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Friedrich J. Bohn | On the dynamics of temperate forests: quantification of several drivers ...

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Helmholtz Centre for Environmental Research – UFZ
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On the dynamics of temperate forests: quantification of several drivers using forest models and inventories

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ON THE DYNAMICS OF TEMPERATE FORESTS: QUANTIFICATION OF SEVERAL DRIVERS USING FOREST MODELS AND INVENTORIES.

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...über Stock und Stein, durch Sand und Hain, bei Nacht und Sonnenschein...

—Tranquilla Trampeltreu —

Michael Ende

ABSTRACT

Forests fulfil a multitude of functions for human society and within global biogeochemical cycles. One central process of forest dynamics is the accumulation of wood due to the growth of trees. The growth rate of forests is influenced by climate, species diversity and forest structure. For instance, various relationships between productivity and biodiversity have been found in forests. However, the processes underlying these relationships remain unclear and theory struggles to explain them coherently. In addition, increasing temperatures due to climate change influence the wood production of forests. Observations show that some temperate forests increase their productivity due to temperature rise, whereas others reduce their productivity. In this thesis we use national forest inventories, yield tables and a forest gap model (FORMIND) to quantify the influence of climate, species composition and forest structure on aboveground wood production (AWP) and its consequences for forest dynamics.

The forest gap model FORMIND, which includes establishment, competition, growth and mortality processes was initially developed for the tropics. To transfer the model to the temperate zone (Bohn et al., 2014, Chapter 2), we added new processes (budburst for deciduous trees) and extended the climate module, which describes the effects of available soil water and temperature on photosynthesis and respiration. This new version of FORMIND includes eight species of the temperate zone, including common species (beech, spruce and pine) and species, which are discussed for future forest stands (oak, poplar, birch, robinia and ash). We showed that the temperate FORMIND-model reproduces well the annual fluxes of gross primary production, autotrophic respiration and above-ground wood production (AWP).

To analyse the importance of forest structure on diversity-productivity-relationships, we developed the new forest factory approach (Bohn and Huth, 2017, Chapter 3). This approach uses simple construction rules together with the FORMIND forest model to generate 379,170 different forest stands. For each forest stand we simulate one year of forest growth to estimate the annual AWP under the given environmental conditions. The forest stands of the forest factory cover young and old, managed and natural, low and high diverse forests. We also developed the new index Ω_{AWP}, which quantifies how optimal species are distributed regarding productivity within a given forest stand.

The simulation results show that changes in forest structure alter AWP in a much stronger way than changes in species composition. Similar patterns can be observed by analysing 5,054 forest plots of the German National Forest Inventory. If we group the forest stands into nine forest types (forest stands of similar forest structure), we find increasing, decreasing, invariant and even bell-shaped relationships between productivity and diversity. These relationships correspond to those obtained in different field studies. We found that the combination of optimal species distribution, basal area and tree height heterogeneity explain productivity of forests quite well and, for the first time, we could explain the different biodiversity-productivity relationships found in field studies.

We analyse how species composition and forest structure influence the temperature sensitivities of temperate forest productivity, and which forests benefit most from increasing temperatures (Chapter 4). For each forest stand of the forest factory, we estimate annual AWP under 320 climate scenarios (of one year length), which differ in mean annual temperature (MAT) and intra-annual temperature amplitude (Q95). The sensitivity of forest productivity against temperature change is quantified as a relative change of AWP for a 1°C temperature rise (SI_{MAT} & SI_{Q95}).

The results show that temperature sensitivity of forest stands (SI_{MAT} & SI_{Q95}) is mainly driven by Ω_{AWP}, which shows a strong positive influence. Forest height is also important, showing a bell-shaped relationship to temperature sensitivity. Forests of all successional stages benefit from rising temperatures, if Ω_{AWP} is high. In addition, young forest stands with low height, low functional diversity and low tree height heterogeneity display positive temperature sensitivity. For later successional states forest stands, which benefits from rising temperatures, have higher species diversity and tree height heterogeneity.

Based on the forest factory, the new concept of forest model application, this thesis quantifies the influence of species diversity, forest structure and temperature change on forest productivity for the temperate forests. In the future our results might help to better quantify biogeochemical fluxes in combination with field measurements and remote sensing data, and it might also contribute to develop new management strategies for forests.

PUBLICATIONS

Two chapters have been published previously:

Chapter 2: Bohn, F.J., Frank, K. and Huth, A. Of climate and its resulting tree growth: simulating the productivity of temperate forests. *Ecological Modelling*, **2014**, 278: 9-17

Chapter 3: Bohn, F.J. and Huth, A. The importance of forest structure to biodiversity-productivity relationships. *Royal Society open science*, **2017**, 3: 160521

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Part I

MAIN PART

1

INTRODUCTION

1.1 OVERVIEW

Forest growth plays a central role for the global carbon cycle and human welfare. By accumulating biomass over time and space, forests sequester carbon dioxide from the atmosphere, exhale life-essential oxygen and transpire water vapour. The growth of around 3.253 billion trees on earth (Crowther et al., 2015) compensates 30% of the anthropogenic CO2-emissions (Pan et al., 2011; IPCC, 2013). Due to transpiration and soil-stabilising roots of these trees, forests protect soils from erosion and build a buffer to prevent water run-off after precipitation events. Global forests form a biomass pool of 296 Gt, which contains 50% of all carbon stored in the biosphere (FAO, 2015). Further, forests provide habitat to 50-70% of all terrestrial species and accommodate the oldest and largest organisms on earth: "Pando", the quaking aspen colony (*Populus tremuloides*) expands over 43.6 hectare and has an age of more than 80,000 years (Mitton and Grant, 1996; DeWoody et al., 2008). The oldest single tree, a *Pinus longaeva*, has survived for more than 5,000 years (actual version of OldList data base Brown, 1996). "Hyperion" a *Sequoia sempervirens* with a dbh of 4.84 meters reaches 115 meters of height (Earle, 2013) and "General Sherman", a *Sequoiadendron giganteum* with a stem diameter at the base of 11.2 m and a height of 83.8 m, weighs around 2,000 tons (Fry and White, 1946).

Figure 1: "The arrival of spring in Woodgate, East Yorkshire in 2011", oil on canvasses (36 x 48" each), 144 x 384" overall, © David Hockney.

Humans have been using forests in many ways for thousands of years. Forests serve as space for hunting and gathering and in modern times for touristic activities. They are a resource of food, spices, medicine, timber and fuel wood. Over various cultural epochs forests occur as a important motif in art (e.g. Bilderzyklus Tageszeiten, Caspar D. Friedrich, 1821/22; Le Reve, Henri J. F. Rousseau, 1910; The arrival of spring in Woodgate, figure 1, David Hockney, 2012), literature (e.g. A midsummer night´s dream, William Shakespeare, 1600; Children´s and Household Tales, Brothers Grimm, 1812; The Lord of the rings, John R. R. Tolkien, 1954 and 1955) or movies (e.g. Bambi, 1956; The village, 2004; Bal – Honig, 2010). In addition, forests protect infrastructure and villages against avalanches and erosion. The forestry sector employs 0.4% of all humans and contributes 1% to the global gross domestic product (FAO, 2015). During the 17th century, the excessive use of wood (mainly for construction and as fuel) let to a rapid decline of forested area in Europe. During this period forest research was initiated, focusing on the effects of different management regimes on wood production. Based on this historic research, foresters suggested the concept of sustainability some 300 years ago (Carlowitz, 1713).

Studies on earth's forest-ecosystems are still essential. The United Nations Climate Change Conference in Paris 2015 (COP 21) requests better quantifications of ecosystem responses to small temperature rises of 1.5 °C since the preindustrial era on regional and local scales (IPCC, 2016). The potential of forests to mitigate the increase of atmospheric CO2 and the risk of carbon emissions from forest is of high interest (Ciais et al., 2005; Pan et al., 2011; Huete, 2016; Seddon et al., 2016). In addition, foresters develop new management strategies to adapt forests to future climates. Studies focus on stabilising above-ground biomass production levels, low vulnerability to climate anomalies and other ecosystem services (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Seidl and Lexer, 2013).

Forest dynamics act at different temporal and spatial scales (Levin, 1992). For instance, enzymatic reactions during the photosynthesis act on a level of seconds within the leaf cells. The germination of seeds takes place within a few days on a few square centimetres of the forest floor. Tree growth acts on the annual scale covering several square meters (tree crowns). Finally, forest succession proceeds over decades or even centuries. It affects areas of several hectares up to large regions and affects forest structure and species compositions. These world-wide dynamics influence the global carbon and water cycle, which feed back into the earth climate.

Forest dynamics are influenced by various factors at different locations in the world. In the temperate zone, three main components are shaping forest dynamics: climatic conditions (such as radiation, temperature or water availability), species composition and forest structure (such as forest height or heterogeneity of tree heights). However, a general quantification and comparison of the influence of these three factors on forest dynamics and especially, the central aspect forest productivity, is missing.

In this thesis, the influences of these three aspects on the dynamics of temperate forests are analysed using field measurements (e.g. the German forest inventory) and a forest gap model. The effect of forest structure on productivity is investigated (a short introduction into this topic is given in § 1.2). The analysis of species-diversity effects on productivity is based on mixtures of up to eight species, which includes common species of the temperate zone (beech, spruce and pine), but also five other species (oak, poplar, birch, robinia and ash; see a short introduction on the link between biodiversity and ecosystem services in § 1.3) Regarding climate, we concentrate on the influence of radiation and temperature on tree productivity processes (see a short introduction on this topic in § 1.4). The introduction also includes a short review section about forest models (§ 1.5) and, at the end, the objectives of this thesis (§ 1.6)

1.2 FOREST STRUCTURE AND FOREST GROWTH

Trees in a forest are surrounded by other trees, which might differ in size and species identity. Over their lifetime trees change in size and shape which influence the competition for resources, such as light and water. Thus, the history of a site influences its current state, as trees of the same age and size could develop very differently due to the stand´s history (Pretzsch, 2009).

First research activities in forestry focused on the development of trees within even-aged monocultural stands, differing only in tree number per area (Cotta, 1821) in order to give foresters recommendations for the stocking density. Therefore, experimental plots that cover 0.2 to 1 hectare, with different management systems, were established and have been monitored. Based on these measurements yield tables were constructed. Variability of growth rates of the same species result from site specific history (mortality/removal of specific trees), from different environmental conditions or from different management activities during the experiment (e.g. reduction of soils water retention capability due to soil compression). The second generation of yield tables combined results from different sites and grouped them into different growth classes depending on the fertility of the site and management regimes. The classification is based on statistical approaches (Schober, 1971; Pretzsch et al., 2002). Based on the current structure of a forest, which can be described by basal area, average stem diameter or forest stand height, the productivity of forest stands can be estimated under constant climate conditions. Foresters determined the stand index (which describes the fertility of a stand) and forest structure and then select the corresponding yield table for their management decisions, if stands were located in a similar climate region (Schober, 1995).

However, environmental changes of the last century were not included in yield tables. For instance, in the second half of the last century nitrogen deposition resulted in higher growth rates as predicted by yield tables (Mund et al., 2002). Currently, nitrogen deposition is decreasing, but the impact of climate change (increasing temperatures and drought events) will become more and more important within the next decades (IPCC, 2013). In addition, a more close-to-nature management with trees of various sizes is seldom covered by yield tables.

All these aspects challenge forest management of the future and motivate the development of computer-based model approaches, which range from statistics-driven model approaches to more complex individual- and process-based models (Pretzsch, 2009). The last group includes forest gap models which are presented in § 1.5 in more detail.

1.3 DIVERSITY AND FOREST GROWTH

Research on the effects of diversity on ecosystem productivity dates back to Darwin (1859):

> *It has been experimentally proved, if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than the former case.*

During the last decades, a range of studies have analysed systematically the effect of species mixtures on ecosystem productivity. Different mixtures of grassland species have been sown on plots of a few square meters. In regular intervals, species not belonging to the mixture were removed. Finally, the biomasses of the plots are harvested once or twice a year. (Tilman et al., 1996; Tilman, 2001; Roscher et al., 2004). In most cases, biomass and the stability of the yield increase with increasing species richness (Hooper et al., 2005; Cardinale et al., 2011). Nevertheless, the single experiments differ in slope and shape of the relationships. In the last years, the effect of diversity on productivity (and other ecosystem services) was also investigated for other ecosystems (Cardinale et al., 2006, 2011). For instance, Cardinale (2011) made experiments with algae and found a positive effect of diversity on biomass production and NO3-uptake rates. Danovaro et al. (2008) analysed 116 deep-sea sites world-wide and found that increasing biodiversity in the benthos supports higher rates of ecosystem processes, and increases efficiency by which these processes are taken place. Bianchi et al. (2006) found that a higher pest suppression due to higher predator diversity results in lower crop injury in agricultural landscapes.

Field experiments with trees that are based on a similar design as the grassland experiments, have been established during the last decade (e.g. Scherer-Lorenzen et al., 2007; Bruelheide et al., 2013), but the trees are still young and consequently results for older forest will only be expected in a few decades. However, some experimental forest stands with two or three species mixtures have been established already in the last century. For instance, Pretzsch et al. (2010) analysed various forest stands including beech and spruce and found higher growth rates in the two-species mixture. Beside experiments, national forest inventories are available (e.g. Vilà et al., 2007, 2013) and forest plot networks of various extensions (e.g. FunDivEURPOE, Baeten et al., 2013). Analyses of larger data sets reveal a positive relationship between tree diversity and forest productivity (e.g. Morin et al., 2011; Zhang et al., 2012; Vilà et al., 2013). However, some studies found also invariant or even decreasing relationships (e.g. Chen and Klinka, 2003; Jacob et al., 2010; Cavard et al., 2010; Holzwarth et al., 2015).

There are different mechanisms proposed to explain the relationship between diversity and productivity. Loreau and Hector (2001) proposed to split the observed net biomass increase statistically into two components, which can be interpreted as complementarity and selection effects. The selection effect is often interpreted as a change in the relative abundance of high-productive species within the mixtures, which drives the change in productivity between monocultures and their mixture (Cardinale et al., 2007). The complementarity effect includes all forms of niche partitioning that might influence biomass production and all forms of indirect and non-additive species interactions (Cardinale et al., 2007). For instance, a mixture, in which shade-tolerant species grow below light-demanding species, would result in a positive complementarity effect (as species occupy different spatial niches, so more trees are placed in the forest and hence forest productivity increases).

Recent studies propose a more mechanistic explanation of the effect of diversity on productivity. Morin et al. (2011) showed with a forest model where high diverse forests have higher leaf areas per area (LAI) and therefore higher productivities. This effect of different LAI vanishes if species do not differ in shade-tolerance, growth rate or maximal size. Effects of trait differences and resulting niche separation and higher productivity were also investigated by Kraft et al. (2015) in two-species grassland-experiments, wherein they alter species abundances. They coupled field parametrised competition models with measurement samplings of functional traits to relate fitness and phenotypic differences to niches. Niche separation, and hence the long time coexistence, can only be explained by combinations of traits, corresponding to differentiation between species in multiple ecological dimensions. The experiments have been conducted with annual plants, but it remains unclear if this concept is transferable to forest stands since they show a much more complex spatial structure. In addition, it is difficult to apply the approach of Kraft et al. (2015) on forests that vary highly in species mixtures and abundances of these species due to the longevity of trees. Hence, a simulation approach as proposed by Morin et al. (2011) can be an alternative to such field experiments with trees.

1.4 CLIMATE VARIABLES AND FOREST GROWTH

Forests grow in different climates worldwide, from tropical over Mediterranean and temperate to boreal biomes. Hence, forests occur in habitats which can be characterized by mean annual temperatures of -5°C to 30°C and by a precipitation of more than 500 mm per year (Kunstler et al., 2016). Nemani et al. (2003) showed that in temperate regions forests´ productivity is mainly driven by a combination of radiation, temperature and precipitation. The reaction of plants to changes in climate can be complex (Davis, 1990). Regarding carbon uptake, it is uncertain how climate change will affect terrestrial ecosystems (Friedlingstein et al., 2006). The net carbon uptake results from two processes: photosynthesis and respiration. Both are influenced non-linearly by several environmental conditions. Photosynthesis, for example, follows a bell shaped curve with increasing temperature, whereby decreasing water availability results in a decrease of productivity if a threshold level is reached (Horn and Schulz, 2011). Respiration on the other hand accelerates exponentially with increasing temperatures (Piao et al., 2010; Mahecha et al., 2010).

Projections on future climate change suggest that regional climates may evolve to states that are different from current climate regimes found on Earth today (Reu et al., 2014). In contrast to agricultural crops, it is difficult to conduct experiments with forest stands in climate chambers under controlled and managed environmental conditions (Grime and Hunt, 1975). Still, some studies modify precipitation by using roofs (Grossiord et al., 2014). Other experiments enrich the air artificially with CO2 (FACE-experiments, Ainsworth and Long, 2005). However, it seems to be impossible to treat a large number of forests (varying species diversity) with different climate scenarios changing only one climate variable and keep all others constant. This is the reason why field experiments should be combined with modeling experiments. One option might be simulation experiments based on process-based models, which include climate dependencies.

1.5 FOREST MODELS

Field studies, as discussed above, need a lot of time, money and many scientists (Anderson-Teixeira et al., 2015). Ecological models provide an additional and alternative opportunity to analyse ecosystems in a "virtual laboratory", as they allow a systematic variation of forest structure, species diversity and/or climatic conditions. Such models should consider the processes of interest in an adequate complexity (Shugart, 1990) and they need to be founded on empirical data and tested against field observations. Several forest models have been developed during the last decades, which are able to calculate forest productivity depending on forest structure, species diversity or climate change. Often and successful applied model types are forest gap models (Bugmann, 2001; Fischer et al., 2016).

1.5.1 *Forest gap models*

In the gap model approach, ecosystems are described as a mosaic of patches whereby each patch represents a different successional state of the ecosystem (Gleason, 1917, 1927, 1939; Watt, 1947; Drury and Nisbet, 1973; Connell and Slatyer, 1977; White and Pickett, 1985; Wissel, 1992; Meurant, 2012). Each patch can be dominated by one large tree. After its death the growing conditions change for all remaining trees (e.g. available light increases; there is now free space wherein trees can grow; and so on). Now, new seedlings establish and former suppressed trees may grow faster. After a while, one tree will become the largest tree again and the cycle runs all over again (Shugart, 1984). Management or natural disturbances can influence this cycle. For instance, suppressed trees might be removed (by e.g. fire or management), or trees did not reach the maximal size due to windfall (especially spruce).

The first computer-based forest gap model was JABOWA (Botkin et al., 1970, 1972a,b). JABOWA simulates mortality, establishment, competition for light and growth of individual trees on small patches of 0.01 to 0.1 hectare size. The geometry of trees has been described as a stem with a two dimensional disc, which represents the crown, on top of the stem. The processes are described by stochastic and deterministic algorithms. For instance, mortality results from stochastic processes (e.g. a constant mortality rate for all trees and/or a stem diameter depending mortality rate). Tree growth in contrast is calculated based on a size-specific maximal potential growth rate, which is reduced by environmental factors such as light availability, soil moisture and temperature during the vegetation period. Beside the analysis of forest productivity, JABOWA allows the analysis of forest structure as individual trees might differ in size, stem diameter and/or height within the forests. Thus, basal area or forest height can be calculated. JABOWA simulates up to 13 different tree species, which are characterized by different parameter sets (e.g. growth rates).

This first gap model, developed to simulate the north-eastern forest of the USA, has inspired a whole generation of scientists that have developed individual and process-based forest models for different regions world-wide. Southern Appalachian forests were modeled with FORET (Shugart and West, 1977) and European temperate forests with FORCE (Kienast, 1987) and TREEDYN (Bossel and Krieger, 1991). The forest gap model approach was also applied to the tropics (FORICO (Doyle, 1981), FORMIX (Bossel and Krieger, 1991) and FORMIND (Köhler and Huth, 1998)) and to boreal forests (FORSKA (Leemans and Prentice, 1989)). Finally, the gap approach was extended to grasslands (VEGOMAT (Smith et al., 1989), GRASMIND (Taubert et al., 2012)).

Some equations of JABOWA and FORET are still found in today´s forest gap models. However, additional processes were included: fire (Kercher and Axelrod, 1981; Fischer, 2013), browsing (Seagle and Liang, 2001; Didion et al., 2009) and management (Liu and Ashton, 1995; Huth et al., 1998; Huth and Ditzer, 2001). Other models describe processes with alternative formulations: for instance, mortality processes are modeled as exogenous, growth-dependent and/or intrinsic process (e.g. Keane et al., 2001). Seidl et al. (2012) developed an alternative approach to simulate light competition. This approach reduces computational time drastically and allows simulating whole landscapes with the forest gap approach.

Temperature dependence of tree growth was already included in FORET and JABOWA. Some studies, investigated the influence of temperature and precipitation change on species composition, forest productivity and stand biomass (Pastor and Post, 1988). The effect of CO_2 fertilization on stand biomass was investigated by Shugart and Emanuel (1985); Solomon (1986), assuming an increase of photosynthesis with increasing CO_2 levels. Dependencies on nitrogen and nutrient cycle were implemented (Aber et al., 1978; Pastor and Post, 1985; Bugmann, 1996) or alternatively a site index, which describes site fertility (Pretzsch et al., 2002). All these approaches have been formulated more or less in an heuristic way, as either stem diameter or the size dependent growth is reduced by several environmental driven factors.

Forest gap models have inspired a second important model type to analyse the dynamics of vegetation: the global dynamic vegetation models (DGVM; Prentice et al. (1992)). DGVMs focus on the global vegetation pattern, carbon balance and water cycle. In these models, the globe is represented by a grid (e.g. 50 km x 50 km). Vegetation is often described by a fractional coverage of populations of different plant functional types in the grid cells. These plant functional types aggregate the variety of species characteristics in a general way. Photosynthesis and respiration of plants are modelled explicitly, in contrast to most forest gap models. The remaining organic carbon is distributed over the different compartments of the plant (Litton et al., 2007), a process called allocation. Thereby, some compartments accumulate carbon over time (e.g. wood, roots), others are renewed regularly (e.g. leaves, fruits). Most DGVMs do not simulate individual plants and hence, structural effects cannot be analysed. Both, photosynthesis and respiration rates depend on environmental conditions (Biome3 (Haxeltine and Prentice, 1996); JeDi (Kleidon and Mooney, 2000); LPJ (Sitch et al., 2003); ORCHIDE,Krinner et al. (2005); Seib-DGVM (an individual-based DGVM) (Sato et al., 2007); JSBACH (Raddatz et al., 2007)). For instance, the photosynthesis rate follows a bell-shaped curve with increasing temperature, whereas maintenance respiration increases exponentially with increasing temperature, as observed in field measurements (Piao et al., 2010; Horn and Schulz, 2011). Such description of the carbon allocation process was also included into a few forest gap models (Gotilwa (Keenan et al., 2008); TREEDYN (Sonntag, 1998); 4C (Lasch et al., 2005); FORMIX (Bossel and Krieger, 1991); FORMIND (Köhler and Huth, 1998)). This more detailed description of a tree comes along with an increase of the number of model parameters, which have to be parameterized (Fontes et al., 2010; Van Oijen et al., 2013). Hence, such forest gap models were parameterized normally only for a limited number of species (e.g. TREE-

DYN only includes picea in Germany; Gotilwa simulates only fagus, pinus, quercus monocultures in Spain).

Different tree species were already included in the gap model JABOWA (Botkin et al., 1970, 1972a,b). However, not all processes were simulated species-specific. For instance, the LAI was calculated species-specifically, but the function and parameters, which estimate the influence of temperature on productivity, were the same for all species. Diversity is often analysed as model output. For instance, Bugmann (1996) and Bugmann and Solomon (2000) showed how species composition depends on environmental conditions. Morin et al. (2011) could detect a positive relationship between species richness and forest productivity in temperate, equilibrium forests (after 1000 years of simulation). In another study, the effect of tree species diversity on productivity varies over time during succession (Holzwarth et al., 2015).

1.6 CURRENT CHALLENGES OF FOREST ECOLOGY RESEARCH

Latest developments in remote sensing have the potential to revolutionize forest ecology research. Higher spectral and spatial resolution of monitoring is now technically feasible. For instance, the satellite MODIS scans the whole earth with 36 different radiation bands from 670 nm (blue light) to 14.4 µm (long wave infra-red), with a spatial resolution down to 250 m and with a temporal resolution down to one or two days. In contrast, air-born remote sensing techniques (drones and air planes) reach much higher spatial resolution but measure only on regional scales. Based on this remote sensing data various indices were developed, which are used to estimate attributes of the vegetation. Such indices process for instance differences of the reflectance intensities between visible light (absorbed by chlorophyll) and near infra-red (reflected by cell structure; see also normalized differenced vegetation index = NDVI (Weier and Herring, 2000)); enhanced vegetation index = EVI; (Solano et al., 2010)). Such observations, which range from local to global, can contribute to detect plant traits (Jetz et al., 2016) or estimate NPP (one of the MODIS-products). However, the quality of such estimation of ecosystem traits and functions are still under discussion. For instance visible light cannot penetrate into deeper vegetation levels in forests, which results in a saturation of vegetation indices. Further, the relation between spectral diversity (reflectance intensities of different bands) and species diversity or functional diversity is still not clear, as the signals can be modified for instance by the aerosol concentration. Nevertheless it might be possible, using current or future satellites (Sentinel-2 launched 2015 and 2017: visible light; FLEX planned for

2022: bioluminescence; tandem-L under discussion: radar), to transform high quality sensing signals into more accurate estimations of ecological states and processes. Such analysis of the biosphere might give new insights into fundamental questions of ecology.

Recently, Seddon et al. (2016) processed satellite measurements (EVI and climate indices) to generate a world map, which quantifies the sensitivity of ecosystems to climate change. This study might be a first step towards the determination of regions which will reach critical thresholds (Scheffer et al., 2009). Such an approach could be one key element for sustainable management concepts and the prevention of irreversible changes of ecosystems (Huete, 2016). However, in Seddon et al. (2016) it remains unclear, why adjacent locations, that belong to the same ecosystem (e.g. temperate forests) differ in their sensitivity. Huete (2016) suggested that structural properties, for instance tree number (Crowther et al., 2015), or trait compositions, which relate to species composition (Musavi et al., 2015), might be responsible to detect sensitivity differences between neighbouring forest stands.

1.6.1 *FORMIND*

The quantification of various aspects, which drive temperate forest dynamics, are of high importance for foresters and stake holders to enable well-considered decisions. Various approaches were developed in ecology and forest research. Besides field data this study uses a forest gap model to investigate the influence of three main factors on forest dynamics: climate, diversity and forest structure. Such a model has to integrate processes regarding these three factors. Furthermore, independent field observations are needed to validate this model. We selected the forest gap model FORMIND (Fischer et al., 2016) for the following reasons: tree productivity in FORMIND is based on a carbon balance by simulating photosynthesis and respiration processes similar to DGVMs. These processes are limited by light, temperature and soil water availability (Gutiérrez, 2010; Fischer, 2013; Bohn et al., 2014). In contrast to other gap models, FORMIND is very detailed regarding the spatial resolution, as it simulates individual tree crown volumes and the competition for light and space of trees. Finally, FORMIND requires a low number of parameters to describe different tree species compared to other models (Bohn et al., 2014).

1.6.2 *Objectives of this study*

We address the following questions:

- FORMIND was initially developed for the tropics, which show a relative homogeneous climate compared to that of the temperate zone. In Chapter 2 the transformation of FORMIND to a temperate forest gap model is presented focusing on the following questions: Which processes need to be adapted or added to enable the simulation of forest dynamics in the temperate zone? How can the huge amount of inventory data be used to parametrise specific species? Can this new FORMIND-version be applied to simulate forest growth for various species? The final temperate model version includes eight species, whose parametrisations follow a new approach (Bohn et al., 2014). All eight species react species-specific to climate conditions. To validate the new model version for the temperate zone, simulated forest productivity was compared to eddy-flux measurements and to yield tables of other European forests.

