**), and portfolio return (**c**). The optimal forest composition refers to the optimized portfolio weights (see Eq. (3)) for block mixtures (circles) and the simulated tree mixtures with the highest VaR under different climate scenarios (triangles) (see also ESM Tables S11–12). The effect of climate change refers to altered survival probabilities (Fig. 2)

gave the highest expected returns but not the highest VaR, compared to all types of mixtures. This is despite the positive effect of mixture on stand stability and tree growth of spruce. Hence, a risk-neutral profit-oriented person would still chose to plant pure spruce stands even when considering the expected losses, due to stand failure (see ESM Tables S10 and S11).

Figure 3a also shows that species selection in mixed stands was more stable under rather extreme climate change scenarios. The optimal share of spruce decreased by 10 percentage points under the most extreme (RCP 8.5) climate scenario compared to the current climate. In the block mixture, species selection was already affected under the moderate RCP 4.5 scenario. Here, the ideal spruce proportion decreased by 20 percentage points for the RCP 8.5 scenario. Yet, the absolute spruce proportion remained for all scenarios still lower for the mixed stand compared to the block mixture.

Being aware of the high prediction error of climate variables on survival time of beech, we also calculated species portfolios that excluded climate change effects for beech. Under this assumption and applying the most severe climate change scenario to spruce, we found that portfolio composition did not change for mixed stands (60% spruce), while the spruce proportion of block mixture dropped to similar levels of 57%. The ideal share of spruce would only fall below 50% if survival of beech, in terms of $S(100)$ (at constant α), was by 45 percentage points higher than that of spruce. For our model, there was no combination within the different climates that could describe such a difference. Thus, even when considering increasing hazard rates in regeneration decisions, a risk-averse forest owner at our study site would opt for establishing stands that are dominated by the more susceptible tree species.

3.4 Sensitivity analyses

Differences in upfront investment costs are a classic driver of investment decisions. In our sensitivity analysis, changes in the establishment costs of spruce, relative to beech by ± 75% (i.e., ± 1500 €), reduced the share of spruce in optimized block mixtures from 100% to only 50% (Fig. 4). This difference in species selection is much larger compared to the simulated effects of climate change. It should be noted that in our baseline assumption, planting costs of beech are assumed to be by 50% higher compared to that of spruce. A relative increase in costs of spruce establishment compared to beech could result from subsidies for forest conversion towards broad-leaved species.

Establishment costs were also found to be a key decision criterion for selecting the optimal type of mixture. While, for our baseline assumption, mixed stands were shown to give a higher VaR compared to block mixtures, this advantage was reduced when assuming higher

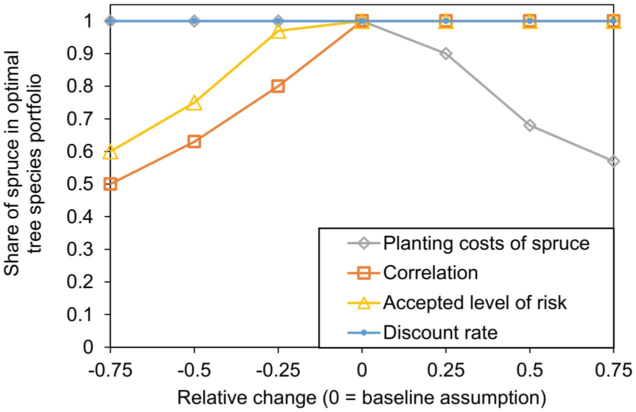

Fig. 4 Sensitivity analysis of further economic drivers of species selection. Results are shown for block mixture. Baseline assumption corresponds to current climate. Absolute values range between 500 and 3500 € ha^{-1} for establishment costs of spruce (while keeping those for beech constant), − 0.75 to + 0.75 for the coefficient of correlation between economic return (i.e., expected annuity) of beech and spruce, 0.4 and 2.6% for the discount rate, and 0.01 to 0.08 for φ (Eq. (2)), representing the accepted level of risk

establishment costs for mixed stands compared to block mixtures. Higher establishment costs could occur, due to the higher complexity, which may result in higher labour costs for stand establishment. In our data example, assuming the planting costs for beech (3000 € ha^{-1}) for all mixed stands clearly reduced their economic advantage (ESM Fig. S3). Under this assumption, pure spruce stands would outcompete mixed stands in terms of VaR. This finding supports the importance of establishment costs in forest investment decisions.