- The influence of tree diversity on forest productivity is an important topic in ecosystem research. Many studies found positive effects of increasing species diversity on forest productivity. However, some studies found also invariant and decreasing relationships. In Chapter 3 (Bohn and Huth, 2017), the influence of forest structure and diversity on forest productivity is analysed answering the following questions: (i) How strong is the effect of forest structure on forest productivity? (ii) How strong is the effect of diversity on forest productivity? (iii) Do different forest structures result in different biodiversity-productivity relationships? Here, a new model approach - the forest factory – is presented, which generates around 400,000 forest stands covering young and old, managed and natural, low- and high-diverse forest stands. For each forest stand we simulate the annual wood production. The simulation results are compared to data of eddy-flux measurements covering a European gradient (7 plots) and the German forest inventory (ca. 5,000 plots).

- Rising temperatures result in increasing or decreasing productivity of temperate forests. In Chapter 4 we investigate whether forest structure and diversity can explain why forest productivity changes due to temperature rise differences between forests. We focus on the following questions: (i) how is the productivity of forest stands (AWP) influenced by an increasing mean annual temperature and (ii) an increasing intra-annual temperature amplitude. (iii) Which forest stands will benefit most from rising temperatures? To analyse these questions, we use the 400,000 forest stands generated by the forest factory and simulate the annual forest productivity using 320 different annual climate scenarios.

This thesis has also contributed to the Helmholtz Alliance "Remote sensing and earth system dynamics," which aims to integrate and use forest (structure) parameters derived from radar remote sensing techniques in monitoring the state and the properties of global forests. The temperate version of FORMIND, which is presented in this thesis, now enables forest simulations in the tropical and temperate zone with the same forest gap model for the first time (Fischer et al., 2016). This temperate version was also used in a model calibration study using Bayesian approaches (Van Oijen et al., 2013), which was supported by the European COSTAction FP603 and it now takes part in several studies supported by the COSTAction FP1304.

2

OF CLIMATE AND ITS RESULTING TREE GROWTH: SIMULATING THE PRODUCTIVITY OF TEMPERATE FORESTS

2.1 ABSTRACT

We parametrize the maintenance respiration of a single tree depending on reference climate parameters (light, temperature, precipitation) and the observed stem diameter increase resulting from that climate. The simulated biomass increment results from photosynthesis under the given climate scenario and is then reduced by maintenance and growth respiration. We incorporate this new carbon allocation algorithm into the established individual-based gap model FORMIND to reproduce the biomass development of typical central European forest stands.

Yield tables for northern Germany recorded over the last century are used for our parametrizations, along with the climate of the area at the time of recording. The model simulates eight tree species based on data on pine, spruce, beech, oak, ash, poplar, birch and robinia. The model dynamics emerge from tree competition, growth and mortality. These processes are calculated on an annual scale. The climate variables (global radiation, air temperature and precipitation) are entered into the model in daily resolution.

This new version of FORMIND version reproduces the forest biomass development represented in the yield tables for northern Germany as well as those for western France. The modelled annual fluxes of gross primary production, woody net primary production and autotrophic respiration correspond with results from eddy flux measurements. Therefore, this version of FORMIND with the new carbon allocation is a suitable tool to investigate the carbon flux, biomass development and potential yield of forests at the individual tree level in the temperate climate zone.

2.2 INTRODUCTION

Forests provide important ecosystem services, such as sequestering carbon or delivering wood (Bonan, 2008). In Europe (excluding the Russian Federation), 32.2% or 2.1 million km^2 of the total land surface is covered by forest (UNECE and FAO, 2011). European forests sequester up to 6.6 tonnes of carbon per hectare and year (Valentini et al., 2000). Janssens et al. (2003) estimate the sequestering rate of all European forest at 363 Tg C a^{-1}, which amounts to almost 20% of European carbon emissions of 1995. Around 4% of these forests are undisturbed by human activity, while 29 % of the managed forests are monocultures and 51% contain two or three species (UNECE and FAO, 2011).

Apart from the ecological aspects, forests are also important for the economy (forestry, manufacture of wood and paper). The forest sector contributed a value of EUR 119.5 billion to the gross value in the year 2008 (which is 1 % of European GDP) and provided jobs for 3.95 million employees in 2010 (UNECE and FAO, 2011). High sequestering rates of carbon and wood production are dependent on different abiotic factors. For example, a moderate increase in temperature can have a positive effect on forest productivity in temperate forests (Solberg et al., 2009). In the case of the extreme European summer of 2003, on the other hand Ciais et al. (2005) estimated a decrease in gross primary production (GPP) of 30 % which resulted in an anomalous net source of carbon dioxide. Consequently, changes in temperature could turn forests into carbon sinks or carbon sources.

As we cannot perform long-term experiments on the effects of a changing climate on forest, one option is to rely on integrated models of ecosystem function to explore the potential effects of change on the development of the ecosystem (e.g. Prentice et al., 1993; Bugmann, 1996; Schmid et al., 2006). They simulate ecosystem development as a result of ecophysiological processes described mechanistically, based on a rich literature on the fundamental ecological processes in forests (e.g. Bossel, 1992; Pacala et al., 1996; Haxeltine and Prentice, 1996; Shugart, 1998).

Process-based spatially explicit forest growth models such as FORMIND (Gutiérrez et al., 2009), FORSKA (Prentice et al., 1993), FORCLIM (Bugmann, 1996), 4C (Lasch et al., 2005) or iLand (Seidl et al., 2012) simulate individual tree growth dependent on climatic conditions. With these models it is possible to investigate temporal and spatial forest dynamics for several hectares and centuries.

Here we adapted the forest model FORMIND for the first time to the European temperate zone. We also consider the experiences with the related TREEDYN3 model (Bossel, 1996; Sonntag, 1998), which is a single species forest growth model for European species.

The FORMIND model has been applied successfully by e.g. Köhler and Huth (2004) to different forests to understand species-rich forest dynamics in tropical rain forests (with up to 25 plant functional types) and to temperate rain forests in Chile (Rüger et al., 2007; Gutiérrez and Huth, 2012). As the productivity of single trees in FORMIND is based on carbon balance, annual sequestering rates as well as the expected biomass yield in case of harvesting can be simulated.

The new version of FORMIND, which is designed to simulate **f**orests of **E**uropean **s**pecies in the **t**emperate zone (FORMIND-fest), includes the following main forest processes: competition, tree growth, recruitment and mortality. As input we use daily time series of incoming light (photo-active photon flux density (PPFD)) above the forest canopy, air temperature, precipitation and potential evapotranspiration (PET). In addition, tree number per hectare, their stem diameter and soil parameters are required.

However, describing and parametrizing different tree species and the effects of climate on their growth processes in a process-based model is a complex task (Fontes et al., 2010). Process-based models have to contend with the following issues (among others): (a) data availability for all needed parameters should be given; (b) a model cannot be completely general in its scope and applicability while at the same time providing locally highly accurate results (Levins, 1966); and (c) the relevant processes to answer the research questions have to be included.

The objective of this study is to present a new climate-dependent allocation algorithm for the forest model FORMIND and its parametrization approach. It should be applicable to the temperate climate zone to address questions concerning annual sequestering rates and wood production of forests.

We use yield tables to parametrize eight tree species. These yield tables describe the forest growth for single species and are based on measurements collected between the last two decades of the 19th century and 1968 (Schober, 1971, 1995). Thus the development of the forests described by the yield tables is not influenced by the high nitrogen deposition which occurred in the last third of the 20th century (De Vries et al., 2006; Kahle, 2008; De Vries et al., 2009; Thomas et al., 2010; Eastaugh et al., 2011; Sutton et al., 2011). We parametrized eight common tree species occurring in central European forests. In doing so, we extended the respiration approach presented in Dislich et al. (2009) by climate dependency.

First, we checked whether we could reproduce the forest development over time documented in the yield tables of Schober (1995), which are used also in parts of the parametrization. Then we validated our parametrization using other yield tables for western France (ENGREF, 1984), which are based on a different climate and therefore differ in growth compared to the yield tables for north-eastern Germany used by us. Finally, we compare the modelled carbon fluxes with eddy flux measurements of temperate forests presented by Luyssaert et al. (2007).

2.3 THE SPATIO-TEMPORAL MODEL

We developed a new version of the gap model FORMIND: FORMIND **f**or **E**uropean **s**pecies in the **t**emperate zone (FORMIND-fest). We incorporated a new algorithm for describing photosynthesis dependence on air temperature and soil water as well as maintenance respiration dependence on air temperature to derive the tree growth. Eight tree types are parametrized to calculate their carbon balance and allometry based on field data on the species *pinus sylvestris*, *picea abies*, *fagus sylvatica*, *quercus robur*, *populus marilandica*, *fraxinus excelsior*, *betula pendula* and *robinia pseudoaccacia*.

2.3.1 *Overview of the forest model FORMIND-fest*

The pristine FORMIND model is a process- and individual-based, three dimensional, grid-based forest growth model. So far, FORMIND has been applied to species-rich forests in the tropics (e.g. Köhler, 2000; Köhler and Huth, 2004; Dislich et al., 2009) and Chilean temperate rain forest (e.g. Rüger et al., 2007; Gutiérrez and Huth, 2012). The FORMIND-fest mode builds upon FORMIND while further developing the calculation of gross primary production (GPP) and maintenance respiration (R_m). It is designed to reproduce forest structure and biomass development in central Europe, which emerge from the physiological attributes of each tree type, the competition for light, the amount of water available and air temperature (figure 2).

The simulated forest area (one hectare) comprises 25 land patches of 20m x 20m in size. These are characterized by vertical light conditions caused by the shade of tree crowns, soil water content, and location within the landscape. Tree positions within a patch are not considered explicitly and therefore light conditions are horizontally homogeneous. However, light conditions differ between the height layers and land patches and depend on the distribution of crowns and the LAI of trees (this is described in detail as the gap model approach in Shugart (1998) and in the Appendix A).

In each land patch, we can simulate trees of different age and size. Trees of the same tree type and size, which are located in the same land patch, are considered as one tree cohort. Actual diameter at breast height (dbh), height, crown diameter and stem volume of trees are derived from their biomass based on their allometric relationships (Appendix A.2). In addition, every tree type has its set of parameters describing its own ecophysiological attributes and mortality (Appendix A.3,A.4,A.5). Thus each tree cohort is characterized by tree type, stem number and above-

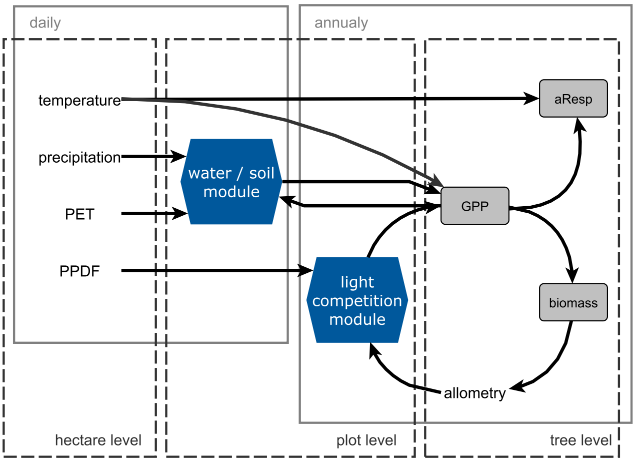


Figure 2: The concept of carbon balance in FORMIND-fest: all climate input variables are equal for the whole simulated area, in our case, one hectare. Precipitation and potential evapostranspiration are used to calculate the GPP limitation factors for all trees in that patch, depending on their GPP. The GPP depends also on the air temperature. The available light for a tree is calculated by the light competition module using the photosynthetic photon flux density (PPFD) giving the available light for all trees in the patch. The GPP is split into autotrophic respiration which is influenced by temperature and biomass increment. The biomass determines the allometry which influences light competition within the patch.

ground biomass of a single tree. Forest dynamics are simulated in annual time steps in the following order: (a) mortality; (b) calculation of light climate in every patch; (c) calculation of the biomass increment dependent on the environmental conditions; (d) calculation of the new allometries of trees. The environmental conditions (air temperature, global radiation, precipitation, potential evapotranspiration) are given as daily times series, with 365 days per year. For more details on (a),(b) and (d) see the Appendix A.4.

2.3.2 *The dependence of biomass increment on the environment*

The annual biomass increment (ΔB) of a tree is the difference between its gross primary production (GPP) and maintenance respiration (R_m), reduced by a growth respiration factor r_g.

$$\Delta B = (GPP - R_m)(1 - r_g) \tag{1}$$

As the GPP of a tree is dependent on the crown area, C_A, the LAI, the irradiation at the top of the tree I_{ind} and the climate-dependent limitation factors of temperature φ_T and water scarcity φ_W.

$$\mathrm{GPP} = \varphi_T \; \varphi_W \; \psi \; C_A P(I_{ind}, LAI) \tag{2}$$

where the photosynthesis per leaf area P is described by a light response curve (of the Michaelis-Menten type) integrated over the whole crown in order to take self-shading of leaves into account. The Michaelis-Menten curve describes a typical saturation relationship between light intensity and production (for more details see the Appendix A.3).

Maintenance respiration results from the temperature-dependent factor κ_T and a base respiration R_b. This R_b depends on the biomass B of the tree.

$$R_m = \kappa_T \; R_b(B) \tag{3}$$

The growth respiration factor is a constant parameter of 0.25 of that carbon which remains from GPP after the reduction of the R_m (Ryan, 1991).

2.3.2.1 *Temperature factors*

PHENOLOGY Only deciduous broad leaf trees in the model have two phenology phases: A dormant phase during winter and a photosynthetically active phase after bud-burst until fall, the vegetation days ψ. The date of bud-burst is reached, when the sum of daily mean air temperatures of days with a threshold temperature T_{th} higher than 5 °C starting on 1 January is higher than a critical temperature (T_{crit}).

$$T_{crit} = -68 + 638e^{-0.01n} \tag{4}$$

where n is the sum of days on which the temperature is below 5°C, starting on 1 November of the previous year. This sub-model is based on the global distribution of leaf onset dates estimated from remote sensing data (Botta et al., 2000). The vegetation period ends when the 10-day running mean air temperature falls below 9°C (Sato et al., 2007). The vegetation period for needle leaf trees is a full year (365 days).

PHOTOSYNTHESIS LIMITATION The temperature dependence of the photosynthesis follows a hump shape reaching values between 0 (for low and high temperature) and 1 (for medial temperatures) (Gutiérrez and Huth, 2012; Haxeltine and Prentice, 1996). The limitation factor of the photosynthesis φ_T is calculated as:

$$\varphi_T = \frac{1}{n} \sum_{1}^{n} \varphi_{T,low} * \varphi_{T,high} \tag{5}$$

where n is the number of days in the vegetation period ψ and $\varphi_{T,low}$ and $\varphi_{T,high}$ are the daily inhibition factors for low and high temperatures $\varphi_{T,high}$

The effect of low temperatures is calculated by an inhibition function:

$$\varphi_{T,low} = (1 + \exp(k_1 * k_2 - T_d))^{-1} \tag{6}$$

where T_d is the daily mean temperature in dimension°C and k_1 and k_2 are constant tree type specific parameters (for their calculation please refer to the Appendix A.3).

Similarly, the effect of high temperatures on photosynthesis is calculated by:

$$\varphi_{T,high} = 1 - 0.01 * \exp(k_3 * (T_d - T_h)) \tag{7}$$

where k_3 is a constant tree type specific parameter (for its calculation see the Appendix A.3), T_d is the daily mean temperature and T_h is the mean temperature of the hottest month, where the reference species occur. Remember, for needle leaf trees the whole year is the vegetation period.

RESPIRATION Maintenance respiration is assumed to increase exponentially with temperature (Prentice et al., 1993). The temperature-dependent factor for maintenance respiration is therefore calculated as:

$$\kappa_T(T_d) = Q_{10}^{(T_d - T_{ref})/10} \tag{8}$$

where T_d is the mean temperature of a certain day, Q_{10} is a constant parameter for all trees and T_{ref} is the reference temperature, for which the correction of the base respiration is 1. We use the annual mean of all κ_T to calculate R_m.

2.3.2.2 *Water/soil module*

A limitation of photosynthesis due to water scarcity φ_W occurs if the soil water falls below the threshold for optimal photosynthesis. If the soil water content is below the permanent wilting point photosynthesis stops (Gutiérrez and Huth, 2012).

The ground is represented as one water pool below every land patch characterized by porosity, conductivity in saturated soil, pore size distribution, residual water content and soil depth. The daily updated soil water content Θ increases after the infiltration of daily precipitation reduced by interception in trees. If the soil is saturated, above-ground run-off occurs. Θ is reduced by daily below-ground run-off and transpiration of trees which depends on photosynthesis. Trees in a patch consume water from the same water pool. If Θ is above a threshold Θ_{msw} which represents Θ when enough soil water is available for optimal photosynthesis of trees, their growth is not reduced. Below the permanent wilting point Θ_{pwp} no photosynthesis is possible. Between these two points photosynthesis of all trees in this land patch as well as their transpiration is redruced.

The limitation factor of photosynthesis because of water scarcity φ_W for all trees is always calculated as:

$$\varphi_W(\Theta) = \begin{cases} 0 & \text{if } \Theta \leqslant \Theta_{pwp} \\ \frac{\Theta - \Theta_{pwp}}{\Theta_{msw} - \Theta_{pwp}} & \text{if } \Theta_{pwp} < \Theta < \Theta_{msw} \\ 1 & \text{if } \Theta \leqslant \Theta_{msw} \end{cases}$$

More details of the water module can be found in Appendix A.3.

2.3.3 *Parametrization*

For better readability species names written in italics refer to real species (or genus), whereas those written in normal type refer to the parametrized virtual tree type, which is oriented on the data of the corresponding real species (or genus).

For all tree types, we use the German yield tables of Schober (1995) to determine the allometric relationships between biomass and dbh as well as between dbh and height, crown diameter, mortality rate and maintenance respiration. To evaluate the developed parametrization we use yield tables for western France (ENGREF, 1984).

Yield tables describe the growth of trees in even-aged forest with only one tree species. To construct yield tables, tree measurements for a large number of forest plots have been compiled and analysed. Trees of the same species can differ in their height growth due to differences in site quality. Forest plots are grouped into different yield classes using statistical methods, based on the mean height development of all forest plots,. For each yield class average basal area, form factor and stem number over time are determined. The corresponding dbh is calculated as quadratic mean, which is the diameter of the tree with mean basal area. Yield tables mostly used 5-year time intervals. (Two exceptions are the German table for ash, which uses 10-year intervals and the French oak table,which uses intervals ranging from 6 to 10 years.) A more detailed description of yield tables can be found in Schober (1971); Pretzsch (2002).

The stem wood volume of a forest for one hectare (fm) is calculated by:

$$fm = \bar{h} * ba * f \tag{9}$$

whereby $\bar{h}$ is the mean height of the forest, ba is the basal area and f is the form factor.

For the parametrization we use only the values for moderately thinned forest stands with the highest height growth rate of trees (site index 1). Moderate thinning management normally removes normally only dead, dying, suppressed and deformed trees. The impact of thinning is considered in the model by calibrating the mortality rate (used in the model) in a way that simulated stem numbers fit to the observed stem numbers in Schober (1995).

For constructing the dbh-height relationship we use the documented quadratic mean of stem diameter and mean tree height values. Mean biomass of a single tree in the yield table is calculated by

$$B = \frac{fm * \rho}{N} \tag{10}$$

whereby fm is the stem wood volume in the yield table, ρ is the wood density and N is the number of trees per hectare in the yield tables. Wood densities were assumed to be constant for every tree species and have been taken from Trendelenburg and Mayer-Wegelin (1955) To estimate the mean crown diameter of a single tree we first calculate the average crown area from yield table data from which we subsequently derive the crown diameter.

$$CA_{tree} = \frac{A * 0.9}{N} \tag{11}$$

whereby A is the forest area (here one hectare) and N is the number of trees per area. To consider small gaps between the crowns as well we used a reduction factor of 0.9 (this corresponds to the packing density of circles in a plane; measurements of such small gaps in beech forest show similar values (Schober, 1971))

Initial slope and maximum photo-productivity of the light response curve for tree types pinus, picea and fagus are taken from the data published by Sonntag (1998) used in the TREEDYN model. We assign these data to light values according to Ellenberg. We interpolate between these data using a power law fit to get initial slope and maximum photo-productivity for the remaining tree types.

The LAI are kept constant using mean values of data presented in Breuer et al. (2003). Tree type robinia is estimated as the mean of *quer-*

cus and *populus*, as these three have the same light values according to Ellenberg.

The base respirations, R_b dependence on biomass can be determined by using the photosynthesis, ΔB and the growth respiration (Eq. 1) if the climate and its resulting biomass increment are known. For this climate κ_T is set to 1. The photosynthesis in the reference climate P^* depends on the irradiation at the top of the tree during the reference climate I^*_{tree}, the LAI and the crown area, which depends on the biomass B. Inserting Eq. 2 in Eq. 1 and solving it to R_b we get:

$$R_b = \varphi^*_T \ \varphi^*_W \ \psi^* \ C_A(B) \ P^*(I^*_{ind}, LAI) - \Delta B(B) \ (1 - r_g) \qquad (12)$$

where the reference limitation factors φ^*_T and φ^*_W and the days of vegetation period ψ^* result from the reference climate.

From the yield tables we derived the growth curve of every tree type. A growth curve describes the dbh increment dependent on the dbh of an average tree. Due to the removal of small trees in forests, a statistical shift in the yield table increment exists. We ignore the statistical shift, because it is still unclear how strong a single tree growth curve differs from the increment documented in the yield tables (see Biber (2010) who quantifies the shift for some spruce stands in Bavaria). However, the resulting growth curves can be transformed into biomass growth curves of one tree based on allometric relationships (see Appendix A.2). Therefore, from the biomass B we derived the crown area and the average increment under the reference climate ΔB. Note that the biomass of leaves and roots is included in R_B and that ΔB corresponds to the woody net primary production wNPP. As the yield tables describe even aged mono cultures with moderate thinning, we assume that all trees have the same height. This results in the assumption that I_{ind} is equal to the global radiation above canopy.

The youngest recording in the yield tables ends in 1967 and most of the others end in the 1950s and go back to the 1880s. For the construction of the yield tables, measurements of forest plots in different years but at the same age are used to derive the age-depend variables. In addition, during the recording periods of the yield table the mean annual temperatures and precipitation change very slightly in north-eastern Germany compared to the temperatures observed in recent decades (see measurements of the Telegrafenberg climate station in Potsdam). Therefore, we assume a constant climate during the recording periods of the yield tables. In addition, the change of forest growth due to nitrogen deposition was low, as this effect appears especially in the last third of the 19th century (Kahle, 2008; Sutton et al., 2011).

We derived the climate input parameters from climate diagrams of the period from 1931 to 1960 published by Müller (1996). We take the stations of Berlin, Bremen, Langenhagen and Lüchow to calculate a mean climate for northern Germany, where all plots of the yield tables are located. Between the monthly values of temperature, irradiation and potential evapotranspiration we interpolate linearly to get the daily time series. The daily precipitation is derived from the monthly value of dry days per month and the monthly sum of precipitation using the precipitation simulation model of Kumagai et al. (2004). Using these time series, we calculate the limitation factors of the reference climate which result in the growth recorded in the yield table.

Based on the above-presented requirements for bud-burst (Eq. 45) and fall, we get the reference vegetation period ψ^*. With it we can calculate the mean global radiation above canopy during the reference vegetation period I^*_{ind}. Using Eq. 5 and the daily temperature time series, we derived the temperature-dependent reference limitation factor for photosynthesis ϕ^*_T. As we were working with class one yield tables (i.e best growing conditions), we assume that the soil characteristics represent the best growing conditions because the climate is the same for all classes of the yield tables in the recording area. Hence, the amount of water available should be the highest in class 1 tables. Therefore we use the soil parameters for loam (Maidment, 1993). Regarding the analysis of Kleidon and Heimann (1998) about maximizing the benefit of root length due to water availability, we assume that the root length is optimal for the water availability. Optimal root length and heigh water availability results in no water stress or mathematically a ϕ^*_W of 1.

The reference limitation factors are tree type specific and are kept constant for all later simulations with other climate scenarios, as we assume that $R_b(B)$ is tree type specific for all trees of a species independent of their climate conditions. Nevertheless R_m is still dependent on air temperature (via κ_T) and the the autotrophic respiration $aResp$, depends additionally on GPP, as $aResp$ include the GPP-dependent growth respiration.

To fit the Q_{10} approach we chose a T_{ref} which results in a κ_T of one for the reference climate. The parameter Q_{10} is set to 2.3, which lies in the middle of the range presented by Piao et al. (2010).

2.4 SCENARIOS

2.4.1 *Climte time series*

We generated 1000 climate time series of daily mean temperature, global radiation, precipitation and potential evapotranspiration for northern Germany using four climate diagrams of Berlin, Bremen, Langenhagen and Lüchow (Müller, 1996) (250 time series per site). We also generated 1000 climate time series for western France using climate diagrams of Paris and Tours (500 time series per site). Thereby we varied the monthly mean temperature assuming a normal distribution. The monthly mean is taken from Müller (1996) and the standard deviation (sd) is set to

$$sd = \frac{T_{max} - T_{min}}{2} * \frac{1}{2.5} \tag{13}$$

where T_{max} is the hottest monthly mean and T_{min} the coldest monthly mean temperature in the recorded time span of the station. We assume that 99% of all values occur between these two extremes, which means three times the sd in a normal distribution.

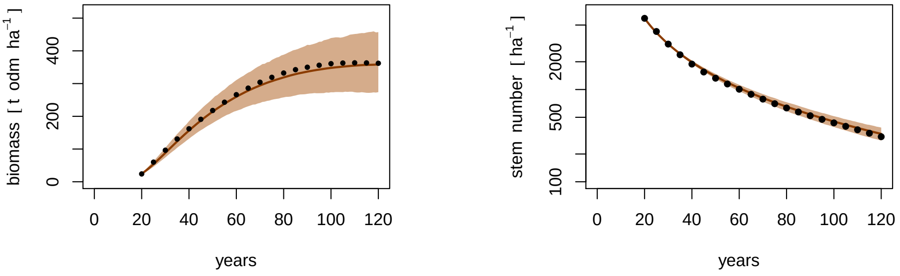
2.4.2 *Initial state of the model*

To compare the yield tables with the simulation output we started the simulations with the same number of trees per hectare as in the respective yield table. All these trees have the same dbh which is given as mean dbh in the yield tables. The tree biomass results from the dbh. As the Θ during early spring is mostly saturated we set Θ to 100 %. We compare the simulation output to the most productive yield table, as we assume that in this case soil fertility does not limit growth.

2.4.3 *Evaluation*

To compare the model output for above-ground biomass with the yield tables, which contain stem volume instead of biomass, we multiply it with rho_t and the age-dependent biomass expansion factor published by Dieter and Elsasser (2002).

Comparing the simulated carbon fluxes with mean eddy flux measurements of temperate humid deciduous forest and evergreen forest as presented by Luyssaert et al. (2007), we built the mean and quantiles of all simulations (northern Germany and western France) for beech and oak to reproduce deciduous forest fluxes of the humid temperate zone. Spruce and fir simulations are used to obtain evergreen forest data.



(a) biomass **(b)** tree number

Figure 3: Biomass as tons of organic dry matter and tree number development over time of tree type spruce on one hectare. Yield table data of Schober (1995) as black dots. Mean of 1000 simulations represented by the dark brown line. Significance interval depicted by paler brown band. All simulations start with the same number of trees as the yield tables.

2.5 RESULTS

We parametrized eight common European tree species for the gap model FORMIND-fest (build 1080) to reproduce (i) the observed growth of one hectare forests over the trees lifetime and (ii) the carbon fluxes of these temperate forests using a new carbon balance approach. The output values are collected after all processes of the current year.

Forest development on one hectare over time is shown for the tree type picea in figure 3. This exemplary forest was initiated as an even-aged monoculture on loamy soil. The climate time series was based on climate data collected at four stations in northern Germany to cover the whole area where the aggregated yield table data were measured. The four stations were located at Berlin-Dahlem, Lüchow, Bremen-Flughafen and Hannover-Langenhagen (Müller, 1996). In total 1000 different time series were generated (250 for each station).

To compare the yield tables measure as total stem volume per hectare, we converted it to biomass by applying wood density and the expansion function with the tree-specific parameters presented by Dieter and Elsasser (2002).

The mean of the simulated biomass development over time represents the yield table data. The significance interval increases over time, because of the different climate time series and mortality rates of single trees, which generate different path dependencies.

To evaluate our whole parameter set we compare the biomass developments over time of even-aged monocultural stands with the simulation results (on loamy soil) for northern Germany (figure 4, all eight species) as well as for France (figure 5, here, measurements exists only for pine, spruce, beech, oak). The climate time series for northern Germany were the same for all species like the one for spruce (described above). For western France we used only two stations to generate 1000 time series: Paris and Tour Müller (1996).

In the case of northern Germany (figure 4) the model output fit the measurements well (all were close to the diagonal, which is the perfect fit.). In the case of western France (figure 5) the simulations of tree types picea and quercus also fit the measurements well. Quercus shows a small growing delay in both figures at the beginning (first 15 simulation years). In France fagus grows too fast (the slope is steeper than the diagonal for the whole simulation) and pinus grows too slowly (the slope is flatter than the diagonal).

The remaining differences between the field data and the simulation output could be explained by different allometric relationships between modelled trees (which are based on the German yield tables) and the French yield tables.

To evaluate the simulated C-fluxes we compare them to the mean measurement of eddy flux studies in the temperate humid biome presented by Luyssaert et al. (2007) (figure 6).

As pine and spruce are the main species in evergreen temperate forest whereas beech and oak represent the main species in the most deciduous forests we took only the results of the tree types pinus, picea, fagus and quercus to compare them with the eddy covariance measurements. As different ages generate different fluxes (Luyssaert et al., 2008) we built the mean, 25% and 75% quantiles of all simulations (with stochastic climate time series for Germany and France as well as mortality). We converted the resulting hectare values to square meter values to compare them with the measurements of GPP, NEP and respiration presented in Luyssaert et al. (2007) (figure 6).

In all cases, the 25-75 quantile interval overlaps between measurements and simulated data, except for respiration of deciduous trees, as the quantile interval of the FLUXNET data was not available. The simulated forest shows lower GPP and respiration for deciduous forests compared to evergreen forests, but nevertheless it shows the different magnitudes of carbon fluxes.

2.6 DISCUSSION

Here we present a forest gap model in which tree growth is based on a carbon balance and climate-dependent carbon allocation. We used three relevant processes of FORMIND (growth, competition and mortality) to

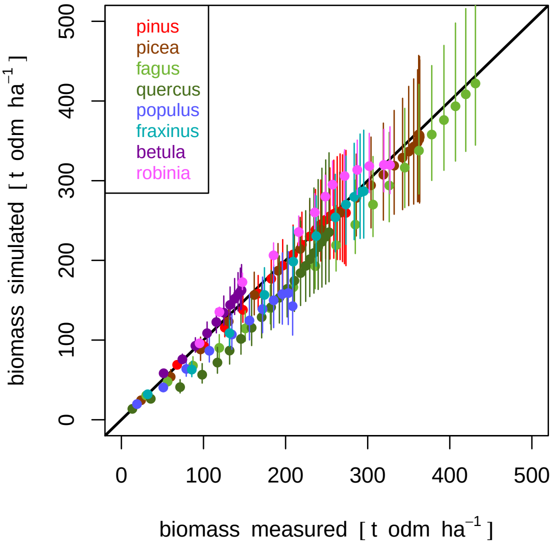


Figure 4: Observed biomass of yield tables in Northern Germany at a certain time are compared against simulated biomass after the same time interval. Biomass is given in tons of organic matter. Dots on y-axis represent the means of 1000 simulations and are compared with measurements on the x-axis every five years. Vertical lines indicate the 95% significance interval.

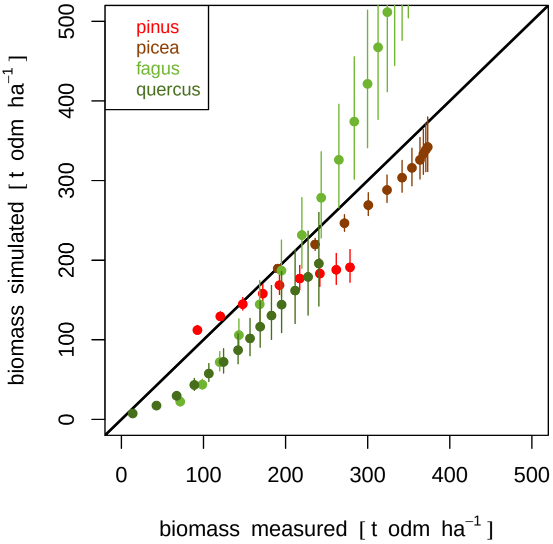
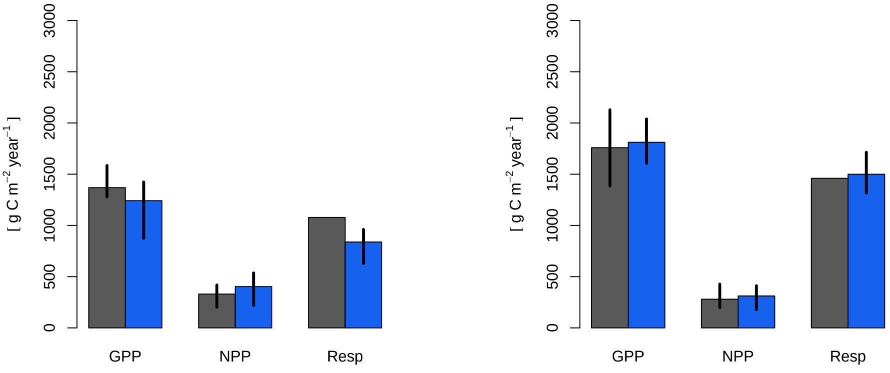


Figure 5: Observed biomass of yield tables for western France at a certain time are compared against simulated biomass after the same time interval. Biomass is given in tons of organic matter. Dots on the y-axis represent means of 1000 simulations and are compared with measurements on the x-axis every five years. Vertical lines indicate the 95% significance interval.



(a) deciduous

(b) evergreen

Figure 6: Measured C-fluxes described by Luyssaert et al. (2007) in gray are compared with simulated C-fluxes of forests of all simulated ages and sites in blue. GPP is the gross primary production (GPP>0 denotes photosynthetic uptake). wNPP is the wood component of net primary uptake (wNPP>0 denotes forest uptake). Resp includes autotrophic respiration and the root and foliage component of the NPP). (a) Evergreen simulations are based on data of the tree types picea and pinus, (b) deciduous simulations on fagus and quercus. The bars represent the means. The lines refer to the data between 25th and 75th percentiles (these data were not available for the measured Resp).

reproduce forest growth according to yield tables with the aim of making the model as simple as possible and easy to parametrize. Nevertheless, it can be applied to different locations in the temperate zone.

Many process-based forest models are designed for single-species and even-aged stands. Therefore they use only a few common species as presented in Fontes et al. (2010). Most forest models discussed in this review (18 of 25) have been developed only for a lower number of species than in this study (eight species). We developed an approach by which the number of species can easily be enlarged if yield tables with corresponding climate data, photosynthetic parameters and wood density are available.

The parameters of carbon allocation of a tree (as well as the allometric parameters) are derived by using the data from yield tables, which contain mean values of stem growth of trees at different locations across northern Germany. The yield tables describe forest development in 5-year intervals (Schober, 1995), thus reducing the effect of inter-anual climate variability on the increments. Hence, single extreme increment measurements of trees hardly affect yield tables, which enables us to concatenate climate data with the diameter increments. Other approaches use only maximal stem increment values of different stem diameters to derive a function which describes the stem diameter increment of a tree under optimal climate conditions (Bugmann, 1996; Pretzsch et al., 2002; Köhler, 2000; Dislich et al., 2009).

We derived the respiration parameters of the tree by using the stem increment values to calculate the carbon allocation and the corresponding primary production of the tree . Therefore we omit the parametrization of maintenance respiration by using direct field measurements. Such measurements are very difficult to take in the field (Piao et al., 2010) and therefore they are often a source of uncertainty in process-based models.

To parametrize one tree type we need 24 parameters, derived from yield tables, climate diagrams, photosynthetic parameters and wood density. Compared to other similar models our number of parameters is at the lower end: SEIB-DGVM need 39 parameters to represent a tree species (Sato et al., 2007). TREEDYN3 needs 34 parameters because of the very detailed modelling of tree growth and the respiration process (Sonntag, 1998). iLand includes fine roots and foliage and therefore it uses 29 tree-specific parameters (Seidl et al., 2012). Only ForClim has only 21 parameters (Bugmann, 1996) and does not contain any mortality parameters. Taking the number of parameters as an indicator of complexity, our model is one of the simplest compared to other forest growth models.

FORMIND is able to predict annual resolution dynamics of stand volume, mean stem diameter, LAI and stand height (as do most process-based forest models (Fontes et al., 2010)). As input variables, we use temperature, rainfall, radiation and potential evapotranspiration in daily resolution. The GPP is calculated using a light response curve integrated over the whole crown of the tree (Thornley and Johnson, 1990). The difference between GPP and respiration (maintenance and growth) results in the woody NPP. Pool-type process based models (e.g. Pietsch et al., 2005; Huber et al., 2013) are mainly used to simulate forests with one species up to the regional scale. However, multi-species gap models could help to investigate highly diverse forest. Such multi-species gap models use stem diameter growth functions (dependent on actual dbh) to describe tree growth. These stem growth curves are modified by reduction factors, which result from the climate variables (e.g. ForClim by Bugmann (1996)). The tree growth in the forest model SORTIE depended on the actual stem radius and the global light index, which are derived after a regression of field data (Pacala et al., 1994, 1996). A new approach used in forest models is the implementation of the radiation use efficiency (RUE) (e.g. in iLand (Seidl et al., 2012)) and presented by Landsberg and Waring (1997)). We use a Michaelis-Menten function as a light response curve, which reproduces the photosynthetic process and primary carbon allocation (Thornley and Johnson, 1990). Note that our approach is able to simulate faster tree growth under other conditions for the trees than the conditions which are used for parametrization.

Many gap models use a modification factor to relate nitrogen concentration in the soil to tree growth (e.g. Seidl et al., 2012). Because the version of FORMIND used here lacks such a factor we assume the parametrization is limited for soils with a similar fertility to soils with good growing conditions prior to 1967 (as these are used for the parametrization). But industrial deposition of nitrogen during recent decades has increased the nitrogen content of soils and thus the productivity of forests (De Vries et al., 2006, 2009). Therefore, future versions of the FORMIND model will have to deal explicitly with nitrogen limitation factors.

For the tested climate scenarios for northern Germany and western France, the new parametrization approach reproduces realistic forest growth and C-fluxes. A comperison of the simulation results with field shows that data all species reproduce forest growth quite well over the whole lifetime. We underestimated the growth of oak trees in both scenarios slightly because the increment function can not represent the fast growth of young oak trees in the field data. The difference of fagus in the simulations and beech in the French data seems to be the result of different estimations of stem volume by Schober (1995) and ENGREF (1984), as trees similar in height and stem diameter have different stem volumes. The ENGREF data set shows a stem volume which is around 33% smaller (for mid and late dbhs) at the same dbh with only around 10% reduced tree height than that in the data set of Schober (1995). The use of different biomass-stem diameter or -height equations for trees with similar height and stem diameter result differences of the biomass. Thereby differences increase for taller trees (Thurnher et al., 2013).

In the case of the conifers, the German stands are more dense (because of different management) which results in a different tree allometry than for stands in France. The German tree crowns are thinner at the same stem diameter because of the limited space but display a higher stem number per hectare. This change in tree crown allometry at the same stem diameter is not currently reflected in the model. Nevertheless, the simulated total forest biomass per hectare fits well to the field data.

The carbon fluxes of the conifer forests are well reproduced. In the case of the deciduous trees, the underestimation of GPP and therefore the underestimation of the autotrophic respiration (aResp) can be explained by the uncertainty of the photosynthetic parameters, especially the initial slope of the light response curve and the maximum rate of photosynthesis.

Surprisingly, the magnitude of the simulated and the measured values is quite similar although the measurements of Luyssaert et al. (2007) were made during increased nitrogen depositions (1990-2004). Hence, FORMIND seems to reproduce the actual mean wNPP of actual European forest quite well (figure 6). Further studies are needed to clarify whether the average soil fertility of today due to industrial depositions is corresponds to the soil fertility which results in the yield class 1 forest stands prior to 1967.

To summarize, our process-based spatially explicit forest growth model simulates the development of forest stands and individual trees for eight European tree species. The parametrization is based on yield tables. The climate which results in the forest development documented in those yield tables and other field measurements can easily be enlarged. To build on experiences with earlier FORMIND applications (e.g. Köhler et al., 2003; Dislich and Huth, 2012; Gutiérrez and Huth, 2012), FORMIND-fest could be a useful tool for investigating the impact of species-rich forest of heterogeneous age structure on sequestration as well as the development of storage during forest succession.

3

THE IMPORTANCE OF FOREST STRUCTURE TO BIODIVERSITY-PRODUCTIVITY RELATIONSHIPS.

3.1 SUMMARY

While various relationships between productivity and biodiversity are found in forests, the processes underlying these relationships remain unclear and theory struggles to coherently explain them. In this work, we analyse diversity–productivity relationships through an examination of forest structure (described by basal area and tree height heterogeneity). We use a new modelling approach, called ‘forest factory’, which generates various forest stands and calculates their annual productivity (above-ground wood increment). Analysing approximately 300,000 forest stands, we find that mean forest productivity does not increase with species diversity. Instead forest structure emerges as the key variable. Similar patterns can be observed by analysing 5054 forest plots of the German National Forest Inventory. Furthermore, we group the forest stands into nine forest structure classes, in which we find increasing, decreasing, invariant and even bell-shaped relationships between productivity and diversity. In addition, we introduce a new index, called optimal species distribution, which describes the ratio of realized to the maximal possible productivity (by shuffling species identities). The optimal species distribution and forest structure indices explain the obtained productivity values quite well (R^2 between 0.7 and 0.95), whereby the influence of these attributes varies within the nine forest structure classes.

3.2 INTRODUCTION

Human activities alter ecosystems and their functions (Hooper et al., 2005). One important function of ecosystems pertains to their productivity. Many biodiversity experiments show higher levels of productivity in species-rich ecosystems than in monocultures (e.g. Tilman et al., 1996; Loreau and Hector, 2001; Cardinale et al., 2007).Nevertheless, the generality (e.g. in forests) of a positive relationship between biodiversity and productivity is still debated because most of the results are derived from grassland experiments (Adler et al., 2011).

In recent years, an increasing number of biodiversity experiments have been designed for forests. However, trees examined in these experiments have often been very young (e.g. Scherer-Lorenzen et al., 2007; Bruelheide et al., 2013). As an alternative method, inventories of natural and managed forests have been analysed. Several field studies of forests have revealed positive effects of biodiversity on productivity (e.g. Edgar and Burk, 2001; Vilà et al., 2007; Paquette and Messier, 2011; Brassard et al., 2011; Vilà et al., 2013; Jucker et al., 2014), but others have found invariant or even negative relationships (e.g. Chen and Klinka, 2003; Jacob et al., 2010; Cavard et al., 2010). A meta-analysis of published field measurements reveals equal abundances of species and a broad variety of light strategies among species as important prerequisites for positive biodiversity–productivity relationships (Zhang et al., 2012).

In addition to field studies and experiments, forest models serve as a means of investigating biodiversity–productivity relationships. They allow the analysis of a variety of species mixtures over long periods. Morin et al. (2011)used a well-established forest gap model (Bugmann, 1996) to show that tree species richness promotes productivity (defined as biomass increments per year) in mature European temperate forests. In addition, the authors show that competition for one resource (here light) is sufficient to generate an increase in forest productivity with species richness.

Despite the widely recognized positive trends found in diversity–productivity relationships in forests, it remains unclear why different relationships can be found. Besides the influence of species diversity it is well known that basal area also influences productivity (e.g. Vilà et al., 2013). Recent studies also highlight the influence of tree size heterogeneity on productivity. For instance, some studies found a negative effect of size heterogeneity in several monocultures (Cordonnier and Kunstler, 2015; Bourdier et al., 2016), whereas Dănescu et al. (2016) revealed positive effects of size heterogeneity (and species diversity) in mixed stands.

In this study, we analyse the role of species diversity and forest structure, which is described by basal area and tree height heterogeneity, on forest productivity. We focus on small-scale forest stands (400 m^2), wherein all trees of a given structure interact due to light competition. Every forest stand is characterized by its tree species mixture and forest structure. We simulated a large set of forest stands by randomizing species identities using a new forest modelling approach, which we refer to as the forest factory approach. The range of investigated forest types includes natural, disturbed and managed forests as well as young and old forests. We estimate the wood production of every tree in the stand using physiological relationships encoded in a process-based forest model. The wood production of all trees in the analysed stands is summed up to estimate instantaneous above-ground wood production

(Bohn et al., 2014). This approach also allows an exploration of the effect of species distribution within a given forest structure. We suggest a new index for analysing this effect.

Using this new forest factory approach, we analyse approximately 300,000 forests stands to answer the following questions: (i) How does forest structure compared with species number influence forest productivity (AWP)? How does especially tree height heterogeneity influence forest productivity? (ii) Do different forest structure types show different biodiversity–productivity relationships? (iii) How does basal area and tree height heterogeneity influence forest productivity compared with optimal species distribution?

3.3 MATERIAL AND METHODS

3.3.1 *Overview of our approach*

The forest factory method involves generating a large number of forest stands that vary in their tree species mixtures and forest structures (figure 7). The creation of forest stands is based on three simple construction rules (see §3.3.3). Forest stands are formed based on different stem diameter distributions, which represent typical forest structures of early to late succession and of managed and unmanaged temperate forests. Species mixtures include the following eight species: pine, spruce, beech, ash, oak, poplar, robinia and birch (255 mixtures in total). These species vary markedly in shade- tolerance, allometry, productivity and responses to climate (more information see Appendix A). Based on environmental conditions, tree productivity is measured for each single tree over 1 year (see §3.3.2) and is summed. We then group forest stands into nine different forest structure classes based on basal area and tree height heterogeneity values (see §3.3.4). Note that we only simulate individual years and do not simulate forest succession over longer time periods (e.g. hundreds of years). Finally, we quantify the influence of forest properties (basal area, tree height heterogeneity and optimal species distribution) on forest productivity (see §3.3.5).

3.3.2 *Productivity of a single tree*

We use processes of a spatially explicit forest gap model (here FORMIND) to estimate tree productivity (above-ground wood production, AWP). Over the last 20 years, this model has been used to study various forests around the world (e.g. Köhler and Huth, 1998, 2004; Groeneveld

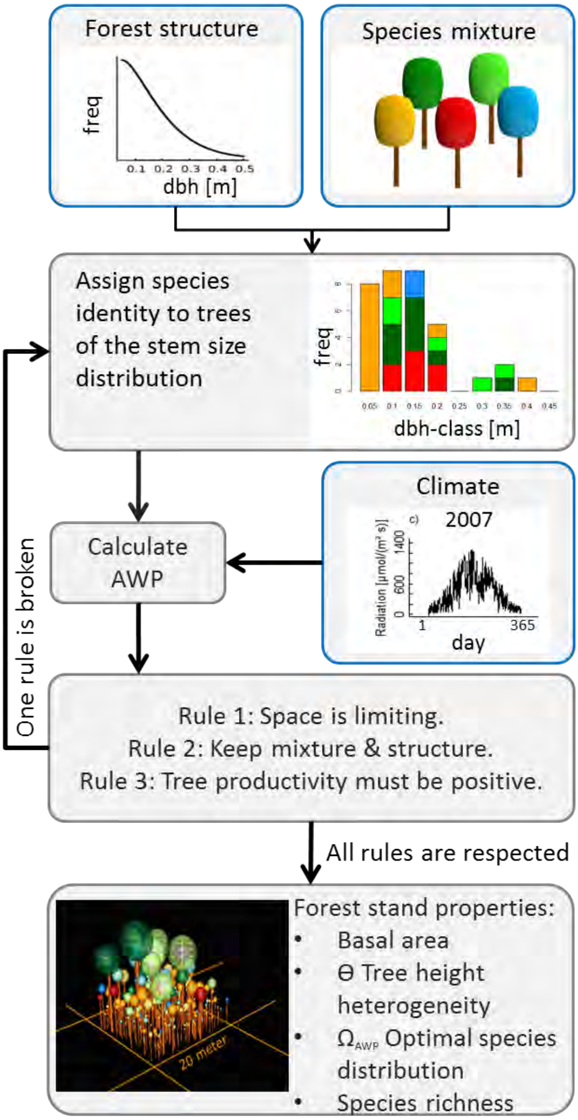


Figure 7: Workflow to generate one forest stand with the forest factory approach. Blue boxes indicate the input variables.

et al., 2009; Gutiérrez and Huth, 2012; Fischer et al., 2014; Kazmierczak et al., 2014; Fischer et al., 2016). The model simulates establishment, mortality, growth of trees including competition for light. Eight tree species have been parametrized for the temperate zone differing in their shade-tolerance, allometric relationships, carbon allocation processes and preferred environmental conditions. In a previous study Bohn et al. (2014), these were parametrized using forest yield tables for Germany and measured species-specific traits and were validated using yield tables for France.

The forest factory method only uses competition and productivity processes of the forest gap model as well as allometric relationships. The allometric relationships used are assumed to be invariant (independent of the competitive environment a tree is found in). However, productivity rates of single trees (AWP_{tree}) are affected by available light, available soil water and air temperature. To estimate these tree-specific environmental conditions, we use daily mean radiation, daily mean air temperature and daily sum of precipitation (1 year simulation). The available light at the top of a tree is the measured radiation level reduced by the shading due to larger trees within a forest stand. The available soil water within a stand results from precipitation, tree evapotranspiration and run-off. We used a climate dataset from a temperate forest in central Germany (eddy flux station at Hainich in the year 2007 Knohl et al. (2003); Appendix C.1, figure C.1).

The productivity rate of a single tree is calculated as the difference between photosynthetic production and respiration. The calculation of photosynthetic production uses species-specfic light-response curves and includes the available light at the top of a tree, crown size and self-shading with its crown.In addition, limitations due to available soil water and air temperature can modify the productivity rate (Gutiérrez and Huth, 2012; Fischer, 2013; Bohn et al., 2014).

The photosynthesis of a tree (P_{tree}) is partly consumed by its maintenance respiration Rm, which is dependent on air temperature and tree biomass (Piao et al., 2010), including allocation to non-wood tree tissues. Remaining organic carbon is transformed for above-ground wood production (AWP_{tree} and into a proportional fraction through growth respiration (r_g)).

$$AWP_{tree} = (P_{tree} - R_m) * (1 - r_g) \tag{14}$$

To get the forest stand AWP, we sum up AWP_{tree} of all trees of the forest stand. Note that changes of AWP due to mortality and establish-

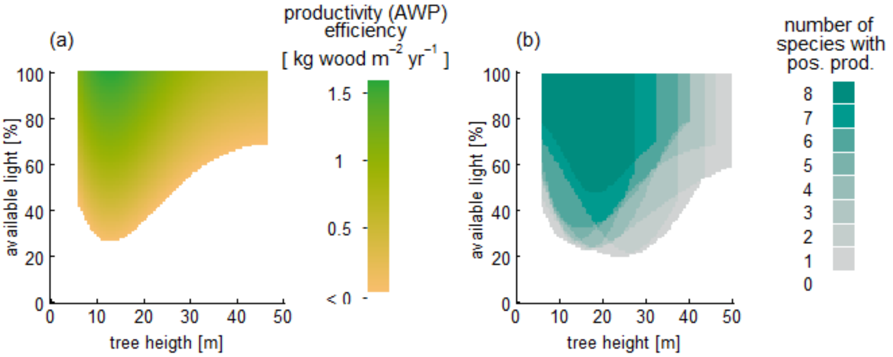


Figure 8: (a) Productivity efficiency ($AWP_{\mathtt{tree}}$ per unit crown area of pine) depends on tree height and available light at the top of a tree under the given environmental conditions at the Hainich station in the year 2007.Productivity efficiencies of tree heights with a diameter at breast height (dbh) smaller than 5 cm and light–height combinations with negative productivity are not plotted (white area). (b) The pancake plot shows how many species exhibit positive productivity under certain light–height conditions.

ment processes within a forest stand are not included (Coomes et al., 2014).

3.3.3 *Construction of forest stands*

Forest stands vary in forest structure and species mixture and each cover an area of 400 m^2 . The creation of forest stands follows three construction rules: (i) Available space limits the number of trees within a forest stand. Thus, the spatially explicit modelled shape of tree crowns limits the maximum number of trees per area. (ii) A predefined forest structure and species mixture is realized. Forest structures are often described based on stem size distributions, which follow a Weibull distribution (e.g. Ryniker et al., 2006; Wang et al., 2009; Taubert et al., 2013)). We use 15 different stem size distributions to describe even-aged (trees with the same stem diameter) and uneven- aged forests (variable stem diameters) of different successional stages (all distributions are shown in detail in Appendix C.2, figure C.3). The stem diameters range between 5 and 50 cm. However, (iii) every tree must exhibit positive productivity. The productivity of a tree is dependent on its species identity, species-specific limitation factors of photosynthesis, tree height and degree of shading from larger trees. As we always use the same climate dataset for construction, photosynthesis limitation factors are constant but species specific (figure 8 a shows productivity for pine while those for other species are shown in Appendix C.2,figure C.4). Productivity levels under the same environmental conditions vary among species, as does the number of possible combinations of light and height levels, which result in positive productivity (figure 8 b areas of positive productivity for all species). As a tree must maintain positive productivity to survive, there are light–height conditions in which some species cannot survive. In such cases, the species identity of a tree (with negative productivity) is replaced by an alternative species identity of the existing mixture, which shows positive productivity. In some cases, when no species identity allows for positive tree productivity, the number of trees is reduced. The presence of fewer trees reduces the shading levels such that one species identity with positive productivity can also be found for shaded trees (for a more detailed account of the creation of forest stands, see Appendix C.3).

In total, we generated 379,170 forest stands. The generated forest stands reach a basal area of up to 60 m^2 and an above-ground biomass of 543 todmha^{-1}. Stem quantities range from 25 to 14 000 stems per hectare.

3.3.4 *Forest productivity and classification*

The analysed productivity of forest stands represents the mean above-ground production over 5 years. Each year is simulated separately using the same initial forest stand (to simulate forest stand productivity under variable climates; Appendix C.1, figure C.2). We used climate data of the Hainich station climate data for the years 2000–2004. It should be noted that the new method used in this study requires much less computation time than do normal forest succession simulations because only a few years need to be simulated for each forest stand to obtain productivity.

We use two simple measures to quantify the structure of forest stands: basal area (BA), which is the sum of all cross sections of stems at breast height per area, and the standard deviation of tree heights within a forest stand to describe tree height heterogeneity (θ). For further analysis, we grouped the dataset into nine structure classes: three basal area classes (small, moderate and large, 5–15, 15–25 and 25–35 $\mathrm{m^2ha^{-1}}$, respectively) and three tree height heterogeneity classes (low, moderate and high, 0.5–2.5, 2.5–4.5 and 4.5–6.5 m, respectively).