In terms of biophysical interactions, we assume that stand failure, i.e., hazard events for beech and spruce occur independently of each other. Given the anticipated increase in extreme weather events stand failure may become more intensively correlated (e.g., through drought or storm events). When testing a perfect correlation of events (reflected by the equal random number in the simulation process), we found a coefficient of correlation of return of 0.45 compared to 0.006 estimated under the baseline assumption. Thus, the high coefficient of correlation displayed in Fig. 4 might be rather unrealistic and not directly comparable to the relative change of other input variables. Yet, the results demonstrate that under a higher correlation of events, the advantage of having beech in the species portfolio will, by trend, be reduced.

Changing the accepted level of risk by decreasing the accepted shortfall probability from a moderate value of 5% to a very risk-averse value of 1% resulted in a 57% smaller optimal proportion of spruce in the block mixture. A moderate change in discount rate did not alter species selection in the block portfolio, when keeping other assumptions constant. Even under very low discount rates beech still could not compete with spruce in our data example.

We found that the optimal species composition in mixed stands was less sensitive to changes in model assumptions. The optimal spruce proportion did not drop below 60% (under current climate) when increasing establishment costs of spruce by 75% or decreasing shortfall probability to 1% (therefore not shown in Fig. 4). Only for an increase in discount rate to 2.6% did the spruce proportion increase to 80%. This reveals that biophysical interactions dominated species selection in mixed stands, while ideal compositions were less susceptible to other input variables.

4 Discussion

In our study, we follow the suggestion of Littell et al. (2011) for the use of climate change modelling in resource planning, which states that "the role of models […] is not to predict the future exactly, but rather to narrow its possible range to a subset of plausible outcomes that identify the vulnerability of specific resources and suggest appropriate management" (Littell et al. 2011, p. 2). While we do not aim to make exact predictions or give precise recommendations for species proportions, we aim to use statistically backed plausible ranges of survival probabilities to investigate their economic effects on regeneration decisions.

Referring back to the first part of our central hypothesis, our results revealed a rather moderate effect of altered survival probabilities on economically optimal species selection. At our example study site, the more susceptible spruce remained the dominant species, even for the most severe climate change scenario. Given the limited time series available for the pan-European mortality data (ICP Level I and Level II data, ESM Tables S1 and S2) and the inherent assessment errors in the dataset (see also Neuner et al. (2015)), prediction errors on climate change responses are still large. Further uncertainty is due to the prediction of future climate variables by the selected circulation model (Littell et al. 2011), which we did not directly address. The estimated survival rates, particularly those for spruce, are, however, rather pessimistic compared to earlier studies. Examples of reported $S(100)$ values for pure stands (current climate) range from 0.69 (based on a literature review in Germany (Beinhofer 2009)) to modelled values of 0.8 for Southwest Germany (Griess et al. 2012) and 0.9, when applying the model by Neuner et al. (2015) to the study site. We corrected our analysis for left truncation, which may explain the lower level of survival compared to earlier studies. Our estimated values for beech fit well to data compiled by Beinhofer (2009) ($S(100) = 0.889$) and Staupendahl (2011) ($S(100) = 0.82$). The estimated relative effects of climate change are, for both species, also in the range of those found by Nothdurft (2013) (referring to mountainous areas in Southwest Germany) and Neuner et al. (2015). Thus, given the survival probabilities used here, it is rather unlikely that the survival probability of spruce is overestimated in relation to that of beech. By reporting the threshold for which spruce would lose its dominant position, our finding appears robust in face of climate change-related uncertainties.