Nearly all structure classes contain forest stands, which include between one and eight species. Only the forest stand with a high BA and high θ cover a range from one to seven species (figure 9, Appendix C.3, figure C.5), which contains only 0.4% of all forest stands. This is a result of random construction processes within the forest factory. Note that the maximum species number of possible species has been assumed to

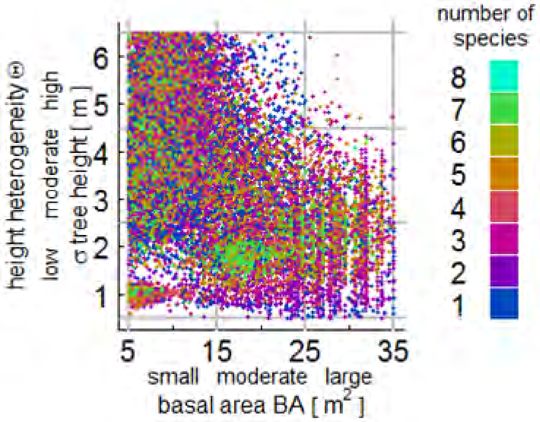


Figure 9: Overview of the 300,000 selected forest stands. Scatter plot between basal area and tree height heterogeneity, where each dot represents one forest stand. Colours denote the number of species within a forest stand. For the sake of clarity, we randomly select 3000 plots for every species quantity (1–7 species) and all forest stands including eight species. Grey lines separate the nine different structure classes of low, moderate and high (0.5–2.5, 2.5–4.5 and 4.5–6.5 m) tree height heterogeneity θ levels and small, moderate and large (5–15, 15–25 and 25–35 m^2ha^{-1}) basal areas. The four smaller pictures in the four corners serve as illustrations of the forest structure classes of the forest stands.

be eight in all cases. The forest stands which belong to one of the nine classes sum up to 299,669 forest stands.

For all stands within the same structure class and with the same species mixture we determine an average productivity ($AWP_{mixture}$). Using this method, all mixtures have the same weight in the structure classes. We then average the $AWP_{mixture}$ of forest stands, which include the same number of species to obtain an average productivity ($AWP_{n,s}$) as a function of the species number for each structure class (figure 12).

There are two ways to analyse aggregate productivity values. First, we can average productivity values for different species quantities while keeping the structure constant (figure 11 a).

$$AWP_S = \frac{1}{n} \sum_{i=1}^{n} AWP_{s,i} \tag{15}$$

In the same way, we can calculate the average productivity level for different structure classes while keeping the species number constant (figure 11 b).

$$AWP_N = \frac{1}{s}\sum_{i=1}^{s} AWP_{n,i} \tag{16}$$

3.3.5 *Quantification of the influence of forest properties on forest productivity*

Forest productivity is dependent on basal area. Thus, the presence of a larger number of trees of the same size increases AWP. Second, AWP is dependent on the vertical tree size structure that we quantified by tree height heterogeneity (θ). Two trees, which do not shade each other, have a higher AWP than the same trees, where one tree shades the other.

Beside basal area and tree height heterogeneity we propose a third forest property index, which we refer to as optimal species distribution in relation to AWP (Ω_{AWP}). Here, we analyse AWP changes due to a change in species identity. For instance, a forest with large beech trees that cover small birch trees has another AWP compared with a forest with birch trees covering beech trees, although the forest structure (and environmental conditions) stays the same. We suggest quantifying this effect by

$$\Omega_{AWP} = \frac{AWP_{obs}}{AWP_{max}} \tag{17}$$

with the observed forest productivity and with the maximum possible AWP of a given forest structure. In calculating, we determine those species identities for every tree found in a forest, which show the maximal AWP (figure 8).Depending on the forest structure, we found compositions of optimal species identities assigned to trees in the forest. For instance, a forest with tall trees and moderate tree height heterogeneity shows optimal AWP if it only consists of beech trees (area A in figure 10). In a forest with moderately sized trees and moderate tree height heterogeneity, different species can exhibit optimal AWP (area B in figure 10). To quantify the importance of these three mechanisms, we made a partitioning of the variance using as explanatory variable: tree height heterogeneity, basal area and Ω_{AWP}.

3.3.6 *Analysis of the German forest inventory*

To compare our results with German forest inventory III (2012), we selected forest plots that (i) host only species considered in this study and

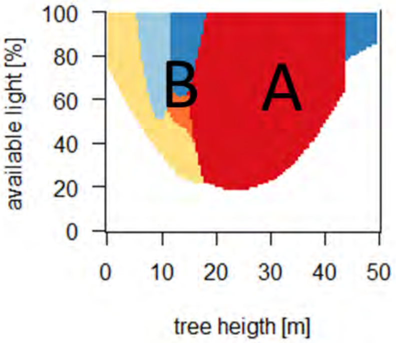


Figure 10: The optimal species distribution plot shows under which conditions (tree height and available light) species present maximum productivity per crown area based on environmental conditions at the Hainich station in the year 2007. Trees in a forest of tall trees of moderate tree height heterogeneity should be found around A, whereas trees in a forest of moderately sized trees and moderate tree height heterogeneity should be found around B. Colours denote different species (light blue, pine; blue, spruce; yellow, robinia; orange, ash; red, beech).

(ii) are located on flat terrain (sloped at less than 15%). As the inventory is based on variable radius sampling, we only considered plots with trees with a maximum diameter at breast height (dbh) of 0.5 m (which results in a maximal area of approx. 400 m^2 of the plots).

We analysed the influence of structure on productivity within the selected plots of the German forest inventory in the same manner as the forest factory and calculated first $AWP_{mixture}$ (with a minimum of two plots per class of every species composition). In total, 5054 forest plots of the German forest inventory were processed. We then calculated AWP_S and AWP_N (see above). Because forest stands with large tree height heterogeneities were rare (2% show height heterogeneity larger 4 m), we calculated results for four new height heterogeneity classes (0–1, 1–2, 2–3, 3–4 m) and added one basal area class (35–45 m^2). A comparable analysis using forest stands of the forest factory uses the same structure classes. Further, we quantify the effect of diversity on productivity by averaging over all structure classes (results in Appendix D.2).

3.4 RESULTS

In this study, forest stands, generated via the forest factory approach, are used to investigate the effects of forest structures and biodiversity levels

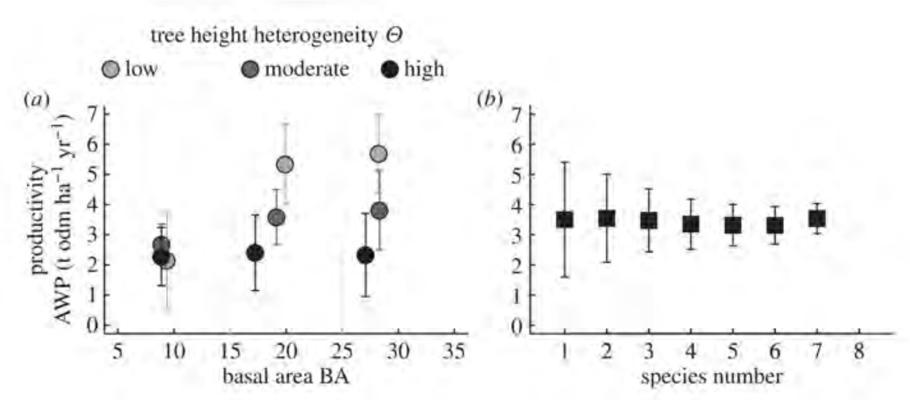


Figure 11: Analysis of mean productivity (above-ground wood production) of the forest stands. (a) Mean productivity of the nine structure classes: small, moderate and large basal area BA (5–15; 15–25; 25–35 $\mathrm{m}^2\mathrm{ha}^{-1}$) and low, moderate and high tree height heterogeneity θ (0.5–2.5; 2.5–4.5; 4.5–6.5 m); (b) mean productivity depending on the numbers of species in a forest stand. Grey bars denote the mean standard deviation.

on productivity (AWP). We classify forest stands into nine different forest structure classes that differ in tree height heterogeneity and basal area (in total, approx. 300,000 forest stands). The tree species diversity levels range from one to eight species.

3.4.1 *Analysis of the forest stands of the forest factory*

The mean productivity of the nine forest structure classes varies from 2.1 to 5.7 t organic dry matter (odm) $\mathrm{ha}^{-1}\mathrm{y}^{-1}$ (figure 11 a). Increasing basal area results in increasing forest stand productivity in cases of low and moderate height heterogeneity. Height heterogeneity is negatively correlated with productivity for stands with moderate and large basal areas. Species richness hardly influences the forest productivity, which remains relatively constant at 3.5 $\mathrm{todmha}^{-1}\mathrm{yr}^{-1}$(figure 11 b). In contrast with the effect of structure, variability of productivity is negatively affected by species richness. This observed effect of structure or diversity on productivity does not change when functional diversity is analysed instead of species number (Appendix D.1, figure D.1). We also analysed the sensitivity of these results to an increase or decrease in the mean annual temperature of 1.5°C. Here, the absolute productivity changes slightly but the general pattern remains the same (Appendix D.1, figure D.1).

When analysing the relationship between tree diversity and productivity for forest stands for each structural class, we found several rela-

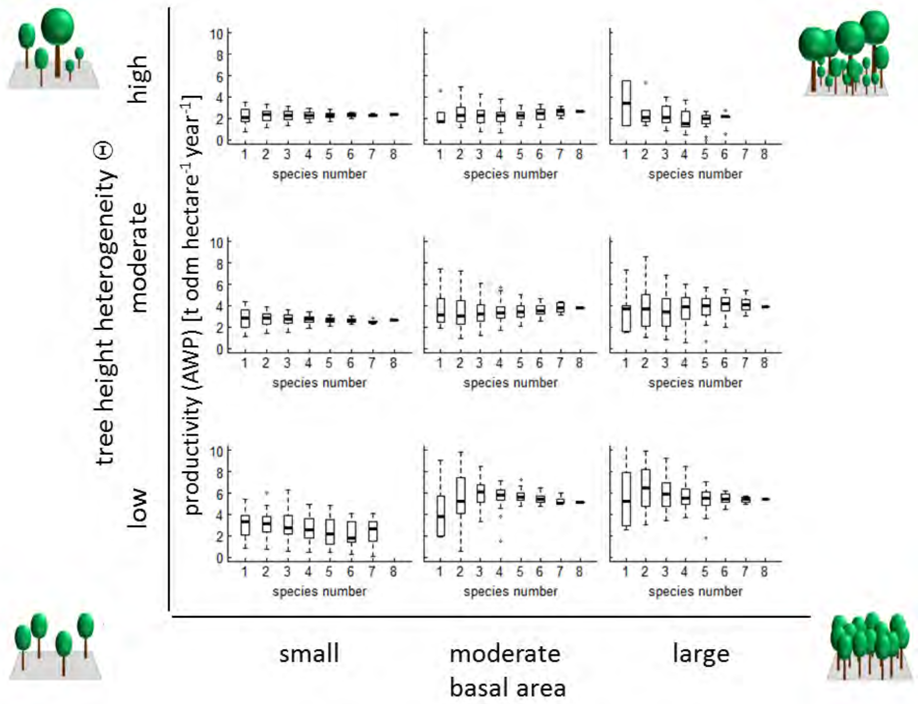


Figure 12: Boxplots of productivity values (AWP) for each number of species among the nine forest structure classes: small, moderate and large basal areas BA (5–15; 15–25; 25–35 $m^2 ha^{-1}$) and low, moderate and high tree height heterogeneity θ (0.5–2.5; 2.5–4.5; 4.5–6.5 m). The four smaller pictures in the four corners illustrate the forest structure classes of the forest stands.

tionships (figure 12): (i) increasing relationships for forest stands with moderate or large BA and moderate θ; (ii) a bell-shaped relationship for forest stands with moderate or large BA and low θ; (iii) invariant relationships for forest stands with small BA and moderate or high θ and (iv) decreasing relationships for forest stands with small BA and high θ. In nearly all cases, the variability of productivity decreases with increasing richness. Overall, from low to high basal area and from high to low tree height heterogeneity increases the effect of species numbers on the diversity–productivity relationship (mean productivity and variability). However, the effect of diversity on productivity among classes is less pronounced than the general effects of structure (figure 11 a and figure 12).

3.4.2 *Quantification of the influence of forest properties on forest productivity*

The three forest properties (basal area, tree height heterogeneity and Ω_{AWP}) influence forest productivity quite strongly but differing in their intensity for different forest classes. For all forest stands, the three mechanisms together explain 70% of the variance, with BA and θ alone explaining 50% (figure 13; all forests). For eight of nine classes, $\Omega_{AWP}$is the most important driver of productivity. Only forests presenting low height heterogeneity small basal areas are more sensitive to structural changes than Ω_{AWP}. With increasing basal area and tree height heterogeneity, Ω_{AWP} becomes increasingly important. Species richness is weakly correlated with the three mechanisms (R^2 values up to 0.25, Appendix D.5, figure D.8). Note that a high correlation between forest properties (BA, θ and Ω_{AWP}) and productivity does not automatically correspond to a high correlation between such mechanisms and diversity. For instance, in forest stands of low height heterogeneity and large basal area, diversity correlates best with tree height heterogeneity ($R^2 = 0.23$), but productivity is mainly determined by Ω_{AWP} ($R^2 = 0.75$), which is not correlated with diversity ($R^2 = 0.01$; Appendix D.5, figure D.8)

3.4.3 *Analysis of the German forest inventory*

We analysed the German forest inventory with the same method as applied to the forest factory. The productivity (AWP) of forest increases with basal area, whereas it decreases with increasing tree height heterogeneity. This pattern is quite similar to the pattern observed in the analysis of the corresponding subsample of the forest factory dataset (figure 14). However, the influence of tree height heterogeneity on forest productivity is higher in the forest factory dataset. For forest stands with high θ, we observe almost constant productivity of forest stands as in the forest stands of the forest factory. According to our analysis, diversity detached from forest structure shows no effect on productivity in the German forest inventory (for further details, see Appendix D.2).

3.5 DISCUSSION

In this study, we presented a new approach (the forest factory method), which allows us to investigate the interplay between tree species diversity, structure and productivity in forest ecosystems. We analysed 300,000 forest stands generated by the forest factory model approach, whose constructions are based on forest gap model algorithms includ-

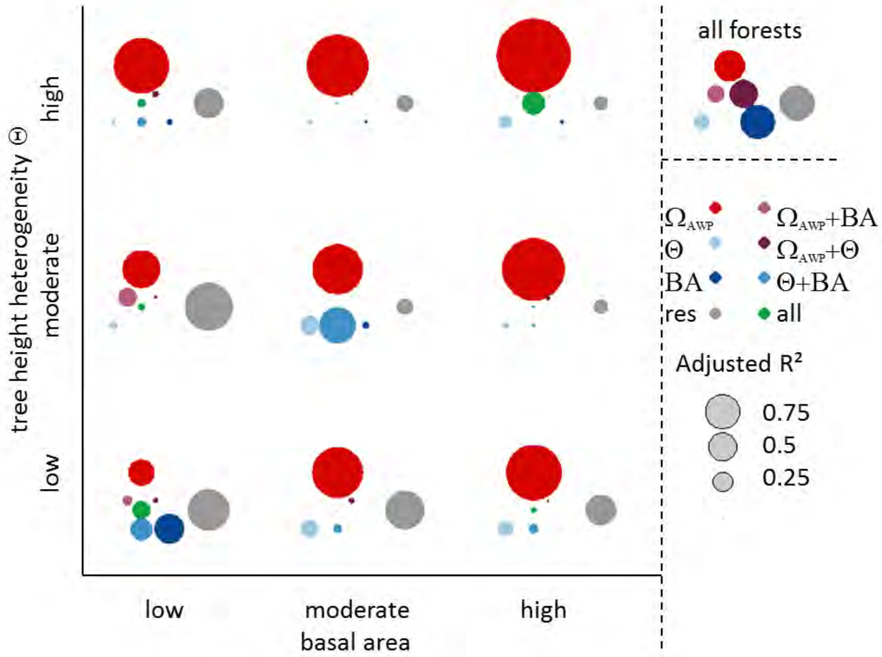


Figure 13: Partition of variance for all forests and for the nine structure classes. Circles denote the adjusted R^2 . Colours represent the different mechanisms (blue, forest structure; red, Ω_{AWP}purple, additional R^2 for combinations of $\Omega_{AWP}$and one structure mechanism; green, additional R 2 when all mechanisms are combined).

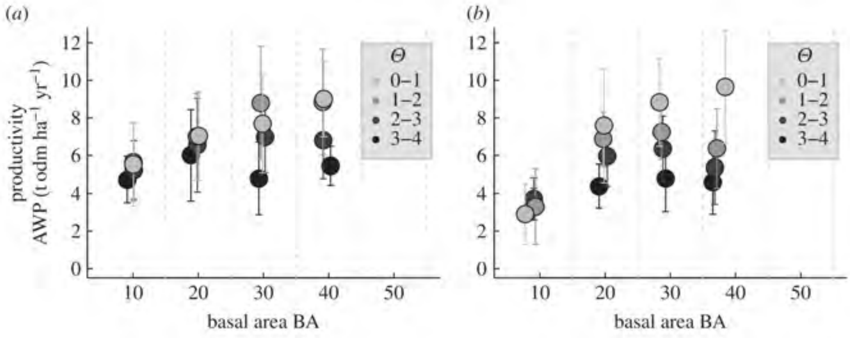


Figure 14: Analysis of mean forest stand productivity (above-ground wood production) of the German forest inventory (a) and forest stands of the forest factory (b) for 16 structure classes. Basal area classes were 5–15, 15–25, 25–35 and 35–45 m^2 ha^{-1} . Tree height heterogeneity (θ) classes were 0–1, 1–2, 2–3 and 3–4 m.

ing species-specific tree allometries, growth processes and inter- individual competition. The analysis revealed strong effects of forest structure on productivity compared with effects of diversity. For different structure classes, we found increasing, constant, decreasing and bell-shaped relationships between species richness and forest productivity.

3.5.1 *The forest factory approach*

The forest factory method applies typical algorithms used in forest models to simulate annual forest growth for a large number of forest stands. The construction of forest stands follows simple rules. Using this method one does not need to simulate forest succession over long periods (e.g. hundreds of years) and hence the computation time required for this approach is quite short. This constitutes an important advantage, as computation time is a strong limiting factor for classical studies that use forest models Seidl and Lexer (2013) . Our approach covers a broad set of successional stages of managed, disturbed and natural forests. We assumed an equal weight for each constructed forest stand. However, it would be possible to include information about frequency of forest stands to adapt the sampling to that of a certain field study. For instance, the German forest inventory includes 20 times more forest stands with $\theta < 1$ m compared with stands with $\theta > 4$ m.

Allometric relationships, modelled tree growth and competition processes behind this analysis have been tested and applied in several studies. Nevertheless, one should be aware of several constraints. For instance, we use average species-specific allometries, which are based on yield tables of monocultures and average values of measured traits (Bohn et al., 2014). The allometries could differ from those of a specific site, as they can be influenced by the individual growth conditions of trees (Jucker et al., 2014). In addition, disturbances and management can modify individual tree allometries. Including allometric processes measures in forest models is an important, but also complex task and should be considered in future work. Please note that the model used does not consider competition for nutrients. According to Zhang et al. (2012), this factor might be of limited relevance to diversity–productivity relationships (because nutrient supplies do not typically change considerably over a few metres and within 1 year).

One important rule for the construction of forest stands is that trees must exhibit positive productivity (third rule of the forest factory). However, trees can also survive for several years in poor conditions. Therefore, in our final analysis, we determined mean productivity levels for five individual years. Thus, our results are not affected by one specific year. They represent the average productivity level for a temperate climate including years characterized by poor and good growing conditions. However, when climatic patterns change for a longer period of time, all species will change their productivity pattern (under the conditions of available light and tree size, figure 8b). A second important point in the forest factory approach is that shade-tolerant trees have a higher probability to occur in the understorey, as these shade-tolerant trees grow also under reduced light conditions. This higher abundance of shade- tolerant species is also found in field studies (Gilbert and Lechowicz, 2004). It is unclear how relevant this effect is within forest stands of the forest factory We, therefore, run an additional analysis to quantify the influence of unequal abundances using only forest stand with more or less equal abundance (FEve greater than 0.9; (Laliberté and Legendre, 2010); Appendix D.6, figure D.10). We found similar patterns as in the original analysis. Only forests with high basal area and high tree height heterogeneity differ in their average productivity from the analysis of the full dataset. In these forests, we found a lower AWP (compared with the full dataset).

In this study, we focus on competition between trees at small spatial scale over short time periods. For larger forests (e.g. several hectares) structural characteristics can differ from small-scale features. For instance, for an old-growth forest, height heterogeneity levels may be quite high if the forest includes small and large trees. Nevertheless, trees could be divided into small-scale regeneration patches with small trees and sections that include mainly large trees. Such a forest would exhibit productivity levels which can be estimated from productivity levels over several forest stands with low tree height heterogeneity. This productivity would be higher (all patches have a low θ) than productivity of a forest consisting of patches including large and small trees on a local scale (all patches have a high θ; figure 11 a). The same consideration could be made for longer time periods (where mean θ is high, whereas for different points in time the θ of forest stands could be quite low).

3.5.2 *Comparisons with field datasets*

Our analysis of the forest factory and the analysis of the German forest inventory show that variables, which characterize forest structure (basal area, tree height heterogeneity), are the dominating drivers of forest productivity for the analysed large datasets (figure 13 and 14). Analysis of other national forest inventories found also strong effects of forest structure. For instance, Vilà et al. (2013) analyse six European forest inventories (the German inventory was not included) and identify basal area as the most important variable to predict forest productivity, whereas diversity was of minor importance. Paquette and Messier (2011) found similar results analysing 15,000 plots of the Canadian forest inventory. However, tree size heterogeneity was not included in these studies. Bourdier et al. (2016) analyse stands of the French forest inventory (approx. 6,000 plots) with one species and found a negative effect of tree size heterogeneity on forest productivity. However, other analysis reveals a positive effect of tree height heterogeneity. For instance, Dănescu et al. (2016) analyse approximately 400 plots (which vary in time and/or location) in southern Germany covering a broad climate gradient. The plots host different mixtures of three species. The positive effect of tree size heterogeneity might be related to the larger size of the analysed stands (plot area $\geqslant$ 0.27 ha). As discussed above, such large area could be a composition of small stands with different forest structures (which may favour higher productivity than a homogeneous structured stand). We also showed that forests with larger height heterogeneity are quite sensitive to optimal species distribution. With increasing Ω_{AWP}forest productivity rises. This seems to outperform the negative effect of height heterogeneity in the stands in southern Germany.

Our analysis of the forest factory dataset (and the German forest inventory) shows no effect of diversity on forest productivity (figure 11; Appendix D.2). However, when the mean productivity for different diversities was calculated (and forest structure was not considered), we found a 10% increase in productivity between one and two species mixtures within the German forest inventory. This corresponds to the results of other studies (e.g. Vilà et al., 2007; Zhang et al., 2012)). This positive relationship may be attributed to the fact that 71% of German forest inventory plots show a θ lower than 2.5 m and basal area values greater than 25 $m^2\ ha^{-1}$. These types of forests, which are mainly driven by the optimal-species-distribution mechanism, show positive relationships between diversity and productivity (figure 13). In Appendix D.8, we discuss additional studies that found positive (e.g. Edgar and Burk, 2001) and negative effects of diversity on productivity (e.g. Jacob et al., 2010) with our results.

3.5.3 *Forest properties*

Additive partitioning can be used to analyse the influence of complementarity and selection effects on diversity–productivity relationships (Loreau and Hector, 2001). This method is based on a comparison of observed yields with expected yields (Appendix D.4 for further details). For our analysis using 300,000 forest stands, no significant trends were found concerning complementarity and selection effects (the best R^2 is 0.01; Appendix D.4, figure D.6). Also for forest stands in the different structure classes we got similar results; both factors could not explain productivity variations (the best R^2 is 0.06). Forest properties (basal area, tree height heterogeneity and Ω_{AWP}) explain forest productivity much better (figure 13).

Different indices were developed to describe forest structure (e.g. Pommerening, 2002). We tested also the effect of mean tree height (by replacing basal area in the analysis, Appendix D.8, figure D.10). We observed similar patterns compared with the original analysis. This might be related to the fact that for the stands of the forest factory basal area and mean height are partly correlated ($R^2 = 0.51$). However, it would be worth analysing the influence of additional structural indices and combination of them on the diversity–productivity relationships (e.g. LAI, Gini index of tree sizes, stem density index).

3.6 CONCLUSION

In this study, we present a novel approach (the forest factory method), which generates possible combinations of forest structures and species mixtures. We show that over a broad range of forest stands, forest structures are the dominant drivers of forest productivity. However, subsamples reveal various diversity–productivity relationships that can be related to forest structure indices or optimal species distribution.

4

SPECIES COMPOSITION AND FOREST STRUCTURE EXPLAIN TEMPERATURE-PRODUCTIVITY RELATIONSHIPS IN TEMPERATE FORESTS.

4.1 SUMMARY

Increasing temperatures due to climate change influence the wood production of forests. Observations show that some temperate forests increase their productivity due to temperature rise, whereas others reduce their productivity. In this study we analyse, how species composition and forest structure properties influence these temperature sensitivities and which forests show the highest increase of productivity due to temperature rise. We describe forest structure by LAI, forest height and tree height heterogeneity. Species composition is characterised by a functional diversity index (Rao´s Q) and optimal species distribution (Ω_{AWP}). This index quantifies how well the current species distribution deals with the given environmental conditions regarding above-ground wood production. We analysed 370,170 forest stands, which are generated by a forest gap model. These forest stands cover a large number of possible forest types. For each forest stand we estimate annual above-ground wood production under 320 climate scenarios (of one year length), which differ in mean annual temperature (MAT) and intra-annual temperature amplitude (Q95). We then quantify the sensitivity of forest productivity against temperature change as relative change of productivity due to a 1°C temperature rise in mean annual temperature and intra-annual temperature amplitude (SI_{MAT} & SI_{Q95}). Ω_{AWP} shows a strong positive influence on both temperature sensitivity indices of forest (SI_{MAT} & SI_{Q95}). Also both indices show a bell-shaped relationship to forest height. The search for forests benefiting most under rising temperature reveal that there are forests in each successional stage which are positively affected by temperature increase. For such forests large suitability-values are important. In case of young forests of low height, low functional diversity and low tree height heterogeneity support a positive temperature sensitivity of forest productivity. During later successional stages higher species diversity and tree height heterogeneity is needed. In this study we highlight the importance of forest structure and optimal species distribution to understand the temperature-productivity-relationships of forests.

4.2 INTRODUCTION

Climate change alters forest growth by modifying photosynthesis and respiration rates of trees (Cao and Woodward, 1998; Barber et al., 2000; Luo, 2007; Peñuelas and Filella, 2009). Changes of forest productivity have been observed over the last decades all over the world (Nemani et al., 2003; Boisvenue and Running, 2006; Seddon et al., 2016). These observations have stimulated discussions if forest management strategies can be adapted to reduce forest vulnerability to climate change, support recovery after extreme events and compensate anthropogenic Co2-emissions (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Bonan, 2008).

Forest productivity is influenced by several factors. Temperature can influence forest productivity strongly besides other climate variables like CO2-fertilisation or nitrogen deposition (Barford et al., 2001; De Vries et al., 2006, 2009; Solberg et al., 2009; Keenan et al., 2013). Temperature modifies photosynthesis, respiration and growth rates of trees (Dillon et al., 2010; Piao et al., 2010; Wang et al., 2011; Jeong et al., 2011; Heskel et al., 2016). Positive effects on forest productivity (e.g. Delpierre et al., 2009; Bontemps et al., 2010; Pan et al., 2013; McMahon et al., 2010) as well as negative effects have been found in the temperate biome (e.g. Barber et al., 2000; Jump et al., 2006; Charru et al., 2010). So far, it is unclear why forests react differently on temperature change.