Expected returns for spruce under climate change are probably rather conservative, as we also excluded further adaptation strategies, such as selection of plant material (Gray and Hamann 2011), thinning concepts, and optimal rotation age, which may not only increase economic performance (Bright and Price 2000; Möllmann and Möhring 2017) but also stand resistance of spruce (Bolte et al. 2009; Jandl et al. 2015). Our dataset suggested a rotation period of 90 years for spruce. Applying shorter rotation periods under the climate change scenarios might increase the economically optimal share of spruce in future tree species portfolios. Hence, the optimal spruce shares for our study site might be slightly underestimated. Future studies could combine both the economic consequences of species diversification and changes in rotation age (see for example Messerer et al. (2017) for a methodological example). Recent studies also suggest an increase in growth performance of spruce under climate change (Gutsch et al. 2016; Thiele et al. 2017), while larger scale species distribution models have anticipated a long-term shift from coniferous to broad-leaved species (Dyderski et al. 2017). We disregarded growth responses to climate variables. However, given the assumptions in our model (based on Clasen (2015)), the cumulative harvested wood volume over a period of 90 years (excluding hazards) was 875 m^3 ha^{-1} for spruce and 453 m^3 ha^{-1} for beech. Thus, in order to compete with spruce, growth volume of beech would have to at least double, given the lower quality and wood price. Yet, the inclusion of growth effects should be considered in further studies, to allow for a trade-off analysis between growth and hazard effects (e.g., Thiele et al. (2017)).

Concerning the second part of our research hypothesis, we found that the type of mixture affected the economically ideal species compositions. Horizontal heterogeneity could also buffer but not completely mitigate the economic consequences of climate change for a risk-averse forest owner. Using the VaR as criterion for economically optimal species composition, mixed stands were more effective in buffering the effects of climate change compared to block mixtures. Yet, in terms of expected returns, pure spruce stands would still outcompete any form of mixture in terms of return for all climate scenarios. Ideal (and thus recommendable) species composition in mixed stands was also more robust in the direction of perturbations in expected survival probabilities compared to that of block mixtures. Thus, mixed stands offer a hedge against uncertainties in future predictions. This finding depends, however, on the biophysical interactions assumed. In our statistical model, the effect of mixture was selected as a linear effect on survival time by the statistical selection procedure, which should be interpreted with caution. Alternatively, Roessiger et al. (2013) assumed that lowering the spruce proportion below 49% would not achieve a more intense stabilization compared to a proportion above this threshold. Our estimated effect of mixture on species resistance appears, however, plausible. For example, Knoke and Seifert (2008) assumed a similar increase in $S(100)$ of spruce from 0.53 in pure stands to 0.81 in mixed stands. Evidence on mixture effects on beech are rare, while available studies point towards positive impacts on stand resistance (Metz et al. 2016; Pretzsch et al. 2010) and no adverse effects on timber quality (Benneter et al. 2018). In our data example, mixed stands would still outcompete block mixtures by 17% in terms of VaR (under constant climate) when excluding the stabilizing effect of species mixture on beech. The assumed effects of mixed stands on timber quality and wood volume hardly influenced the objective function of our analysis. Excluding the factors given in ESM Table S8 led to a slight increase in the VaR of the optimal species portfolio by 2% (53 € ha^{-1} $year^{-1}$), as the assumed negative effects of mixture on timber quality and volume growth of beech are disregarded. This small change did also not affect the optimal species proportions in the mixed stand portfolio. Yet, we found that decisions on the type of mixture will also strongly depend on the differences in establishment costs between them, which have seldom been systematically studied.

Diversification in mixed stands is not restricted to horizontal heterogeneity alone. Vertical heterogeneity was not considered in our study, given our focus on regeneration planning subsequent to a regional storm event. However, fostering uneven-aged forests will also offer advantages in terms of time diversification (Couture et al. 2016; Messerer et al. 2017; Roessiger et al. 2013) and aspects of flexibility—as considered in real option approaches (Schou et al. 2012; Schou et al. 2015), while further increasing stand resistance (Díaz-Yáñez et al. 2017). In our study, we refer to adaptation to climate change by adjusting species selection of future forest generations. This decision is mainly driven by economic considerations and the risk attitude of the decision-maker. This perspective uses a static approach of infinity, meaning that if the forest owner suffers from stand failure, the initially chosen tree composition will still be used for regeneration. This assumption appears plausible as future tree generations partly stem from natural regeneration (see ESM Table S7). However, changing information on climate change may update knowledge and beliefs and change decisions in the future. Using our simulation results for informing a Bayesian simulation approach (Yousefpour et al. 2014, 2017) could be a fruitful field for future research.

We found that economic input parameters, such as establishment costs, discount rates, or correlations, affected species composition at a similar magnitude compared to climate change, thus supporting and extending the findings by Neuner and Knoke (2017). This result should, by no means, undermine the importance of adaptation strategies towards climate change. But, it demonstrates that regeneration strategies for climate-smart forestry should still carefully consider classic drivers of investment decisions, particularly establishment costs. We found that optimal species proportions in mixed stands were more robust towards perturbations in these drivers. Hence, mixed stands might offer an important hedge against both climate and market uncertainty.