Besides the influence of climate, forest productivity is also affected by forest properties which can be grouped into two classes: forest structure and species composition (figure 15). For instance, changes in productivity can result from changes in basal area (Vilà et al., 2013), tree height heterogeneity (Bohn and Huth, 2017), or LAI (Asner et al., 2003). Furthermore, forest productivity increases often with an increasing number of species (Vilà et al., 2007; Zhang et al., 2012).

Forest stands which differ in their forest properties might respond differently to the same climate change (Huete, 2016). For instance the positive effect of increasing temperature on forest productivity fades with forest age in temperate deciduous forests (e.g. McMahon et al., 2010; Bontemps et al., 2010). It has also been observed that higher diversity can buffer the effect of intra-annual variability on forest productivity, as species react differently to the same climate conditions (Morin et al., 2014). Nevertheless, these studies include only a few forest properties and seldom cover both species composition and forest structure indices as key variables. Hence it remains unclear how forest properties influence forest productivity change due to temperature rise and which forests will benefit from rising temperatures.

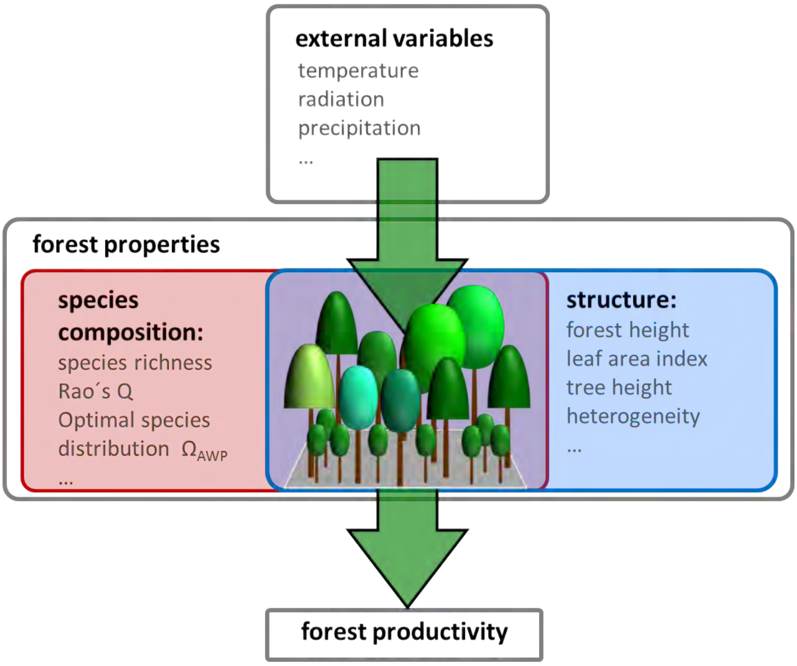


Figure 15: Overview of factors influencing forest productivity. External variables in this study are temperature, radiation, precipitation whereas forest properties are divided into two groups: species composition properties (including the Rao´s Q as a measure of functional diversity and suitability) and forest structure properties (including forest height, leaf area index and tree height heterogeneity).

As far as we know, there is no data set available which covers different forest types systematically (low and high diverse forest with various forest structures) under almost identical climate conditions. Even if a larger number of forest stands would be available, it would be difficult to manipulate temperature keeping other climate variables constant (e.g. radiation). An alternative option is the application of forest models which can be used to estimate application forest productivity under different climate conditions (e.g. Lasch et al., 2005; Bohn et al., 2014). For instance, Reyer et al. (2014) investigated the effect of climatic changes on forests by simulating 135 forest stands 30 years into the future. There are also model-based studies, which systematically analysed the effect of species diversity on productivity and stability over long periods (Morin et al., 2011, 2014). However, disturbed or managed forest stands and the influence of climate change was not included in such analysis.

In this study we therefore propose a new simulation-based approach. First, we generate a huge number of forest stands covering various forest structures and species mixtures (for up to eight temperate tree species). Annual forest productivity (above-ground wood production, AWP) is then calculated for all forest stands based on climate scenarios, which differ in the mean annual temperature (MAT) and the intra-annual temperature amplitude (Q95). We aim to analyse (i) how the productivity of forest stands (AWP) is influenced by an increasing mean annual temperature and (ii) an increasing intra-annual temperature amplitude. (iii) Which forest stands will benefit most from rising temperatures?

4.3 METHODS

To analyse the effect of temperature on the productivity of forest stands we use a model approach called “forest factory” (Bohn and Huth, 2017). With this approach we generate 370,170 different forest stands (see § 4.3.1). The used 320 climate scenarios differ in mean annual temperature (MAT) and intra-annual temperature amplitude (Q95). For all forest stands and climate scenarios we estimated the annual above ground wood production (AWP). Finally, we calculated the stand-specific sensitivity of productivity against temperature change ($SI_{MAT}$and SI_{Q95}) as relative change of forest productivity per temperature change of 1°C (see § 4.3.2). To relate these sensitivities to forest structure and species diversity we characterised every forest stand with five properties (see § 4.3.3). We analysed the influence of the five forest properties on temperature sensitivity values using boosted regression trees (see § 4.3.4). Finally we assume forest height as proxy for the successional stage of forests and analysed which combination of forest properties depending on height results in the highest sensitivity values (see § 4.3.5).

4.3.1 *The forest factory approach*

The forest factory combines 15 different forest types (a gradient of stem size distributions covering young and old, disturbed and undisturbed forest types) with 256 species mixtures (all possible combinations of pine, spruce, beech, oak, ash, poplar, birch and robinia). It generates forest stands with the size of 400 m^2 using the following rules: (i) Space limits the maximal number of trees. (ii) Every tree must have a positive productivity under a typical temperate climate. To calcualte the productivity of all tree within the forest stand, we use a climate time series of the year 2007, measured at the Hainich national park, Central Germany. Bohn and Huth (2017) presented a detailed description and discussion of the forest factory. Parameter sets and algorithms used in the forest factory are based on the FORMIND-model version for temperate forests (see Appendix A, Bohn et al., 2014; Fischer et al., 2016).

4.3.2 *The forest productivity under temperature variation*

The productivity (AWP) of a single tree is calculated as the difference between climate driven photosynthesis and respiration rates. The photosynthesis rate (P_{tree}) is based on the available light at the top of the tree, the crown size and self-shading within the crown. The available light at the top of a tree depends on the radiation above the canopy, reduced by the shading of larger trees within the forest stand. Furthermore, productivity can be limited by available soil water and due to air temperature (Gutiérrez, 2010; Fischer, 2013; Bohn et al., 2014). The available soil water within the stand is influenced by precipitation, interception, evapotranspiration of trees and run-off. Available soil water and air temperature are used to calculate a photosynthesis-limiting factor ϕ for each tree (Bohn et al., 2014).

One part of the photosynthesis production of a tree (P_{tree}) is allocated to its maintenance respiration (and to non-wood tissues; R_m), which depends on tree biomass and temperature dependent factor ψ (Piao et al., 2010). The remaining organic carbon is transformed into new aboveground wood (AWP_{tree}) and a proportional fraction is used as growth respiration (r_g).

$$AWP_{tree} = (\phi P_{tree} - \psi R_m)(1 - r_g) \tag{18}$$

AWP_{tree} is summed up over all trees to get the productivity of the forest stand – AWP (A more detailed description of modelled growth processes can be found in Appendix A).

To generate a set of 320 annual climate scenarios, we use as starting point daily climate measurements of the Hainich station in central Germany between 2000 and 2004. This time series includes mean daily radiation, precipitation and air temperature (see Appendix E, figure E.1). We subdivide this time series into fife distinct time series of one year length. In a first step we increase/decrease the mean annual temperature of each year by adding/subtracting 0.5°C steps between -1.5°C up to +2°C. Second, we change the amplitude of the annual temperature cycle for these time series by modifying the standard deviation of each year by 4% steps between –12 % up to +16 %. This result in five scenario sets (each including 64 time series of one year length), wherein temperature varies, but radiation and precipitation stay constant. Temperature change is quantified using two indices: (i) mean annual temperature (MAT) and (ii) intra-annual temperature amplitude (Q95), which is calculated as the 95 % inter quantile range of all daily temperature values of a given year. In this study we exclude the effects of nitrogen and CO_2 fertilization (as both do not vary strongly within one year) or extreme anomalies (e.g. pathogen attacks) on forest productivity. Figure 16 shows the above-ground wood production (AWP) for three different forest stands depending on mean annual temperature.

We analysed the sensitivity of every forest stand against temperature change by following the approach of Piao et al. (2010). For every forest stand a general linear model is fitted relating forest productivity and the two temperature indices MAT, Q95 and the nuisance parameter year.

$$AWP = \alpha x_{MAT} + \beta x_{Q95} + \gamma x_{year} + \epsilon \tag{19}$$

For every forest we calculated the relative change of productivity due to an increase of 1°C:

$$\begin{aligned} SI_{MAT} &= \frac{\alpha}{\overline{\overline{AWP}}} \\ SI_{Q95} &= \frac{\beta}{\overline{\overline{AWP}}} \end{aligned} \tag{20}$$

In our analysis we excluded all forests stands, whose AWP turns negative if temperature rises by 1°C (2% of all stands).

We also determined the sensitivity of forests to temperature change using the German forest inventory to validate our results. However, the inventory does not include LAI measurements. We therefore used BA

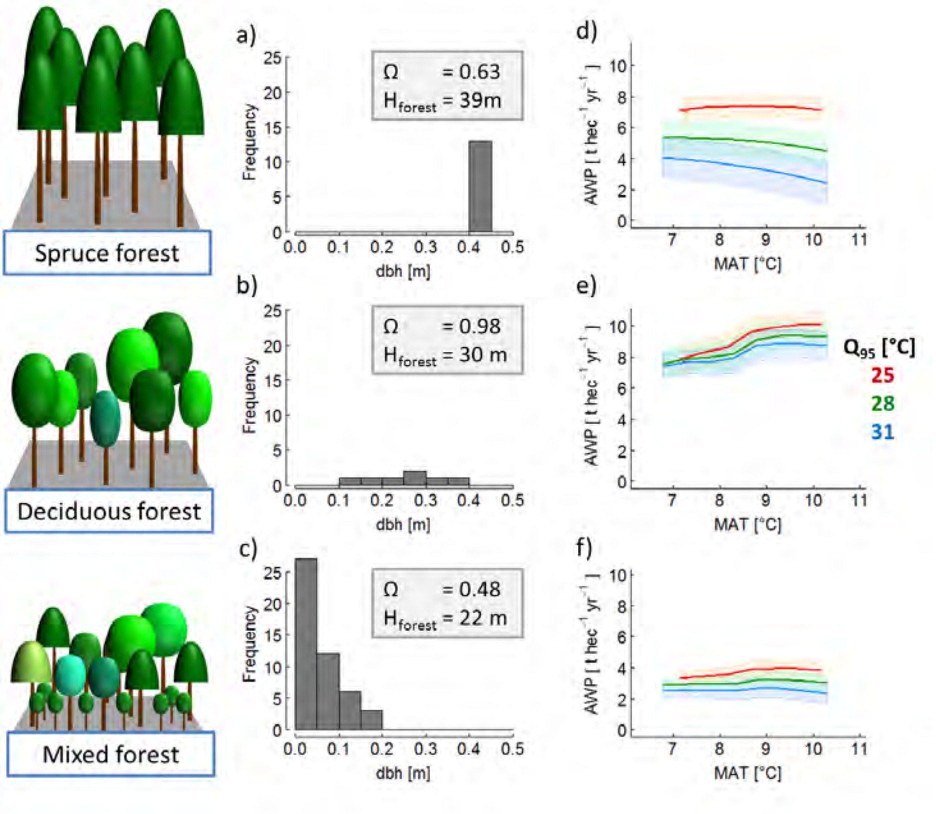


Figure 16: Three different forest examples: an even-aged spruce forest a & b; a mixed forest including only deciduous species c & d; a mixed forest including needle leaf a deciduous trees e & f. a-c) show the stem size distribution of the three examples and suitability values as well as maximal forest height. d-f) shows the above-ground wood production (AWP) depending on mean annual temperature increase (x-axes) and on mean intra-annual temperature amplitude (colours) over those five years with identical temperature modifications. Bands indicate the standard deviation of AWP for the five years with identical temperature modifications.

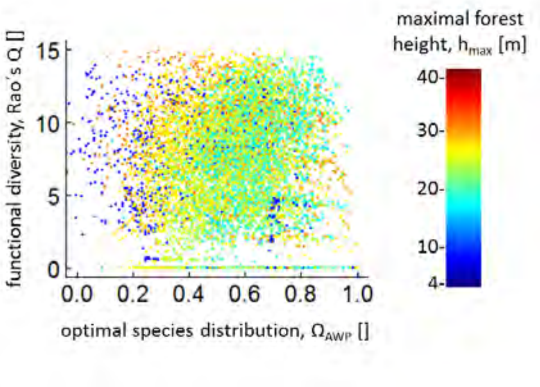


Figure 17: The scatterplot shows the relation between Ω_{AWP} (optimal species distribution), Rao´s Q (functional diversity) and h_{max}(maximal forest height in colour). Each dot represents one forest stand (n=10,000, randomly selected).

assuming it would serve as proxy for LAI and select subsamples of forest stands with a similar structure (BA, tree height heterogeneity, forest height, same species mixtures). In addition, we used elevation as proxy for mean annual temperature, assuming temperature changes of 0.65 °C per 100 metres on average (Foken and Nappo, 2008). Only in the case of spruce and beech monocultures we found enough data to calculate SI_{MAT}-values for several forest structures (see Appendix E.3, figure E.3, E.4). The correlation between the sensitivity values based on field data and simulation data was quite high ($R^2 = 0.65$).

4.3.3 *Five forest properties to describe forest stands*

We used three indices to describe the forest structure: leaf area index (LAI), maximal forest height (h_{max}) and tree height heterogeneity (θ). h_{max} corresponds to the height of the largest tree in a forest stand and θ is quantified by the standard deviation of the tree heights. These indices are easy to derive for forest inventory data, which include tree height information.

To describe species composition, we used Rao´s Q and optimal species distribution (Ω_{AWP}). Rao´s Q quantifies functional diversity based on species abundances and differences in species traits (Botta-Dukát, 2005). Ω_{AWP} analyses instead the optimal location of species within the forest structure. Ω_{AWP} is defined as the ratio of the forest´s productivity to maximal possible productivity of this forest. The optimal productivity of the forest can be estimated by varying only species identities of trees within the forest stand (Bohn and Huth, 2017). All five indices are nearly uncorrelated with the investigated forest stands (figure 2; Appendix E.2 table 10).

4.3.4 *Boosted regression trees*

We used boosted regression trees (BRT) to quantify the influence of the five forest properties on $SI_{MAT}$and SI_{Q95}. BRT is a machine learning algorithm using multiple decision (or regression) trees. This algorithm is able to deal with unidentified distributions (De´Ath, 2007; Elith et al., 2008). Each model is fitted in a forward stage-wise procedure to predict the response of the dependent variable (SI_{MAT}or SI_{Q95}) to multiple predictors (θ, h_{max}, LAI, Rao´s Q, Ω_{AWP}). To omit an over fitting regarding maximal forest height we classified forest stands into 18 classes (H_{max}), which differ in forest height (width of the classes is 2 meters, starting with 4 to 6 metres and finishing with 36 to 38 metres). The BRT try in an iterative process to minimize the squared error between predicted SI values and those of the data set, whereby one part of the data is used for fitting procedure and the other part is used for computing out-of-sample estimates of the loss function (Ridgeway, 10.2015). This BRT-analysis was performed by the R-package gbm 2.1.1 (Ridgeway, 10.2015).

For the machine learning procedure we used a quarter of the data (randomly sampled). To get the best model we varied the following four BRT parameters: learning rate (0.1, 0.05 and 0.01), the bag-fractions (0.33, 0.5 and 0.66), the interaction depth (1, 3 and 5) and the cross-validation (3-, 6- and 9-fold) applying the Gaussian error structure. The best fitted BRTs for both SI_{MAT} and SI_{Q95} show a learning rate of 0.1, a bag-fraction of 0.66, an interaction depth of 5 and 3-fold–cross validation. These two models were used for all further analyses.

4.3.5 *Finding the most benefiting forest stands for different succession stages*

Here we assumed that forest height can be used as proxy for the successional stages of a forest. In every height class (H_{max}) we selected those 5% of forests which have the highest sensitivity values ($SI_{MAT}$and SI_{Q95}). We removed the forest height classes between 10 and 14 metres, as they contain only a few forests (15), and analysed for all other classes the relationship between H_{max} and the forest properties (Ω_{AWP}, Rao´s Q, LAI and θ).

4.4 RESULTS

We analysed the sensitivity of productivity (AWP) to temperature for forest stands, which differ in forest properties (optimal species distribution (Ω_{AWP}), functional diversity (Rao´s Q), tree height heterogeneity

(θ), forest height class (H_{max}) and LAI). For each forest stands the annual above-ground wood production (AWP) was estimated using 320 different climate scenarios. We then estimated the changes in productivity due to the changes of mean annual temperature (SI_{MAT}) and amplitude of the intra-annual temperature amplitude (SI_{Q95}). For the analysed forest stands the mean $SI_{MAT}$is 1.5% $C^{\circ -1}$and the mean $SI_{Q95}$is -5.4% $C^{\circ -1}$(see frequency distributions in Appendix F.1, figure F.1)

A boosted regression tree algorithm has been used to analyse how the five forest properties influence the temperature sensitivity of forests. To test the fitted BRT algorithm, we compare the SI-values of the remaining 75% of the forest stands, which were not used in the fitting process, with the SI-value-prediction of the BRT algorithm (figure 18). The BRT estimate the mean annual temperature sensitivity values (SI_{MAT}) quite well. We found a high R^2 of 0.84 and an RMSE of ± 2.9% $C^{\circ -1}$ (Appendix F.2 figure F.3) The accuracy of the SI_{Q95}-prediction is a bit higher. Analysing the SI_{MAT}-values for a subset of the forest stands which have sensitivity larger than –5% $C^{\circ -1}$(90% of the data), the RMSE decreases to ±1.5% $C^{\circ -1}$. Similarly analysing only those SI_{Q95}-values, which have sensitivity larger than –15% $C^{\circ -1}$(93% of the data), RMSE decreases to ±1.1% $C^{\circ -1}$(see Appendix F.2 figure F.4).

According to this analysis, Ω_{AWP} is the most relevant forest property to explain temperature sensitivities (figure 18; Ω_{AWP} has a relative influence of 87% for SI_{MAT} and 89% for SI_{Q95}; see also Appendix F.2, figure E.4). However the influence of Ω_{AWP} on temperature sensitivity is reduced in case of high Ω_{AWP}-levels. The second relevant forest property is forest height (H_{max}). Forests with heights between 25 and 30 metres benefit most from increasing mean annual temperatures. The other three properties (LAI, Rao´s Q, θ) have a low influence on SI_{MAT}.

The relationships between forest properties and intra-annual temperature amplitude sensitivity (SI_{Q95}) are similar to those found for SI_{MAT}. However an increasing intra-annual temperature amplitude always reduces productivity, whereas an increasing mean annual temperature can have a positive effect on forest productivity.

We also filtered those forest stands which show the highest SI_{MAT}-values in a certain forest height class (5% of forest stands within each height class; figure 19). In all forest classes the filtered forest stands benefit from increasing temperatures. The analysis of their forest properties reveals that they all have high Ω_{AWP} levels. In young forests (low forest height) high temperature sensitivity values can be observed for forest stands with low functional diversity and low tree height heterogeneity (θ). For older forests (of intermediate and high forest height) high temperature sensitivity can be observed for intermediate levels of functional

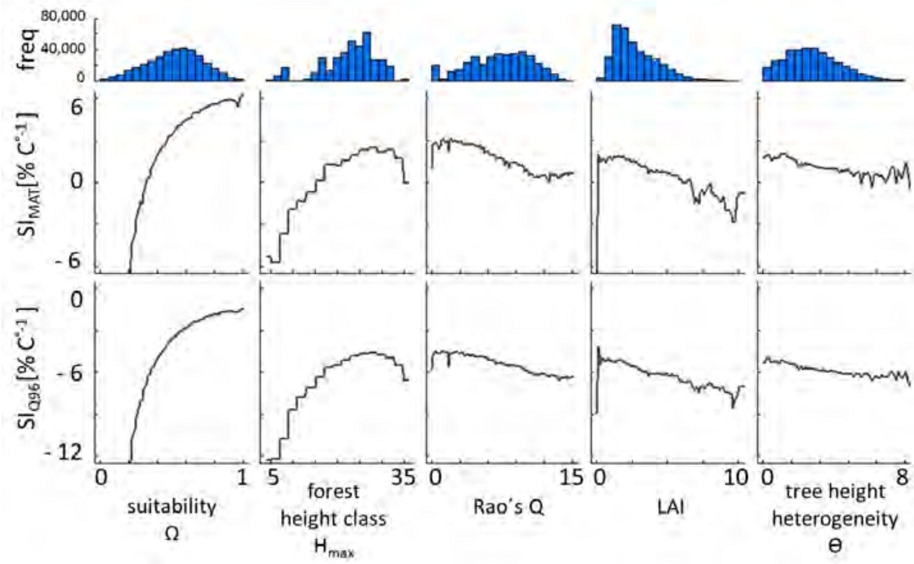


Figure 18: Partial dependency plots of the five forest properties Ω_{AWP}(optimal species distribution), forest height class H_{max}, Rao´s Q (functional diversity), θ(tree height heterogeneity) and LAI (leaf area index) for SI_{MAT} (Sensitivity against changes of the mean annual temperature) and SI_{Q95} (Sensitivity against changes of the intra-annual temperature amplitude). Histograms show frequency of forest property values in the analysed data set.

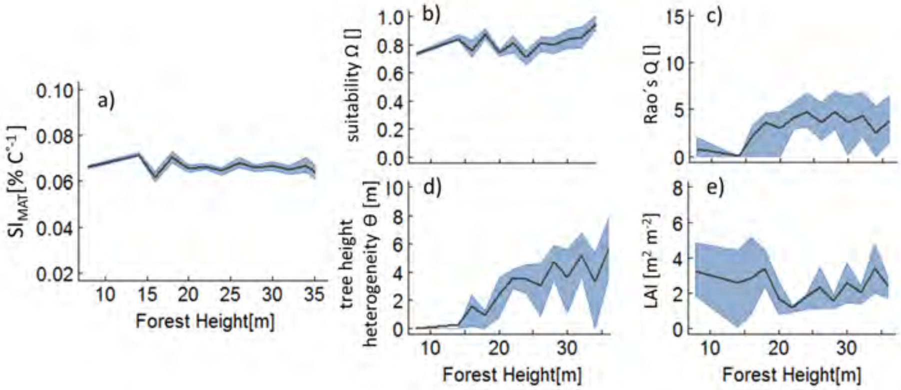


Figure 19: Analysis of those forests, which show the highest 5% of the SI-values depending of forest height. Lines indicate mean values of the subsamples and the grey band indicates the inter quartile range. Figure a) shows temperature sensitivity of productivity against forest height, analysing only the best 5%. b) to d) shows the change of the remaining forest properties within the subsamples (Ω_{AWP} = optimal species distribution; θ = tree height heterogeneity; LAI = leaf area index; Rao´s Q quantifies functional diversity).

diversity. Interestingly, for three variables (Rao´s Q, θ and LAI) the relationships change their character between young and intermediate forest heights. We obtain similar simulation patterns for SI_{Q95}(Appendix F.3, figure F.5).

4.5 DISCUSSION

In this study we analysed how temperature changes affect forest productivity (AWP) and quantify the effect of five different forest properties in this relationship. We analysed the forest productivities (AWP) of 370,170 forest stands based on 320 different climate scenarios. The analysis shows that the two considered forest properties explain the temperature sensitivity of AWP remarkably well. The most relevant property is optimal species distribution (Ω_{AWP}) followed by forest height (H_{max}). Furthermore, we investigated which type of forests stand benefit most from increasing temperatures.

4.5.1 *The study design*

In this theoretical study we present a new approach to investigating effects of climate change (here temperature) on forest productivity (AWP). This approach extends field observations and long term model simulations, as it allows the analysis of forests which already exist, but which also might exist in the future due to management changes and/or disturbances. In case of field observations it is quite difficult to explore the influence of a single climate variable (e.g. temperature) on one target variable (e.g. AWP), as in most cases several variables alter at the same time. Process-based models are one option to analyse such relationships and to separate these effects.

The used forest model simulates photosynthesis and respiration processes of trees, whereby both are influenced by climate (Nemani et al., 2003). The used process formulations are based on well-established algorithms (e.g. Haxeltine and Prentice, 1996; Sato et al., 2007; Bohn et al., 2014, see Appendix A). Simulations of forest growth with the FORMIND-model have been validated in other studies (Fischer et al., 2016). For instance, simulated forest productivity has been successfully compared to Eddy flux sites, the national German forest inventory (Bohn and Huth, 2017) and European yield tables (Bohn et al., 2014).

An advantage of the forest factory approach is the huge set of forest stands that can be analysed (in this study 370,170 stands). The dataset includes forest stand, which often occur in temperate forest (even-aged spruce, pine and beech stands). However, it also includes hypothetical forest stands that could occur through alternative forest management or disturbances (fire, bark beetles, ...). Hence, our data set of forest stands covers a much larger variety of forest property combinations compared to long term forest simulations with the focus on forests in their equilibrium stage (e.g. Morin et al., 2011) or on monocultures (e.g. Reyer et al., 2014). However, it would be possible to reconstruct a forest succession based on the forest factory by selecting forest stands in appropriate order.

Long term simulations with ecosystem models which process modelled climate projections, face a trade-off between cascade uncertainty and path dependency (Wilby and Dessai, 2010; Lindner et al., 2014). The accumulations of model uncertainties over such a process chain result in an increasing uncertainty. Our study design tries to minimize this uncertainty and omits path dependencies by including only those processes which might be relevant for the research question. In this study, for instance, we omit the effect of climate change on regeneration and mortality.

Furthermore, using several climate variables as model input but analysing only the effect of one variable might interpret its effect incorrectly. For instance temperature and radiation often correlate and both can increase productivity. We therefore vary in this study only one variable to guarantee no correlations between the remaining climate variables and the target climate variable. As an increase of global mean temperature of 1.5°C to 2°C cannot be avoided under the RCP2.5 climate scenarios (IPCC, 2013) this study focuses on temperature change. This scenario predicts only small changes of annual precipitation levels for many areas of the temporal biome. However, other scenarios which result in a stronger climate change predict an increase in droughts and changes in annual temperature cycles.

We chose two variables to characterize the intra-annual temperature cycle. Higher MAT result in longer vegetation periods, especially if other resources are sufficiently available, and lead to higher forest productivity (Luo, 2007). On the other hand high temperatures increase respiration (Piao et al., 2010), resulting in higher respiration rates in years with a high intra-annual temperature amplitude (whereby MAT could stay constant).

The here obtained temperature sensitivity values are in the same range as found for temperate ecosystems in heating experiments (+4.4 ± 2.2 $\% \, C^{\circ -1}$, Lu et al., 2013). Within the 16 analysed studies, the experimental plots show almost identical environmental conditions (soil, radiation, precipitation) and species composition. To heat the plots green houses or infra-red heaters were used. Another study based on natural forest stands in New Zeeland found an AWP increase between 5 and 20% $C^{\circ -1}$for forests assuming no change in forest structure and species composition (Coomes et al., 2014). The investigated plots were spread all over New Zeeland and warmer temperature coincides with higher radiation (Mackintosh, 2016). Hence, the analysed temperature effect also includes the influence of radiation. In our setting, the influence of temperature is independent of radiation (as in Lu et al., 2013). We also found a good correlation between SI values derived from growth measurements of the German forest inventory and simulated SI values based on the forest factory (Appendix E.3, figure E.4).