In our study, we identified optimal species mixtures according to the VaR criterion. This criterion corresponds to the objective of avoiding situations with very low return expectations. This is a rather conservative measure of portfolio selection, which may be applicable for the management of natural resources (Härtl et al. 2013). In line with classic portfolio theory, the approach is based on the assumption of normally distributed returns, which may not always be met, particularly under the occurrence of rather extreme events (Fasen et al. 2014). It is furthermore a very data-intensive approach, as expected returns, risks, and correlations between alternatives are derived from the Monte Carlo simulation. In situations with scarce data and non-normally distributed returns, robust portfolio optimization techniques may offer an alternative approach (Knoke et al. 2017; Messerer et al. 2017).

Our approach could be further extended and improved by a larger number of species (Brunette et al. 2017), for which survival functions are currently under development. This could substantially change the proportion of spruce for our example site, particularly when including more economically competitive species, such as Douglas fir (Beinhofer and Knoke 2010; Knoke et al. 2017). Furthermore, economic considerations may not be the only drivers of regeneration decisions, while provision of multiple ecosystem services might further support the establishment of mixed stands rather than pure stands or block mixtures (Knoke et al. 2017).

5 Conclusions

The bio-economic modelling approach reveals that survival probabilities are a crucial aspect to consider in regeneration planning. This finding also underlines the economic relevance of empiric tree survival modelling and the importance of continuous tree mortality observations, such as those available from the ICP Forest or the German crown condition databases. Continuing and expanding this monitoring network will improve future bio-economic modelling approaches. Particularly, the effects of stand mixtures on stand resistance are of high economic importance.

Our findings also support current policies towards incentivizing mixed stands. Mixing species may be an important measure to increase forest stability, while also maintaining high shares of economically desirable species. This applies, for example, to spruce in Central Europe with its high importance for the wood-processing industry. Our results also demonstrate that incentives related to establishment costs may impact the forest owner's regeneration decisions more intensively than expectations on increasing natural hazards.

Our approach combines an empiric and mechanistic model and builds on sensitivity analysis. Understanding and communicating the economic consequences of uncertain input factors can help to design purposeful adaptation strategies and regeneration planning.

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Statement on data availability All biophysical and economic input coefficients to reproduce and further apply our bio-economic model are provided in the Electronic Supplementary Material. The original tree mortality data used for parametrization of the statistical model is available from the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (www.icp-forest.net), and climate data is freely available from the WorldClim database (www.worldclim.org). Model codes are available from the authors upon request.

Compliance with ethical standards

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

Appendix

Table 1 Coefficients derived from AFT-fitted Weibull distribution to predict survival probability of spruce and beech based on the European dataset

Covariate	Coefficient	SE
Spruce		
Share of spruce	0.719	0.055
Sum of precipitation of warmest quarter	− 0.001	0.000
Mean temperature warmest quarter	0.066	0.008
$\ln(\beta^a)$	6.229	0.159
$\ln(\alpha)$	0.259	0.020
Beech		
Share of beech	0.577	0.012
Minimum temperature in coldest month	− 0.039	0.016
Maximum temperature warmest month	0.089	0.105
$\ln(\beta^a)$	8.179	0.402
$\ln(\alpha)$	0.241	0.051

Exp(Coefficient) is the acceleration factor. It corresponds to the ratio of survival times to any fixed value of $S(t)$. An acceleration factor greater (less) than one indicates that the covariate decreases (increases) time to death. Thus, a positive coefficient translates to an acceleration factor > 1, i.e., the effect on survival of the respective variable is negative. The entire model written in R language is available from the authors upon request

SE standard error of coefficient

[a] Scale parameter is reparametrized for different values of coefficients using the following formula:

$$\beta_{\text{reparametrized}} = \frac{\beta}{\exp(\text{coef}1\times x1)\times\exp(\text{coef}2\times x2)\times\exp(\text{coef}3\times x3)}$$

where coef denotes the coefficient and x the value of the corresponding explanatory variable. See ESM Table S9 for scale parameters derived for the study site

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