4.5.2 *The influence of forest structure on temperature sensitivity*

To understand the relationship between forest structure and temperature sensitivity we investigated the SI_{MAT}values of single pine trees in forest stands (figure 20). Based on the height of a tree and its available light it is possible to calculate the SI-values for every condition a tree can be

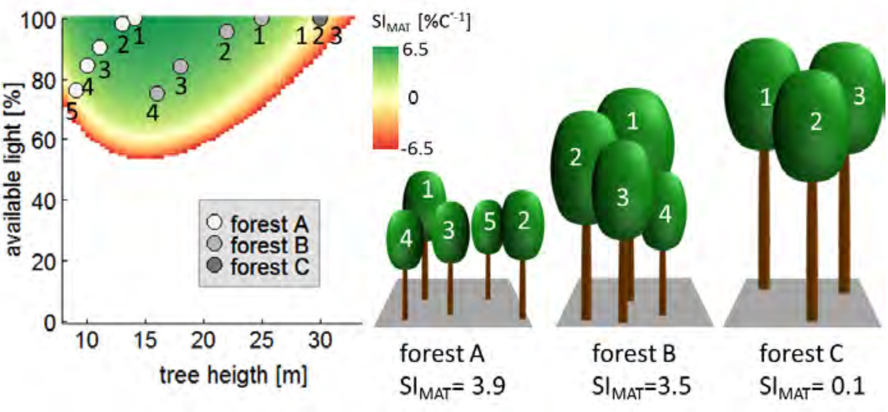


Figure 20: Analysis of SI_{MAT}values of single trees within three different forests. The diagram shows for every combination of tree height and available light the calculated SI_{MAT}-value (> -6.5% $C^{\circ-1}$) of pine. The dots indicate the different trees of the three forest examples, whereby the grey tone indicate the forest, which the tree belongs to and the number indicate the specific tree of that forest. Note that in the case of forest C all trees have the same height and the same light, so that all three dots are at the same place in the diagram. White area are combinations of height and available light which results in SI_{MAT}-values below -6.5% $C^{\circ-1}$.

found in (see a detailed discussion of these calculations in Appendix F.4). In forests of even-aged pine trees, all trees have the same height and get full light (e.g. forest C in figure 20). Such even-aged forests show a bell-shaped relationship between forest height and temperature sensitivity (figure 20, SI_{MAT}values for 100% available light in dependence of tree height).

In forests, which consist of trees with different heights (but similar LAI), smaller trees receive less light due to shading. Two cases will be discussed: first, all trees have not reached their maximal SI-values (forest "A", figure 20) and second all trees passed their maximal SI-values of their individual light conditions (forest B, figure 20). In the case of forest "A", trees in the shade of larger trees always have lower SI-values. Hence the temperature sensitivity of this forest is lower than the sensitivity of an even-aged forests whose trees have the same size as the largest trees in the first forest (e.g. forest "A" compared to a forest consisting of several trees "1"). This consideration explains why young forests (low H_{max}) with the highest SI-values show low height heterogeneity (figure 20). In the case of forest "B", SI-values of the shaded trees can still be similar (or even higher) than the SI-values of the largest trees in the forest (SI-values of tree "1" shows similar values than tree "2","3" and "4" of forest "B"). This result in similar or even higher SI-values compared to even-aged forest (with similar LAI), which consist only of the largest trees (e.g. forest "B" compared to a forest consisting of several trees "1" of forest "B"). Hence, older forest (high H_{max}) benefit from increasing temperature if their trees show different heights (higher θ; see figure 20).

4.5.3 *The effect of species composition on temperature sensitivity*

In this study we introduce a new index Ω_{AWP} called optimal species distribution. Ω_{AWP} describes the ratio of realised forest productivity to the maximal possible productivity of a forest, which can be reached by mixing species identities of trees in the given forest stand. Its huge importance on forest temperature sensitivity might be illustrated by the following considerations: If species are unfavourable distributed within the forest (low Ω_{AWP}) the AWP of this forest is low and in consequence the SI-value is low as well (see also Appendix F.4).

Increasing functional diversity (Rao´s Q) has a stabilising effect (in case of mean temperature sensitivity). This corresponds to results of Morin et al. (2014) and theoretical consideration of Yachi and Loreau (1999). The analysis of the single species can give additional insights into the mechanisms behind: those species which benefit most from temperature increase, are robinia, poplar and beech in our simulation. The highest functional diversity (Rao´s Q) on the other hand occurs in mixtures with trees of deciduous and needle leaf trees (Appendix F.5 figure F.8). As only two needle leaf species are in the here considered species pool, low Rao´s Q values are dominated by mixtures of deciduous trees (56 possible combinations), which benefit more from temperature increase compared to mixtures including both functional types (figure 18; Appendix F.5 figure F.8).

We developed two diagrams to understand the relationship between Ω_{AWP} and temperature sensitivity in the forest with the highest SI-values (figure 19). These diagrams show the species with the highest Ω_{AWP} (or SI-value) for every combination of tree height and light availability (figure 21). Interestingly, the species with the highest Ω_{AWP} differ in many cases from the species which benefit most from rising temperatures under the same conditions. This has important consequences. The highest benefit due to increasing temperatures show forests with high but surprisingly not maximal Ω_{AWP} (figure 19) and deciduous trees benefit more than coniferous trees from rising temperatures (figure 21 b). Hence, young forests should consist of deciduous trees, although the highest productivity value can be obtained by coniferous trees of trees smaller than 20 metres (figure 21, forest "A"). Forests with high θ and large trees, obtain the highest sensitivity values, if intermediate sized trees differ in their species identity from the largest trees (figure 21, forest "B").

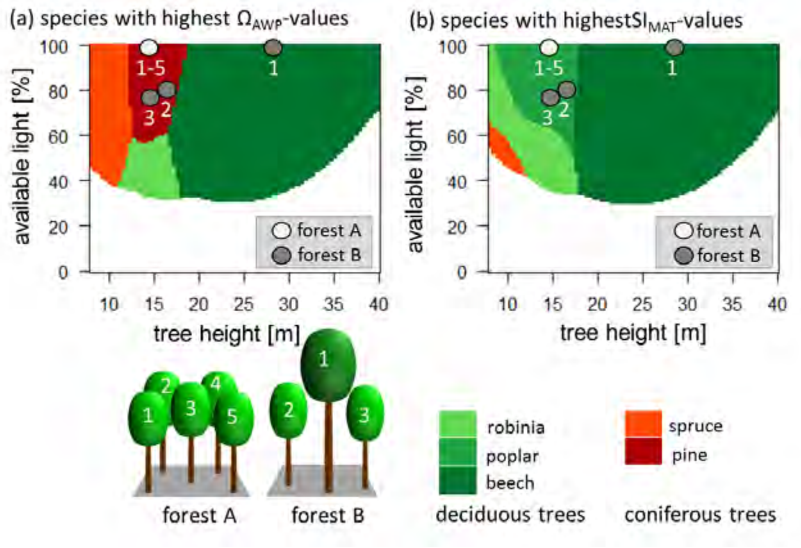


Figure 21: graphic a) shows which species show the highest increase of productivity due to increasing temperatures at different heights under different light conditions. Graphic b) shows which species show the highest productivity at different heights and different light conditions. Red colours indicate coniferous trees, whereas green colours indicate deciduous trees. Darker colours indicate late successional species, whereas lighter colours indicate pioneers. The dots indicates the different trees of the two forest examples, whereby the grey tone indicate the forest which the tree belongs to and the number indicates the specific tree of that forest. White areas indicate height-light combinations where no species have a positive AWP.

4.6 CONCLUSION

The temperature sensitivity of forests is driven by forest structure and species diversity. Most relevant for the temperature-productivity-relationship are optimal species distribution (Ω_{AWP}) and forest height. Forests which benefit most from temperature rise consist of deciduous tree species. Thereby young forests need low and old forests need high tree height heterogeneity.

5

CONCLUSION

Forest dynamics are influenced by various factors in the temperate zone. In this thesis, the influence of three important factors (climate, forest structure, and biodiversity) on the dynamics of temperate forests is analysed using large-scale inventory data (e.g. German forest inventory), eddy flux measurements, yield tables, and simulations of an individual-based forest model (FORMIND).

5.1 EXTENDING THE APPLICATION RANGE OF A FOREST MODEL: THE FORMIND VERSION FOR TEMPERATE FORESTS

Forest gap models, which synthesize important processes of the existing knowledge on tree growth, allow to analyse impacts of climate on forest growth. Such analysis can help to disentangle effects of single climate variables on different aspects of forest dynamics, for instance productivity (Bugmann, 2001; Fischer et al., 2016). As environmental conditions differ between tropical and temperate zones, it has been challenging to transfer the tropical forest model (FORMIND) to the temperature zone by keeping the structure of processes (establishment, competition, growth, and mortality) and a low number of parameters.

For the temperate version of FORMIND we incorporated budburst-process for deciduous trees into the model (Chapter 2). This module was inspired by the SEIB-DGVM-model (Sato et al., 2007). In addition, we continued the development of modules for temperature and water dependency of aboveground wood production of trees, which was inspired by previous work of Gutiérrez (2010) and the LPJ-model (Sitch et al., 2003).

Yield tables (Schober, 1995) and trait information from descriptions of temperate tree species (e.g. Sonntag, 1998; Piao et al., 2010) enable a new parameterization approach (in contrast to previous used methods for tropical forests). Parameter values for the photosynthetic processes are taken from literature (see Appendix A). Yield tables, which date back to the 18th century and have been extend to the 1950´s, contain information about tree allometry and growth rate (above-ground wood production, AWP). The difference between photosynthesis rate and AWP can be divided into a growth respiration rate (fixed proportion of AWP) and a size dependent maintenance respiration rate (which includes also allocation to non-wood tissues). This maintenance respiration rate has been determined using a photosynthesis model in combination with AWP-values from yield tables (for even-aged monocultures). The photosynthesis rate has been modeled with climate data for North Germany between 1931 and 1960 (Müller, 1996). The assumed climate scenarios influence maintenance respiration and photosynthesis rates in simulations and hence a climate dependent growth (AWP) of single trees can be derived (similar to global vegetation models). In several analyses, we showed that the adapted FORMIND-model using the parameter set of eight temperate species (pine, spruce, beech, oak, ash, poplar, birch, and robinia) can be applied successfully within the temperate zone (Chapter 2, 3 & 4). In addition, using a Bayesian approach for parameter fitting, the model can even be applied to boreal forests (Van Oijen et al., 2013) and new species can be parameterized quite easily if their growth is documented in yield tables.

One part of this thesis focuses on above-ground wood productivity and its relationship to diversity, forest structure and temperature change (Chapter 3 & 4). To include a large number of forest stands into our analysis, we developed the "forest factory" approach (Chapter 3). The forest factory generates a huge set of forest stands (in total 379,170) and simulates one year of forest growth, whereby all trees must have a positive above-ground wood production. In addition, the number of trees is limited by the available space. Forest stands of the forest factory differ in species composition and forest structure (covering young and old as well as managed and natural forests). This approach takes a relatively short computational time to generate a large number of forest stands and to estimate their productivity (and other fluxes) under given environmental conditions compared to long-term simulations (Morin et al., 2011; Seidl and Lexer, 2013; Reyer et al., 2014). Nevertheless, it is also possible to reconstruct successional dynamics by combining forest stands, which relate to different successional phases. The forest factory is a new concept for using forest models that allows the analysis of a large number of forest stands.

5.2 QUANTIFICATION OF FOREST STRUCTURE AND SPECIES DIVERSITY

For analysing a large number of forest stands it is useful to quantify properties of forests related to structure and diversity. Our aim was to find a small number of indices for our analysis, which show no multicollinearity and are relatively easy to interpret.

We used the following forest properties to describe forest structure: basal area, leaf area index (LAI), forest height and tree height heterogeneity. Basal area measures the cross section of tree trunks in a given area and correlate with LAI (leaf area per square meter). In Chapter 3 we use basal area, in Chapter 4 LAI. Tree height heterogeneity θ, a new developed index, quantifies how strong the height between the trees differs within a forest stand. Forest height relates to the height of the largest tree in a forest stand. If height measurements of trees are not available, similar indices might be derived using stem diameter (dbh) instead of tree height. All these structure indices are relatively easy to measure in the field or can be derived from available data sets (e.g. the national forest inventory). They show no collinearity and are also better interpretable than e.g. parameters describing the shape of stem size distribution-functions.

To describe species composition we used species number, functional diversity (Rao´s Q) and optimal species distribution (Ω_{AWP}). Species number is the simplest index to describe species richness. However, this index does not consider the differences in functionality and species abundance. Both of these aspects are included in the calculation of Rao´s Q, an index to describe functional diversity (Botta-Dukát, 2005). Further, the location of single trees in a forest is important for the forest structure. For instance, productivity differs between forests, if shade tolerant species grow below light demanding species or vice versa. We therefore developed the new index called optimal species distribution (Ω_{AWP}), which quantifies how species are optimally distributed concerning productivity within a given forest stand. To quantify Ω_{AWP} using field data it is necessary to use a model for estimating the forest productivity (AWP) of the forest with optimal distributed species. Further, Ω_{AWP} and Rao´s Q do not correlate (Chapter 4) and show no multicollinearity with other used structure indices (Appendix E.2, table 10)

5.3 DIFFERENT DRIVERS OF FOREST PRODUCTIVITY: SPECIES RICHNESS AND STRUCTURE

Forests differ in structure and species composition. However, it remains unclear how forest properties influence forest productivity and if different species-diversity-relationships can be assigned to different forest types (e.g. young vs. old forest stands).

In Chapter 3 we showed that changes in structure (basal area and tree height heterogeneity) alter forest productivity (AWP) much stronger than changes in species composition (species richness or Rao´s Q). This pattern was found for forest stands of the forest factory as well as for the analysis of the German forest inventory (5,054 plots). Furthermore, different diversity-productivity-relationships could be related to different forest types (forests stands with similar forest structure). The derived relationships correspond to relationships obtained in different field studies (e.g. Edgar and Burk, 2001; Jacob et al., 2010; Zhang et al., 2012; Vilà et al., 2013).

Forest productivity could be explained quite well by the combination of basal area, tree height heterogeneity, and optimal species distribution (Ω_{AWP}). Within all forest types Ω_{AWP} is an important forest property. Please note, Ω_{AWP} correlates only weakly with species richness in most forest types. The relevance of basal area and tree height heterogeneity vary between the different forest types. For instance, basal area has a larger impact on forest productivity in forests with lower basal area than those with high. Hence, we recommend that future studies that investigate diversity-productivity-relationships should include information on the forest structure in their analysis. An additional conclusion of this thesis is that studies regarding structure-productivity-relationships should consider the distribution of species within the forest.

5.4 FOREST PRODUCTIVITY AND RISING TEMPERATURES

Temperature is one of the important climate variables which affects forest growth. In Chapter 4 we develop a modelling approach to investigate how forest properties influence the temperature-productivity-relationship of forests.

Forest stands of the forest factory are used to simulate forest productivity under different annual climate scenarios. For every forest stand the relative change of forest productivity (AWP) is calculated due to a 1°C-increase in temperature. Estimated sensitivity levels for seven forest types of the German forest inventory (based on 1,301 plots) correspond to simulation based sensitivity levels. Finally, effects of forest structure and species composition on temperature sensitivity are analyzed using a boosted regression tree approach. We found that an optimal species distribution within the forest structure (high Ω_{AWP} level) is important for a positive temperature sensitivity of forest productivity. Also forest height is an important factor, whereby forest stands of intermediate height benefit from rising temperatures and forest stands with small or large forest-height-level have disadvantages.

Beside the links between forest productivity and temperature increase, it is interesting to assess if and how forest management can be adapted so that forest productivity remains on the current level or can even benefit from climate change (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Bonan, 2008). We examine forest properties of those forest stands, which benefit most under rising temperatures. For all successional stages (which differ in forest height H_{max}), an optimal distribution of species is important (high Ω_{AWP} level). Young forests benefit most from increasing temperatures, if forests consist of pioneer species of the same size. With increasing forest height, however, forests profit from trees with various sizes belonging to different species. If forests are managed based on the here presented results, forest productivity can increase from rising temperatures.

5.5 LIMITATIONS OF THE APPROACHES

5.5.1 *FORMIND*

Although FORMIND is a well-established and thoroughly validated modell, one should be aware of its inherent constraints. FORMIND includes a relatively simple soil water module (one-bucket). Further, our simulations do not include nitrogen dependencies of tree growth. It would be interesting to couple FORMIND with more advanced biogeochemical soil models (e.g. LandscapeDNDC Kraus et al., 2015) to predict carbon, water and nitrogen pools and fluxes of the soil in more detail. This would improve the feedback of soil water and nitrogen to above-ground processes. Further, the current used allocation process distributes the available carbon into above-ground wood, growth respiration and maintenance respiration (which includes also other tissues). Hence, it would be worth to implement also allocation to root biomass (following the approach of Kleidon and Heimann, 1998) and/or to leaves (following the LPJ approach of Sitch et al., 2003) for future studies. In Chapter 3 & 4, we highlight the effect of forest structure on forest productivity. Global vegetation models do not include structure in most cases. The addition of structural aspects into these models could therefore affect several processes (e.g. photosynthesis, growth or establishment) and change the model results.

5.5.2 *Forest factory*

The main idea of the forest factory is to enable analysis of all possible forest stands. The forest factory, which is presented in this thesis, includes some limitations. For example, our forest factory only includes trees with a stem diameter between 5 and 50 cm and uses 15 stem diameter distributions to create different forest structures. In addition, the resulting forests include as many trees as possible (dense forests). Finally, we applied the presented concept in this thesis only to temperate forests. In the near future, a second version of the forest factory is planned to overcome these limitations. It will be expended by (i) allowing all possible tree sizes, (ii) using more flexible description of forest structure including also forest stands with low densities and (iii) processing trait based plant functional types for all biomes instead of a few temperate species. The new version of the forest factory will enable the analysis of forest productivity, but also all other forest pools (e.g. biomass) and fluxes (of the carbon and water cycles). The quality of the second forest factory can be validated by comparisons with new national inventories, data from eddy flux towers and forest megaplots of the ForestGeo network.

5.6 OUTLOOK

FORMIND

Chapter 4 showed that some forest types benefit more from increased temperatures than others. Thus, one interesting question is how do natural systems evolve with climate change in terms of forest structure and species composition? Does a forest system optimize species composition and forest structure regarding productivity (or biomass)? Long term simulations of forests with the FORMIND-model could be used to analyse changes of forest structure and species composition (especially Ω_{AWP}) in forests. Such a study should include a growth rate dependent mortality as already implemented in FORMIND (Fischer et al., 2016).

Forest factory

The forest factory approach can also be used for other interesting applications: For instance, the effect of other environmental forces (like droughts) on forest productivity, evapotranspiration or living biomass is also of high interest. The forest factory can also serve as a null-model for future field studies (e.g BEF-China (Yang et al., 2013), BioTree (Scherer-Lorenzen et al., 2007)) by selecting (or rebuilding) the experimental forest plots and estimate productivity and fluxes. Differences to observed fluxes would point out the existence of missing processes Oliveira et al. (e.g. hydraulic lift, 2005). In addition, it would be possible to create forest stands of two species with different abundances (as presented by Kraft et al. (2015) for grasslands) or tree sizes. Fitness (number of seeds produced per seed lost in Kraft et al., 2015) could be replaced in the model-approach by AWP and the traits corresponding to the species parameters. Coexistence of two species can be explored in long-term simulations. Current work of Roedig et al. (personal communication) allows an individual based simulation of the whole Amazon using remote sensing and climate data in combination with long-term FORMIND-simulations. However, many forests of the world are plantations or managed forests, and so their fluxes differ from the fluxes of undisturbed natural forests. Based on remote sensing, climate and - if available - management information it could be possible to select the most probable forest stands of the forest factory for various landscapes.

Sampling experiments

The forest factory can also be used to examine how sampling strategies affect results of field studies. Studies using field data normally do not show equal frequency of forest types, as natural processes or management favour certain forest types (e.g. Zhang et al., 2012). For instance, the German forest inventory is dominated by even-aged forest stands including often only one tree species. In case of such national forest inventories, a comparison between the species-diversity-relationship of the original data set and a data subset, which shows equal frequencies of different successional stages (but same frequency of species mixtures) might be worth to analyse. In general such sampling experiments using filtered subsamples of the forest factory data set might help to answer the following question: can various diversity-productivity-relationships emerge from different sampling strategies?

Theory building

In Chapter 3 we found a strong influence of basal area in combination with tree height heterogeneity on forest productivity in the German forest inventory. Due to our simulations results we would expect that this pattern should be a general pattern for temperate European forests. It could be tested for other temperate forests by analysing appropriate national forest inventories. It would be also interesting to check if the general pattern changes in other climate regions (tropics, boreal zone). This could be tested with the data from the world-wide ForestGeo network, which includes inventories that recorded every tree in areas up to 50 hectares (Anderson-Teixeira et al., 2015).

We average productivity for different forest structure classes to analyze productivity-structure-relationships (Chapter 3) and use boosted regression trees to quantify the effect of forest properties on temperature sensitivity (Chapter 4). Both analyses might contribute and give inspirations for research concerning mechanistic formulas, which relate forest structure and species diversity indices to forest productivity or to temperature sensitivity of forest. Such formulas would help to reveal more general mechanisms in forest ecology.

Field experiments

Such theories may inspire field ecologist to design new experiments (which might be easier realized in grasslands) which focus on the structure of an ecosystem, and not only on species composition. For instance, it might be interesting to compare forest or grasslands with same LAI (which could be corrected by removing single leafs) but different height structures (H_{max}, θ). Such an experiment would help to quantify how good LAI-related remote sensing indices (e.g. EVI, or NDVI) can be used to predict productivity. In addition it would be also interesting how the structure of grasslands (LAI, H_{max}, θ) affect the sensitivity of carbon fluxes due to changes in temperature or during drought events.

Linking forest structure with remote sensing

Remote sensing techniques now generate huge amounts of data with high spatial and temporal resolution. Forest models like FORMIND will soon have modules that generate various remote sensing signals from the virtual forests (Knapp et al. personal communication). Here the transmission, absorption, and reflectance due to leaves in case of Lidar and due to branches in case of L-band radar are simulated. Based on such simulations with the forest factory and large field data sets, which include several national forest inventories, megaplots of ForestGeo and remote sensing data, it would be worth to develop transfer functions between structural forest properties (e.g LAI, H_{max}, Basal area, θ) and remote sensing based indices. However, this aim has to deal with different challenges. For instance, the field-measured attributes of a tree (biomass, height, etc.) are pinned to the position of its stem, whereas the optical remote sensing signal based on the leaves within the crown (Ferraz et al., 2016). In addition, the detection of the understory is impossible with optical methods and even with Lidar and radar it is still challenging (Duncanson et al., 2015). Finally, it is a topic of contemporary discussion whether it is even possible to identify a single species or function type from remotely sensed data, which would be necessary to determine species diversity indices (species richness, Rao´s Q). It is very likely impossible to determine Ω_{AWP} from remote sensing.

The remote sensing based indices can be related to various ecosystem services. For instance, vegetation productivity (NPP and GPP) can be estimated for the whole earth based on different spectral indices Weier and Herring (NDVI, EVI; 2000), which relate to LAI. However, this thesis highlights the importance of height heterogeneity of trees on forest productivity. With future satellites (like tandem-L), it could be possible to create remote sensing based indices that quantify tree height heterogeneity, which then might be combined with other structure describing indices (which relate to forest height and basal area) and NDVI (or EVI) to improve the estimation of carbon fluxes and pools (biomass) in forests on the global level. The detection of tree crowns within a forest based on Lidar-data is possible if the point density per square meter is high enough (Ferraz et al., 2016). Based on such a 3D canopy map it could be possible to calculate the light competition of the trees using the FORMIND algorithms for competition. Based on the available light for the different crowns it might be possible to calculate AWP using the detected crown geometry and the growth function of FORMIND. In contrast to classical approaches, where the difference in biomass during two flight campaigns is used to estimate growth rates of forests, this approach would give AWP rates based one single flight campaign.

This thesis was only possible due to the work of many field ecologists and foresters, who collect myriads of data, dating back more than 150 years. Founded on these data, a forest model was developed that enables the forest factory and the analysis of this thesis. We hope that this theoretical work, will inspire field ecologist to design new experiments and foresters to develop adaptive forest management strategies to changing conditions. This new knowledge will hopefully lead to thoughtful interactions with the forest, which might result in a beneficial coevolution of nature and human society.

Part II

APPENDICES

A

MODEL DESCRIPTION

A.1 GENERAL CONCEPT

FORMIND (temperate version) is an individual-based, spatially explicit and process-based model designed for simulating species-rich vegetation communities. This document introduces only a specific version of FORMIND (temperate version) which excludes recruitment and disturbance events. For a full model description of FORMIND (temperate version) please go to the FORMIND homepage www.formind.org. Here you will find alternative model versions of FORMIND, which currently be applied (i.e. the choices of different geometries for the vegetation, the climatic zone and various disturbance events).

In FORMIND (temperate version) vegetation is simulated on an area of size A_{area}, which is a composite of regularly ordered, quadratic patches of size A_{patch} [m^2] uniquely described by their location within the area (figure A.1). Individual trees grow within the patches, but do not have spatially explicit positions within a patch.

Individual plants of the same type and age, which are located in the same patch, are summarized by a so-called cohort. Each cohort is uniquely described by its type, the number of identical individuals, their age and the size of one single individual (i.e. above-ground biomass). The number of identical individuals and their size change during the simulation according to a type-specific set of ecophysiological and morphological parameters used within the modelled processes. The modelled processes are simulated on different levels: (i) area-level, (ii) patch-level or (iii) on the level of a representative individual of a cohort, which we refer to the following as individual.

Within each time step t_y the following main processes are calculated :

- § A.3 Mortality: Mortality is calculated for cohorts or, in case of crowding, mortality on the patch level per model time step t_y.
- § A.4 Environment: The patches of the simulation area are homogeneously concerning climatic input variables. Based on these input parameters, the environment of the trees is specified. For example, the radiation above canopy and day length are equal for all patches.

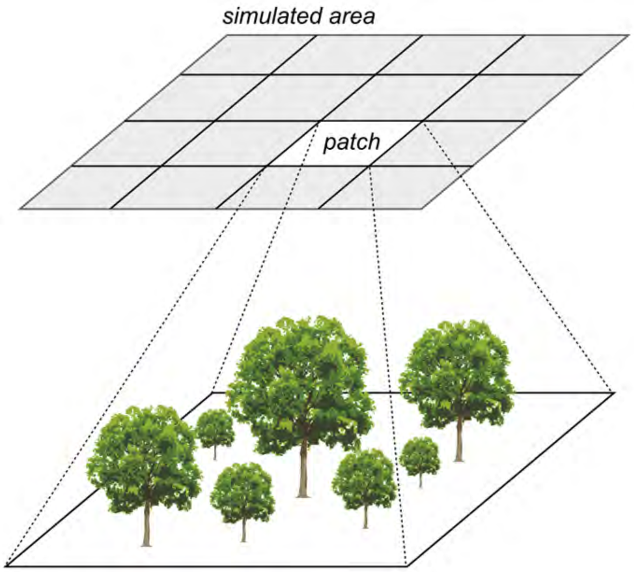


Figure A.1: Illustration of the simulated area and its composition of regularly ordered patches. Individual trees do not have spatially explicit positions within the patches. Only for an illustrative purpose, we show positioned trees on an exemplary patch.

The vertical attenuation of the incoming radiation (i.e. light climate) is calculated for each patch based on the vegetation, so that light intensity at different heights can differ between patches dependent on the number of trees shading each other. Reduced light availability for shaded individuals can result in a reduced gross photosynthesis. Limited soil water resources can also reduce the gross photosynthesis of an individual. In the same manner as the light climate, soil water contents can differ between patches during the simulation, although the initial soil water content and other soil properties (e.g. soil porosity) are equal for all patches. Differences in soil water content between patches are dependent on the number of trees per patch, which take up soil water resources. Further, type-specific effect of air temperature can also limit gross photosynthesis and affect respiration of an individual. All limitations are calculated in time steps of higher resolution than t_y.

- § A.5 Growth: The growth of a single tree is determined by its gross productivity, respiration and type-specific morphological parameters. Respiration is calculated on the level of an individual. An increase in biomass per tree is modelled as the difference between gross photosynthesis and respiration. The allocation of the resulting biomass in- crease (including the increase of geometrical properties according to chapter B) act on the level of a tree.

The modelled processes, which are summarized within the above mentioned main processes, are scheduled in a serial way. For details on the modelled processes and their schedule see figure A.2.

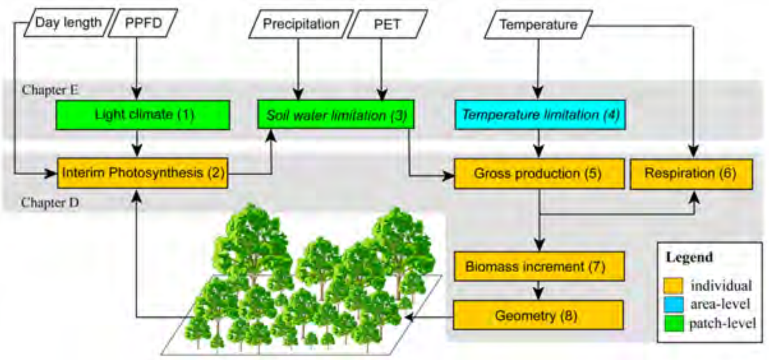


Figure A.2: Block diagram of the modelled processes. Different colours indicate the spatial scale on which each process is calculated (blue = area, green = patch, orange= individual). Italic written boxes show processes which are simulated with time steps of higher resolution than t_y. Numbers in brackets within each box show the serial order of their calculation within one time step t_y. Grey frames that underly these boxes group them according to the above mentioned main processes and their corresponding chapters. Rhombuses indicate climatic input parameters with the following abbreviations: PET – potential evapotranspiration, PPFD – photoactive photon flux density.

For the purpose of calculations within the processes of light climate and crowding mortality, the above-ground space is discretised into vertical height layers of constant width Δ h. Table 1 shows general input parameters.

Table 1: Parameters describing space and time.

Parameter	Value	Unit
t_y	1	year
A_{area}	1	hectare
A_{patch}	400	m^2
Δh	0.5	m

A.2 GEOMETRY

Although individual trees in real forests should not have necessarily identical shapes, we model each tree by a cylindrical stem and a cylindrical crown (Fig. 3). The geometry of an individual can be described completely by the following size characteristics: stem diameter (D), height (H), crown diameter (C_D), crown length (C_L) and crown projection area ((C_A) as shown in figure A.3.

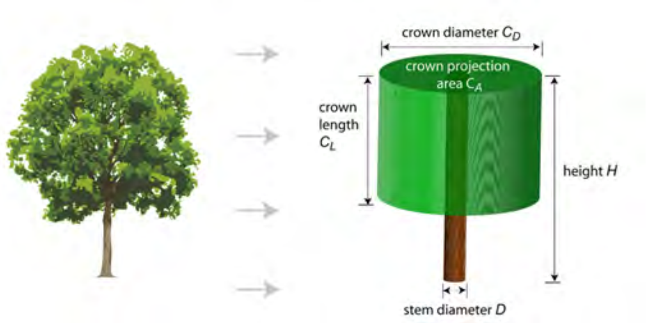


Figure A.3: Geometrical representation of a single tree . The following abbreviations describe size characteristics of the modelled tree geometry: D - stem diameter, H - height, C_D - crown diameter, C_L - crown length, C_A crown projection area.

These characteristics are applied to all individuals of the cohort. Parameters of these functional relationships depend on the pft assignment of each cohort. In the following all relationships are described according to a representative individual of a cohort.

Above-ground dry biomass B [t] relates to stem diameter D [m] by:

$$B = \exp\left(b_1 * (D - b_3) * \frac{2 * b_2 + (D - b_3)}{b_2 + (D - b_3)}\right) \qquad (21)$$

whereby b_1, b_2 and b_3 are type-specific parameters. Here the power law presented by Ter-Mikaelian and Korzukhin (1997) is modified in the exponent by a negative Michaelis-Menten function.

The height H [m] relates to D [cm] by:

$$H = \frac{D}{\frac{1}{h_1} + \frac{D}{h_2}} \qquad (22)$$

whereby h_1 and h_2 are pft-specific parameters (Köhler, 2000).

The crown diameter (C_D) [m²] relates to D [cm] by:

$$C_D = D\left(c_{D1} + c_{D2} * \exp\left(-c_{D3} * D\right)\right) \qquad (23)$$

whereby c_{D1}, c_{D2} and c_{D3} are pft-specific parameters. We modified the formula published by Dislich et al. (2009).

Crown length C_L [m] of all trees is modelled in relation to the height h [m] of an individual by:

$$C_L = c_{L1} * H \tag{24}$$

whereby c_{L1} is the percentage of height which is attributed to the crown.

Crown projection area C_A is the area of the conical crown:

$$C_A = \frac{\pi}{4} C_D \tag{25}$$

The leaf area index relates to D [cm] by.

$$LAI = l_1 \, D^{l_2} \tag{26}$$

whereby l_1 and l_2 are type-specific parameters.

Table 2: Summary of the type-specific morphological parameters. They are derived from the yield tables of Schober (1995) yield class 1 with moderate thinning (populus is only available for yield class 2). The data in the yield tables are aggregations of many single tree measurements in an age-homogeneous forest which are managed by the same standardized long-term experiment program.

tree type	b_1	b_2	b_3	h_1	h_2	c_1	c_2	c_3
pinus	1.185	5.657	3.676	1.259	75.762	0.156	0.152	0.204
picea	1.029	3.204	3.717	1.326	101.33	0.128	0.102	0.089
fagus	1.202	5.727	3.475	1.916	61.036	0.155	0.125	0.066
quercus	1.151	5.187	3.586	1.879	45.341	0.173	0.054	0.066
populus	1.266	5.636	3.809	1.286	62.651	0.173	0.614	0.087
fraxinus	1.192	5.957	3.534	1.976	52.925	0.171	0.146	0.066
betula	1.091	6.394	3.671	1.711	51.488	0.207	1.760	0.277
robinia	1.217	9.175	3.586	1.400	45.315	0.161	0.493	0.120

A.3 MORTALITY

The following different types of mortality occur in the model: diameter dependent mortality m_d; and crowding mortality due to limited space.

The growth-dependent mortality indicates a functional relationship between D and mortality. The dbh-dependent mortality is calculated as:

$$m(D) = m_0 * D^{m_1} \tag{27}$$

Per time step t_y for each cohort the number of individuals N is reduced with a summed up mortality rate m_{tot} of:

$$M = m_d + m_b + m_i \tag{28}$$

The reduction of individuals is performed either stochastically or deterministically. If the number of individuals per cohort is less than a pre-defined number N_M or the stem diameter of a representative individual is greater than or equal to a pre-defined threshold D_M, then for each individual per cohort the rate m_{tot} represents its probability of dying. Otherwise, the number of dying individuals per cohort is determined by multiplying and rounding the individual number N with the total mortality rate m_{tot}.

- **crowding mortality** Crowding mortality occurs, when the cumulative crown area of tree crowns exceeds the patch area at any height layer. For each representative individual a reduction factor r_c is calculated based on the coverage of the height layers. The factor r_c is the reciprocal of the maximum coverage (cumulative crown area per patch area) according to those height layers to which the individual´s crown belongs (see Table 1 and section A.4) . Crowding mortality reduces the number of individuals in a cohort if the calculated r_c of the representative individual is smaller than 0.99. The number of dying individuals is determined by:

  $$N_c = N\ (1 - r_c) \tag{29}$$

  As the space conditions including the reduction factor are updated after individuals have died due to crowding, the next space limitation event is delayed by one time step t_y delayed. Space limitation or self-thinning can be interpreted as competition for space.

Overall, per time step t_y for each cohort the change in the number of individuals N is determined by:

$$dN/dt = -(m_{tot} * N + N_c) \tag{30}$$

Table 3: Tree type specific leaf area index parameters. We use the mean of measurements presented in Breuer et al. (2003). The number of measurements used is written in parenthesis. Robinia is estimated as the mean of quercus and populus, which all have the same light values described by Ellenberg.

tree type	l_0	l_1
pinus	3.6 (2)	0
picea	7.7 (4)	0
fagus	6.1 (6)	0
quercus	5.4 (4)	0
populus	4.6 (7)	0
fraxinus	5.0 (1)	0
betula	5.3 (1)	0
robinia	5.0 (0)	0

Table 4: Tree type specific mortality parameters based on the yield tables of Schober (1995)

tree type	m_1	m_2	r^2
pinus	0.00383	-1.271	0.002
picea	0.00630	-0.953	0.001
fagus	0.00890	-0.761	0.001
quercus	0.00657	-0.950	0.002
populus	0.01707	-0.894	0.004
fraxinus	0.00272	-1.505	0.002
betula	0.01841	-0.210	0.018
robinia	0.01202	-0.373	0.008

whereby the event-driven crowding mortality (with N_c tree dying) occurs before every time step.

A.4 COMPETITION & ENVIRONMENTAL LIMITATIONS

A.4.1 *Light climate*

An individual tree on a patch receives full incoming radiation. An increasing number of individual trees of different heights on a patch results in shading within the canopy. With decreasing height from the canopy down to the ground, light is increasingly attenuated and thus, shading of smaller individuals increases. The vertical distribution of light availability in a patch denotes its light climate.

To calculate light conditions at different heights within the canopy, the entire above-ground space is divided into layers of constant width Δh. For each patch, the leaf area for each height layer is calculated. Therefore the layers occupied by a tree crown lie between l_{max} and l_{min}. These are determined by crown length c_l and the tree's height h:

$$l_{max} = \frac{h}{\Delta h} \tag{31}$$

$$l_{min} = \frac{h - c_l}{\Delta h} \tag{32}$$

For those height layers, between l_{min} and l_{max}, the contribution of the tree's leaf area in each height layer i is distributed equally among the layers:

$$\bar{L}_i = \frac{LAI\ C_A}{A_{pat}} \frac{\Delta h}{C_L} \tag{33}$$

whereby $\bar{L}_i$ is the patch-based leaf area index contribution of an individual tree to the height layer i, LAI is the leaf area index of the tree, C_A is the projection area of the tree's crown, C_L is the crown length of the tree's crown, A_{pat} is the area expansion of the patch, and Δh the constant width of the above-ground, discretized space. Summing up the contributions of leaf area of all trees on a patch to their respective height layers results in the patch-based community leaf area index $\hat{L}$ for each height layer i:

$$\hat{L} = \sum_{all\ individuals} k\ \bar{L} \tag{34}$$

whereby k denotes the light extinction coefficient of an individual and the leaf area index contribution of the trees to height layer i.

Using this information, the radiation each tree intercepts can be determined. For each tree the patch-based leaf area indices of all height layers greater than the individual tree's height are summed up. Light attenuation through the canopy is calculated using the approach of Monsi (1953), which is equivalent to the Beer-Lambert law. The incoming radiation I_{ind} per t_y on top of an individual, which is on top of the height layer the individual tree reaches, is calculated by:

$$I_{ind} = I_0 \exp\left(\sum_{i>l_{max}} \hat{L}\right) \tag{35}$$

where I_0 is the mean radiation above canopy of t_y during the vegetation period and $\hat{L}$ the patch-based community leaf area index of height layer i.

By determining the irradiance that reaches the top of the tree crown, competition for light between individuals is considered.

A.4.1.1 *Water cycle*

The individual's uptake of water resources from the soil, taking into account on the one hand its demand and on the other hand the available soil water. The individual's water demand Θ_{dem}, which is equal to its potential transpiration, is modelled using the water use efficiency concept (Lambers et al., 2008):

$$\Theta_{dem} = \frac{GPP}{WUE} \tag{36}$$

whereby GPP denotes the gross primary productivity of one tree in [tODM/ha/y] and WUE the water use efficiency parameter in [gODM/kg (H_2O)]. Soil depth S_d is divided into layers of constant width Δs. We assume roots to be equally distributed among the soil per patch. Using the information about the individual's water demand per patch, the patch-based total water demand of all trees on the patch can be determined:

$$\Theta_{tot} = \sum_{all\ individuals} \Theta_{dem} \tag{37}$$

To determine the fraction of demanded water an individual can take up from soil while competing with other individuals, the calculations of Granier et al. (1999) are used. For each tree, the fraction of demanded water, which can be taken up is determined based on the remaining soil water content Θ_{rem} after subtraction of the potential demands:

$$\Theta_{rem} = \Theta_{soil} - \Theta_{tot} \tag{38}$$

whereby Θ_{soil} is the available soil volumetric water content in [V%]. The remaining soil water content Θ_{rem} defines the content of soil water that would remain in soil after uptake of the total potential water demands.

The limitation factor of photosynthesis due to water scarcity φ_W for all trees is always calculated as:

$$\varphi_W(\Theta_{rem}) = \begin{cases} 0 & \text{if } \Theta_{rem} \leqslant \Theta_{pwp} \\ \frac{\Theta - \Theta_{pwp}}{\Theta_{msw} - \Theta_{pwp}} & \text{if } \Theta_{pwp} < \Theta_{rem} < \Theta_{msw} \\ 1 & \text{if } \Theta_{rem} \leqslant \Theta_{msw} \end{cases}$$

whereby Θ_{pwp} is the permanent wilting point and Θ_{msw} is the minimum soil water content required for normal photosynthesis. Between these two endpoints a linear constraint is assumed following Granier et al. (1999). Θ_{msw} is determined by:

$$\Theta_{msw} = \Theta_{pwp} + \frac{1}{3}(F_c - \Theta_{pwp}) \tag{39}$$

whereby F_c is the field capacity of the soil (Granier et al., 1999).

The soil water content Θ is computed using a differential equation of time step t_d, which quantifies temporal changes in the soil water depending on precipitation iP_0, interception I_{int}, run-off R_{off}, and transpiration T_{tran} Kumagai et al. (2004):

$$\frac{d\Theta}{dt_d} = P_0(t_d) - I_{int}(t_d) - R_{off}(t_d) - T_{tran}(t_d) \tag{40}$$

The interception I_{int} is assumed to be directly proportional to the leaf area index of a specific patch area Liang et al. (1994):

$$I_{int}(t_d) = \min(k_L * LAI, P_0(t_d)) \tag{41}$$

where k_L is the interception constant. On the surface we consider two different run-offs: surface run-off and subsurface run-off. Surface run-off $R_{off\rightarrow}$ is defined in the following way:

$$R_{off\rightarrow} = \max(0, \Theta(t_d) + iP_0(t_d) - I_{int}(t_d) - P_{por}) \tag{42}$$

Table 5: Water circle relevant parameters

parameter	unit	value	reference
WUE	$\text{g odm kg}^{-1}\text{H}_2\text{O}^{-1}$	6.0	Larcher (1994)
Θ_{pwp}	V%	19.4	Maidment et al. (1992)
F_c	V%	31.0	Maidment et al. (1992)
k_L	mm d^{-1}	0.2	Dickinson (1984)
por	V%	46.3	Maidment et al. (1992)
k_s	m s^{-1}	$3.66\ 10^{-6}$	Maidment et al. (1992)
Θ_r	V%	2.7	Maidment et al. (1992)

whereby P_{por} is the porosity, which is defined as the maximum water intake of the soil.

For the calculation of the subsurface run-off $R_{off\downarrow}$ due to gravitation, we used the Brooks-Corey relation Liang et al. (1994):

$$R_{off\downarrow} = k_s \left(\frac{\Theta(t_d) - \Theta_{res}}{P_{por} - \Theta_{res}} \right)^{\frac{2}{\lambda}+3} \tag{43}$$

whereby k_s is the fully saturated conductivity, Θ_{res} the residual water content, and λ the pore size distribution index.

Transpiration T_{tran} is calculated based on the water use efficiency concept (Lambers et al., 2008):

$$T_{tran}(t_d) = \frac{GPP_{pat}(t_d)}{WUE} \tag{44}$$

whereby WUE is the water use efficiency and $GPP_{pat}(t_d)$ is the photosynthesis rate of the trees in the patch (evenly distributed over the sub time steps t_{day}). The sum of transpiration and interception is limited by the potential evapotranspiration PET. The PET is the maximum amount of water that would be transpired and evaporated if there were enough water available.

A.4.1.2 *Temperature*

Temperature affects the carbon balance of a pft via different processes: Phenology, which is the number of photoactive days; photosynthesis and respiration, which are both modified by a temperature-dependent limitation factor.

- **Phenology**: Only deciduous broad leaf trees in the model have two phenology phases: A dormant phase during winter and a photosynthetically active period φ_{act} [days] after bud-burst until fall (the vegetation period). The date of bud-burst is reached, when the sum of daily mean air temperatures of days with a temperature higher than 5 °C starting on January 1^{st} is higher then a critical temperature (T_{crit}).

  $$T_{crit} = -68 + 638e^{-0.01n} \tag{45}$$

  where n is the sum of days for which the temperature is below 5°C, starting on November 1^{st} of the previous year. This algorithm is based on the global distribution of leaf onset dates estimated from remote sensing data (Botta et al., 2000). The photo-active period ends when the 10-day running mean air temperature falls below 9°C (Sato et al., 2007). The photo-active period of needle leaf trees is a full year (365 days).

- **Photosynthesis limitation:** The temperature dependence of the photosynthesis limitation factor φ_T is calculated as :

  $$\varphi_T = \frac{1}{n} \sum_{1}^{n} \varphi_{T,l} * \varphi_{T,h} \tag{46}$$

  where n is the number of days in the time step t_y and $\varphi_{T,l}$ and $\varphi_{T,h}$ are the daily inhibition factors for low and high temperatures $\varphi_{T,h}$ (Gutiérrez and Huth, 2012; Haxeltine and Prentice, 1996). The effect of low temperatures is calculated by:

  $$\varphi_{T,l} = (1 + \exp(k_1 * k_2 - T))^{-1} \tag{47}$$

  where T is the input variable daily mean temperature in °C and k_1 and k_2 are tree type specific parameters.

  Similarly, the effect of high temperatures on photosynthesis is calculated by:

  $$\varphi_{T,h} = 1 - 0.01 * \exp(k_3 * (T - T_{hot})) \tag{48}$$

  where k_3 is a tree type specific parameter, T is the daily mean temperature and T_{hot} is the mean temperature of the hottest month, where the species occur.

The parameters k_1 and k_2 are calculated as:

$$k_1 = \frac{2\ \log(0.01/0.99)}{T_{CO_2l} - T_{cold}} \tag{49}$$

$$k_2 = 0.5\ (T_{CO_2l} + T_{cold}) \tag{50}$$

where T_{CO_2l} and T_{cold} are parameters representing the lower temperature limit for CO_2 assimilation and the mean temperature of the coldest month where the tree species occur, respectively.

The parameter k_3 is calculated as:

$$k_3 = \frac{\log(0.99/0.01)}{T_{CO_2h} - T_{hot}} \tag{51}$$

whereby T_{CO_2h} and T_{hot} are parameters representing the higher temperature limit for CO_2 assimilation and the mean temperature of the warmest month where the tree species occur, respectively.

- **Respiration** Maintenance respiration is assumed to increase exponentially with temperature (Prentice et al., 1993): The calculation of the temperature-dependent factor for maintenance respiration is therefore calculated as

  $$\kappa_T(T) = Q_{10}^{T - T_{ref}/10} \tag{52}$$

  whereby T is the mean temperature of a certain day, Q_{10} is a constant parameter for all trees and T_{ref} is the reference temperature, for which the correction of the base respiration is 1 (see section A.5). For the time step t_y we use the mean of all κ_T within that time step.

A.5 CARBON ALLOCATION

A.5.1 *Photosynthesis of one tree*

Based on the incoming irradiance on top of an individual I_{ind} corresponding to its height, organic carbon is produced. I_{ind} needs correction to obtain the irradiance on the surface of a single leaf rather than on the top of the entire individual:

$$I_{leaf} = \frac{k}{1 - m}\ I_{ind} \tag{53}$$

Table 6: Warmest and coldest month where the tree species occur based on distribution maps and the climate diagrams of Müller (1996).

tree type	T_{hot} °C	T_{cold} °C	T_{ref} °C	Q_{10}
pinus	26.55	-2.33	10.47	2.3
picea	26.55	-9.9	10.47	2.3
fagus	22.00	-3.2	10.47	2.3
quercus	23.5	-3.9	10.47	2.3
populus	27.0	-6.90	10.47	2.3
fraxinus	25.55	-6.61	10.47	2.3
betula	21.5	-9.9	10.47	2.3
robinia	24.5	-9.1	10.47	2.3

where k is the species-specific light extinction coefficient, m the transmission coefficient of leaves and I_S the incoming irradiance on top of an individual. This factor consisting of k and m accounts for self-shading within the crown of the individual.

Gross primary production is modelled using the approach of Thornley and Johnson (1990). It is based on the single-leaf photosynthesis modelled by a Michaelis-Menten function – a typical saturation function describing the relation between absorbed radiation and gross photosynthetic rate P_{leaf}:

$$P_{leaf}(I_{leaf}) = \frac{\alpha\,\hat{I_S}\,p_{max}}{\alpha\,I_{leaf} + p_{max}} \tag{54}$$

where α is the quantum efficiency, also known as the initial slope of the species-specific light response curve, I_{leaf} is the incoming irradiance on the surface of a single leaf dependent on the leaf area distribution within the canopy and p_{max} is the maximum gross photosynthetic rate.

To obtain the actual gross photosynthetic rate of an entire individual per year, the single-leaf photosynthesis of the equation is integrated over the individual's leaf area index (LAI)

$$P_{tree} = \int_0^{LAI} P_{leaf}(I_{ind}(L))dL \tag{55}$$

This results in the potential photosynthesis of an individual tree per year as first presented by Thornley and Johnson (1990):

$$P(I_{ind}) = \frac{p_{max}}{k} \ln \frac{\alpha\,k\,I_{ind} + p_{max}(1-m)}{\alpha\,k\,I_{ind}\,e^{-kLAI} + p_{max}(1-m)} \tag{56}$$

The instantaneous rate of photosynthesis per square meter P has to be multiplied by the crown area C_A, the duration of the tree specific photo-active period over the year φ_{act}, the limitation factors of water φ_W and temperature φ_T and finally the conversion coefficient $codm$ from absorbed CO_2 to organic dry mass:

$$GPP_{tree} = P_{tree}\ C_A\ \varphi_{act}\ \varphi_T\ \varphi_W\ codm \qquad (57)$$

Radiation input I_S is assumed to be the average daily radiation from sunrise to sunset. The photo-active period is calculated as

$$\phi_{act} = 60 * 60 * L_{day} * \psi \qquad (58)$$

whereby L_{day} is the mean length of the day during the vegetation period ψ [days].

Table 7: Tree type specific photosynthetic parameters based on data published by Sonntag (1998) (a). The rest is interpolated

tree type	p_{max} $\mu mol_{CO_2}/m^2s$	α $\mu mol_{CO_2}/\mu mol_{photons}$
pinus	18.82 a	0.0364 a
picea	14.1 a	0.0402 a
fagus	13.14 a	0.0644 a
quercus	16.87	0.0368
populus	14.69	0.0385
fraxinus	13.44	0.0471
betula	18.81	0.0364
robinia	14.1	0.0402

Table 8: General parameters of forest

name	value	unit
m	0.1	-
k	0.7	-

A.5.2 *biomass increment:*

Gross primary production is first reduced by maintenance respiration R_m and growth respiration r_g then consumes then a constant fraction of the remaining biomass production ΔB (Dislich et al., 2009).

$$\Delta B = (GPP - R_m) * (1 - r_g) \tag{59}$$

Thereby, the growth respiration factor r_g is set to 0.25 for every tree type Ryan (1991).

A.5.3 *Maintenance respiration:*

The maintenance respiration results from the temperature-dependent factor κ_T of t_y and the biomass-dependent base respirationR_b:

$$R_m = \kappa_T \; R_b(B) \tag{60}$$

That base respiration results from a parametrization climate and a resulting observed growth in the field which is used only for the parametrization. Solving Eq. 59 for R_m and replacing P with $\check{P}$ as the photosynthesis calculated for the given parametrization climate and $\Delta\check{B}$ as observed growth, we get:

$$R_b = G\check{P}P - \Delta\check{B}(1 - r_g) \tag{61}$$

All trees of the observation data must have same height in a given year so that the resulting observed growth results from full light conditions. In other words: no shading between the trees is assumed and this situation mostly occurs in monocultures. Using the parametrization climate as input for the limitation factor calculations of section A.4 and replacing them in Eq.57 we get:

$$G\check{P}P = \check{P}(I_{\check{ind}}, \check{\psi}, \check{B}) \; C_A \; \phi_{\check{act}} \; codm \; \check{\varphi}_T \; \check{\varphi}_W \tag{62}$$

where $(I_{\check{ind}}$ is the radiation at top of the tree of the parametrization climate.

Biomass increment is proportional to ΔD (21). Therefore the observed diameter increments under the parametrization climate can be transformed to biomass increments $\Delta\check{B}$. The diameter increment depends on the actual diameter by:

$$\Delta D = d_1 \; d_2 \; d_3 (d_2 \; D)^{d_3 - 1} \; exp\left((d_2 D)^{d_3}\right) \tag{63}$$

where d_1, d_2, d_3 are type specific parameters.

Table 9: Tree type-specific carbon balance parameters

tree type	ψ^*	I_r^*	$\varphi_T^* * \varphi_W^*$	d_1	d_2	d_3
pinus	1.00	503.79	0.9998	$1.83\ 10^{-3}$	3.216	1.253
picea			0.9975	$5.67\ 10^{-3}$	0.820	1.064
fagus	0.4839	761.23	0.9985	$4.70\ 10^{-3}$	1.252	1.39
quercus			0.9992	$7.06\ 10^{-3}$	0.703	1.184
populus			0.9999	$14.32\ 10^{-3}$	1.396	1.220
fraxinus			0.9997	$2.04\ 10^{-3}$	3.651	1.512
betula			0.9981	$3.74\ 10^{-3}$	1.445	1.445
robinia			0.9995	$3.12\ 10^{-3}$	3.393	1.120

B

ADDITIONAL INFORMATION REGARDING RESULTS AND DISCUSSION OF CHAPTER 2

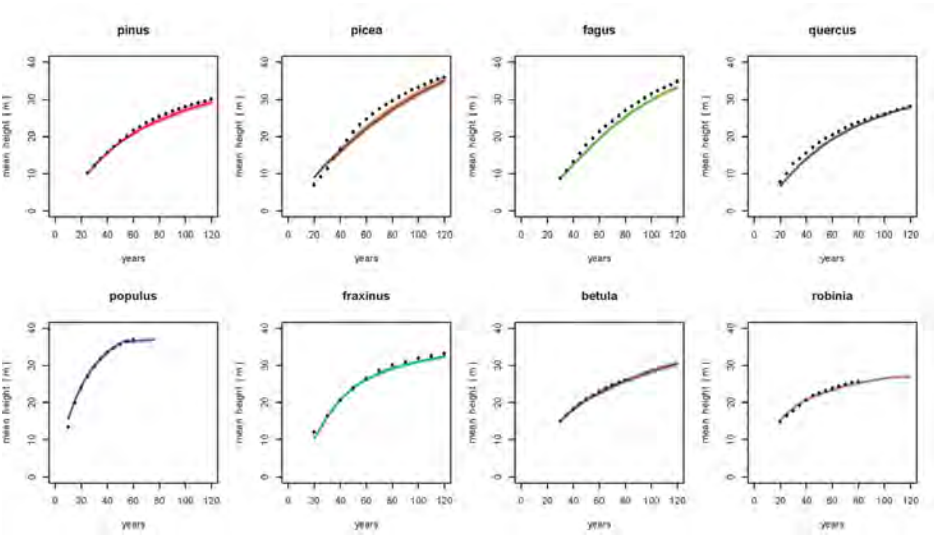


Figure B.1: Mean height development of trees over time of all eight species. Black dots show the yield table data in Schober (1995) for Germany. Mean of 1000 simulations represented by lines. Significance interval represented as grey band. All simulations start with the same initial conditions as the yield tables.

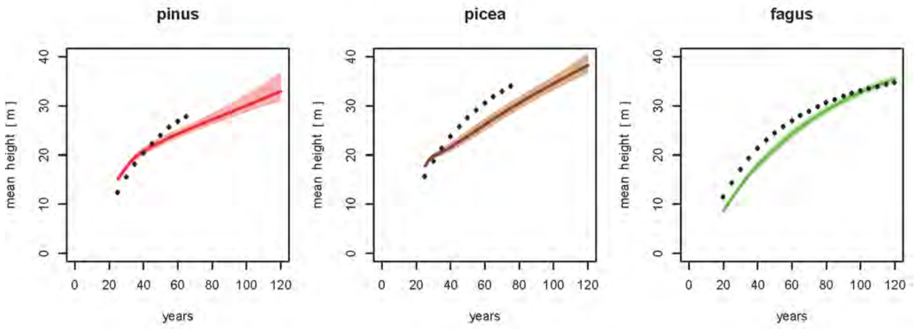


Figure B.2: Mean height development of trees over time of Pinus, Picea and Fagus. Black dots show the yield table data in ENGREF (1984) for France. Mean of 1000 simulations represented by lines. Significance interval represented as grey band. All simulations start with the same number of trees as the yield tables.

C

ADDITIONAL INFORMATION REGARDING METHODS AND VALIDATION OF CHAPTER 3

C.1 CLIMATE DATA

Two climate time series are used in this study. The first one (figure C.1) consists of one "typical" year and it is needed in the forest factory for the creation process of the forest stands. The second one (figure C.2) consists of five years, which are used to calculated average productivities of these five independent scenario years. Note, tree allometries stay constant for all five scenarios.

C.2 DETAILED DESCRIPTION OF GENERATION OF THE FOREST PATCHES

The used stem size distributions are based on a Weibull-distribution (e.g. Ryniker et al., 2006; Taubert et al., 2013) . The peaks of the stem size distribution are set at a stem diameter of 5,15,25,35 and 45 cm whereby the 95% quantile are set at a stem diameter of 6,16,26,36 and 46 cm (figure C.3). We selected this 15 stem size distribution to cover a broad range of forest structure in a systematic way and to limit calculation time. With this setting, we include 65% of all forest plots of the German forest inventory (35% are forest plots, which include at least on tree with a dbh larger than 50cm). However, larger maximal stem diameters are possible.

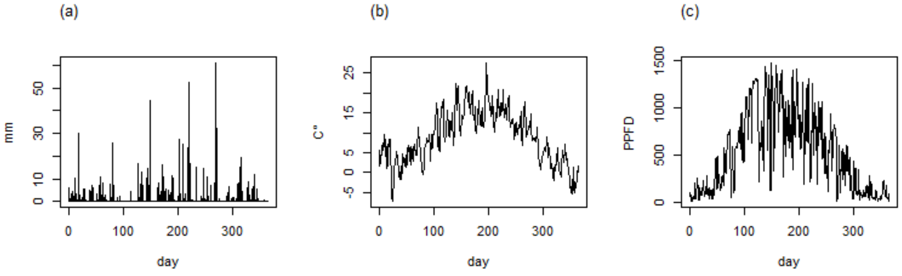


Figure C.1: Overview of climate conditions used as input for the forest stand creation. The climate data set was measured at FLUXNET-station Hainich in 2007. (a) daily precipitation (mm), (b) daily air temperature (°C), (c) daily incoming radiation (photoactive photon flux density (μmol m^{-2} s^{-1})).

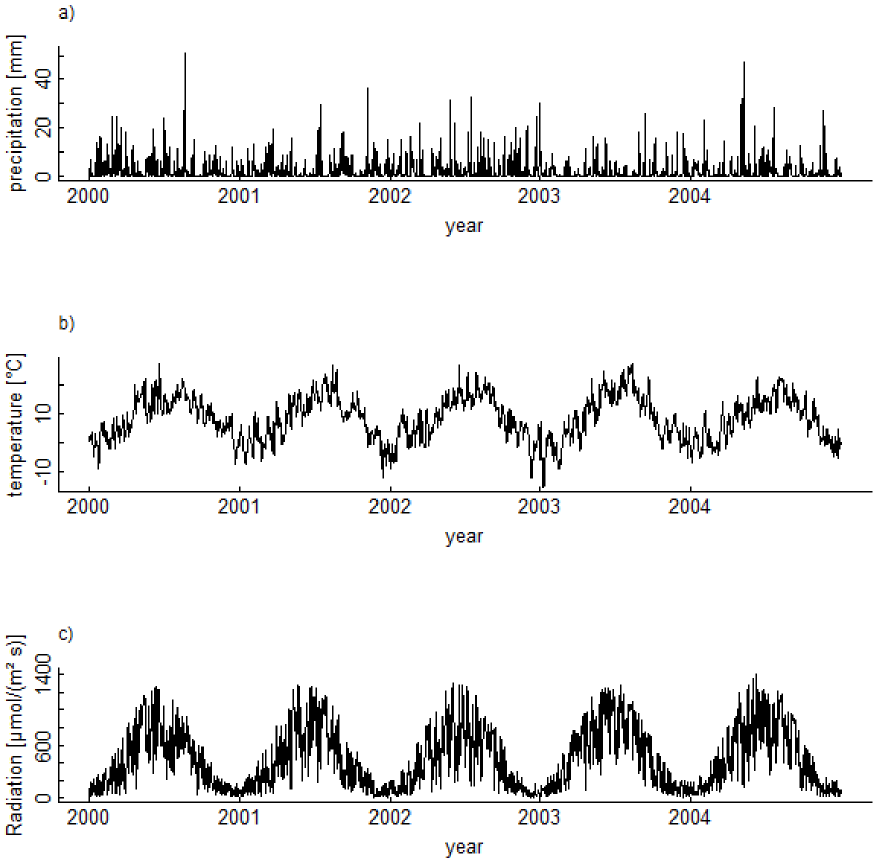


Figure C.2: Overview of climate conditions used as input for the final productivity calculation. The climate data set was measured at FLUXNET-station Hainich from 2000 to 2004. (a) daily precipitation (mm), (b) daily air temperature (°C), (c) daily incoming radiation (photoactive photon flux density µmol/(m^2s)).

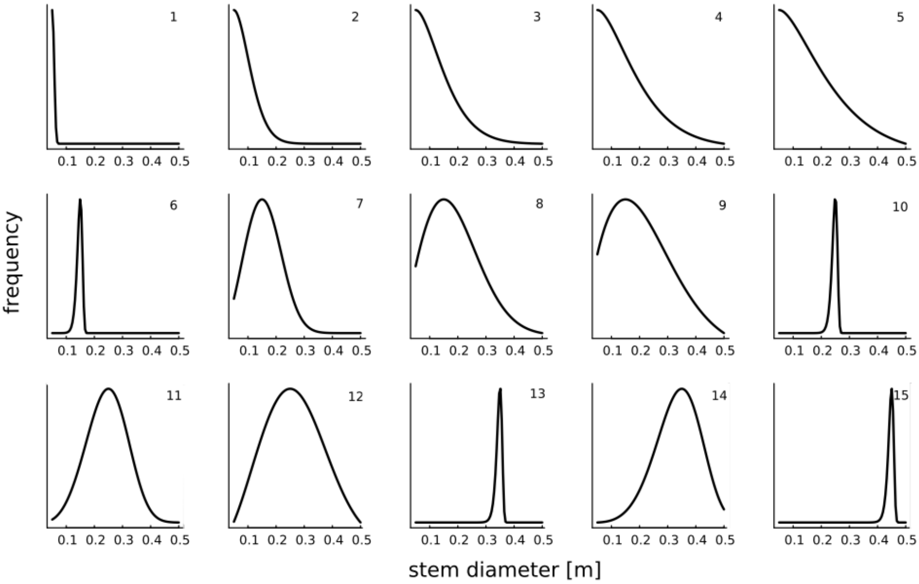


Figure C.3: Overview of the different stem size distributions.

For every combination of species mixtures and stem size distributions we generate 100 patches of $400m^2$ (= 4 hectare in total). For every hectare (25 patches) we execute step one and step two.

Step one: The input stem size distribution contains no information regarding the total number of stems. We therefore determine how many trees can be found per hectare by iteratively adding trees to reproduce the character of the stem size distribution as well as possible (rule 2). The only limitation in this step is the space occupied by the tree crowns (rule 1). Species identities of trees are chosen randomly from the current species composition. Note that species differ in their crown allometries, which results in different stem numbers for different species composition, but the same stem size distribution. This step results in the maximal stem number per hectare of the current stem size distribution (see figure 7).

Step two: We start the placement of trees in the 25 patches of the stem size distribution resulting from step 1 with the largest tree (defined by the largest stem diameter) followed by the next smaller one. Every tree is assigned to one of the patches randomly. Before every tree placement we check

- ...if there is enough space in the patch for the tree crown. If not another patch is selected randomly. If no patch could take up the tree the total number of trees for the current hectare is reduced and the filling process of step two restarts.

- ...if the assigned species identity of the tree has a positive productivity under the current light and environmental conditions (see figure 8 in the paper). If this is not the case another species identity (if available) is tested for positive productivity. If no species identity (of the current mixture) has a positive productivity, another patch is selected and the placement starts with the original species identity. If no patch could host the current tree the total number of trees in the hectare is reduced and the filling process of step two restarts. c
- ...if the change in light conditions results in a negative productivity of any other tree in the patch. If this is the case, we check if a species identity with same stem diameter and positive productivity is available, which shades other trees less than the original one so that all trees have a positive productivity. If not all criteria are fulfilled another patch is selected. If no patch could host the tree the total number of trees for the current hectare is reduced and the filling process of step two restarts.

Note, if the tree number of the stem size distribution must be reduced, the reduction is executed in a way that keeps the shape of distribution at the hectare scale as good as possible.

The described procedure is implemented in R 3.2.2

C.3 FOREST STAND PROPERTIES

We also analysed the relationship between basal area and θdepending on species richness (figure C.5).

C.4 VALIDATION OF AWP CALCULATION

We use eddy flux measurements to determine how well the forest factory method reproduces forest productivity under different climatic conditions (boreal and temperate). We also use German forest inventory II and III data to determine whether differences in forest structures and species mixture influence productivity. Note that the species-specific parameterization has already been tested successfully against the yield tables presented by Bohn et al. (2014).

For the validation with eddy flux measurements (Luyssaert et al., 2007), we select sites with a homogenous forest structure, with trees of similar height within the footprint and with one dominant species (even-aged forests). For such sites, it is reasonable to assume that productivity

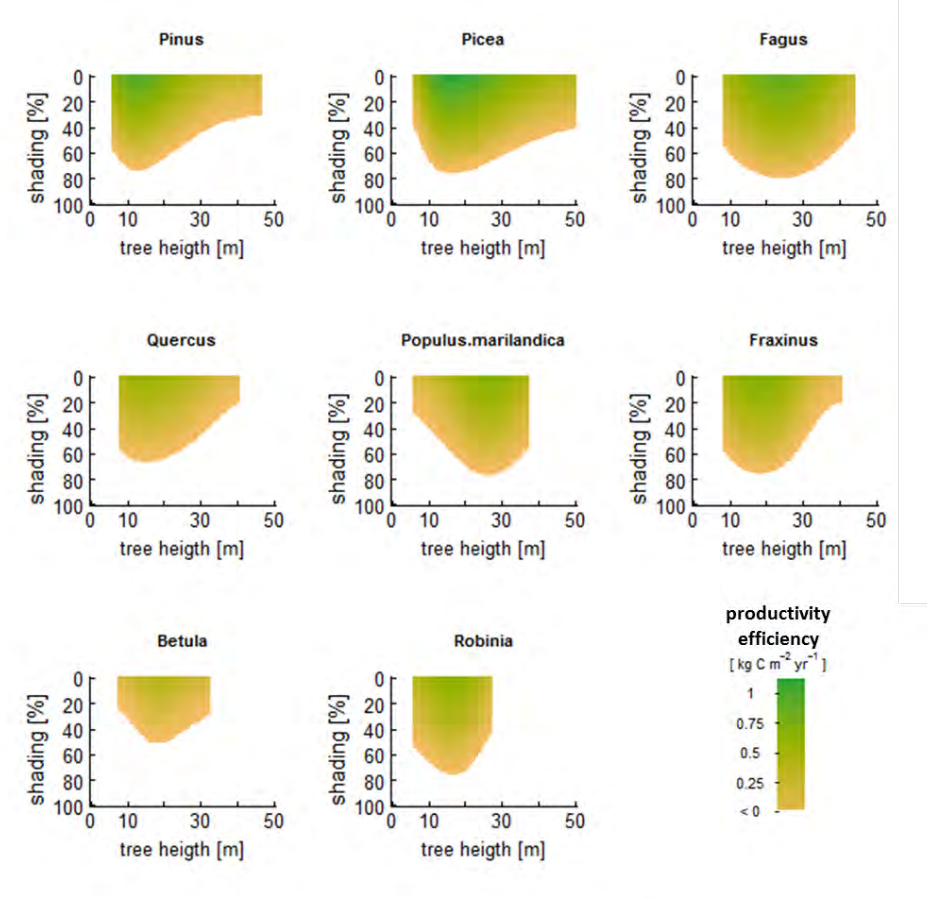


Figure C.4: productivity efficiency (AWPtree per unit crown area) of all eight species. Productivity depends on tree height and available light at the top of the tree under the given environmental conditions (Hainich 2007). Productivity efficiencies of tree heights with a dbh smaller than 5 cm and light-height combinations with negative productivity are not plotted (white area).

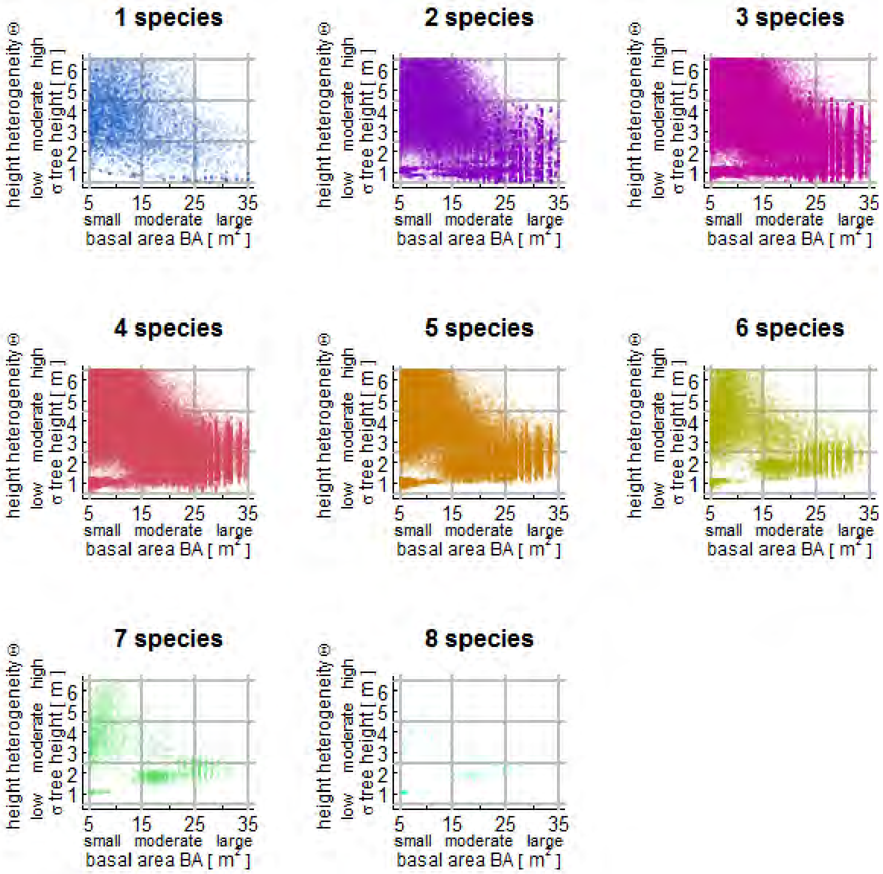


Figure C.5: Overview of the all forest stands. Scatterplots between basal area and tree height heterogeneity, where each dot represents one forest stand. Grey lines separate the nine different structure classes of low, moderate and high tree height heterogeneity levels (0.5-2.5 m, 2.5-4.5 m and 4.5-6.5 m) and small, moderate and large basal areas (5-15 m^2, 15-25 m^2 and 25-35 m^2).

per area is scale independent. From our dataset, we selected a forest stand from the forest factory model which hosts the identical species and which has the same LAI and forest height recorded for the flux site. The forest stand productivity was calculated from climate data measured at the sites. For temperate forests, productivity was reproduced effectively (figure C.5 a). However, simulated and observed productivity were found to be less prevalent in the boreal zone.

To compare our AWP-estimation with the German forest inventory III (2012), we selected forest plots that (i) host only species considered in this study and (iii) are located on flat terrain (sloped at less than 15 %). As the inventory is based on variable radius sampling, we only consider plots with trees with a maximum dbh of 0.5 meters (which results in a maximal area of 400 m^2 of the plots).

To construct the plots, we used the average height and dbh of each tree for inventories II and III. For the productivity calculations, we used Hainich station climate data (for 2000 to 2004) because plot-specific climate data were not available. We omitted stands presenting negative productivity (0.97% stands were removed). Simulated forest stand productivity levels correspond quite well with the observed stand productivity level (figure C.6 b; figure C.7 shows analysis with all values). Our slight underestimation of AWP (a = 0.85) may be a product of the assumed climate because the climate at the Hainich site is slightly colder than the average climate for Germany (the site is located at 430 m o.s.l). Such differences may also be attributable to specific tree allometries and local environmental conditions.

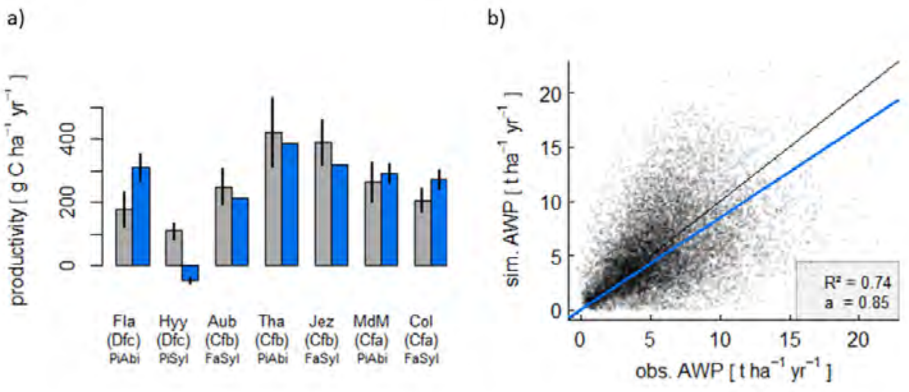


Figure C.6: Validation for (a) eddy flux measured wood productivity (dark grey) and modelled AWP (blue). The following sites were selected: Flakaliden (Sweden), Hyytiala (Finland), Aubure (France), Tharand (Germany), Jezeri (Czech Republic), Monte di Mezzo and Collelongo (Italy). Dfc sites are located in a wet boreal climatic zone with cold summers, whereas Cfa and Cfb are located in a wet temperate climatic zone with hot (Cfa) and warm (Cfb) summers. Dominant species found in the sites are spruce (PiAbi), pine (PiSyl) and beech (FaSyl). b) Observed aboveground wood production for German forest inventory III compared to simulated values. The black line represents the 1:1 line, and the blue line represents the linear fit between observed and simulated values using a linear model (a*x ; R^2 = 0.74; a =0.85).

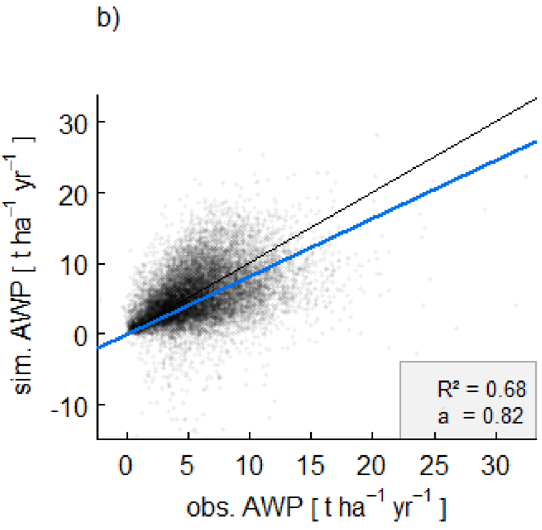


Figure C.7: Validation graphic including all forest plots. Every point represent compares the productivity of a forest plot of the German forest inventory with the simulated productivity of that plot. Points are transparent.

D

ADDITIONAL INFORMATION REGARDING RESULTS AND DISCUSSION OF CHAPTER 3

D.1 IMPACT OF TEMPERATURE AND FUNCTIONAL DIVERSITY ON THE RESULTS

To explore the sensitivity of the results in figure 11 to changes in the temperature of the used climate time series, we reconduct the full analysis using a modified climate time series (we alter the temperature time series by 1.5°C, resulting in a mean annual temperature of 6.8°C and 9.8°C). In general, the observed pattern persists (figure D.1, first & second rows). There is a slightly positive effect for forest stands with low height heterogeneity but a negative effect for forests with high height heterogeneity. Additionally, the variability of the productivity between the forest stands increases with increasing temperatures. To analyse the effect of functional diversity on productivity (instead of richness), we calculate Rao´s Q (Rao, 1982; Laliberté and Legendre, 2010) using all of the physiological parameters that are related to the productivity calculation (n=12). However, the effect of functional diversity on productivity is negligible (figure D.1). The variability in productivity did not decrease with increasing Rao´s Q as it did for species number.

D.2 ANALYSIS OF THE SPECIES RICHNESS WITHIN THE GERMAN FOREST INVENTORY

We analyse the relationship between diversity and productivity by using two different methods. First, we calculate the AWP_N for the plots of the German forest inventory based on AWP_{mixsture}, which consists only of beech, spruce or pine trees or one of their mixtures. This selection was made because other mixtures occur only in a small number of forest structure classes (in total we analysed 5,054 forest stands). Second, we calculate the mean productivity of all plots containing the same number of species (as conducted, for example, by (Vilà et al., 2007). With the second analysis, we find an increase in productivity of 10 % between one and two species mixtures, which corresponds to the findings of other studies (e.g. Vilà et al., 2007). The calculated AWP_N instead shows no effect of diversity, which corresponds to the analysis of the forest factory (figure D.2, and figure 11). When the mean productivity for all forested

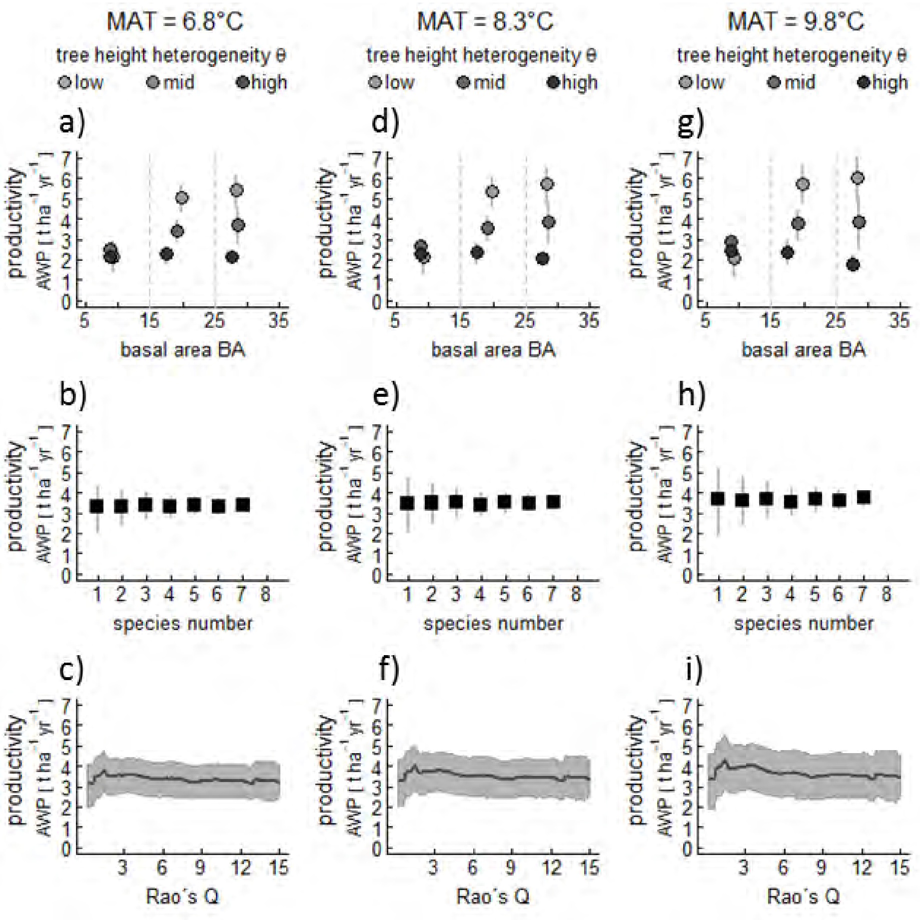


Figure D.1: Sensitivity of forest stand productivity (above-ground wood production) against mean annual temperature (MAT). Left column based on simulation with a MAT of 6.8°C (figure a), b), c), middle column (figure d), e), f)) based on the measured data of Hainich and right column based on a simulation with a MAT of 9.8°C (figure g), h), i)). Mean productivity of the nine structure classes fig(a), d), g)): low, mid and high basal area BA (5-15 m^2 hectare-1; 15-25 m^2 hectare-1; 25-35 m^2 hectare-1) and low mid and high tree height heterogeneity Θ (0.5-2.5 m; 2.5-4.5 m; 4.5-6.5 m); Mean productivity depending on species number (figure b), e), h) of forest stand. Mean productivity depending on Rao´s Q (figure c), f), i)). Grey bars indicate the interquartile range.

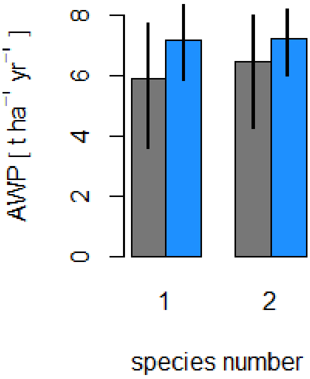


Figure D.2: Mean productivity of forest stands (above-ground wood production) depending on species number for stands of the German forest inventory, which includes only beech, spruce and pine and their mixtures. Grey bars represent the mean productivity over all plots with the corresponding species number. Blue bars represent mean productivity ($= AWP_N$ of the Manuscript), where we build the mean over all $AWP_{s,n}$ while keeping the species number constant. Lines represent the interquartile range.

areas with a certain number of species was calculated, we found a 10 % increase in productivity between one and two species mixtures. This corresponds to the results of other inventories (e.g. Vilà et al., 2007, Catalonian forest inventory). This positive relationship may be attributed to the fact that 71% of German forest inventory plots show height heterogeneity levels of less than 2.5 and basal areas of greater than 25 m^2. For these structure classes, our results show a positive diversity-productivity relationship (see figure 12).

D.3 FOREST STANDS WITH ONLY ONE OR TWO SPECIES

The relationship between forest structure and productivity (figure D.1) can be analysed for stands with only one species. Thereby the general pattern (productivity increases with increasing basal area and decreasing height heterogeneity) can be found in all mixtures (figure D.4,D.5). However, monocultures vary in their absolute productivity values (figure D.4), but monocultures and AWP_N for all monocultures shows the general pattern quite well. In case of two species mixture with beech (figure D.5) the differences of the productivity-structure-relationships between the mixtures are much lower and vanish almost completely for species mixtures with more than two species

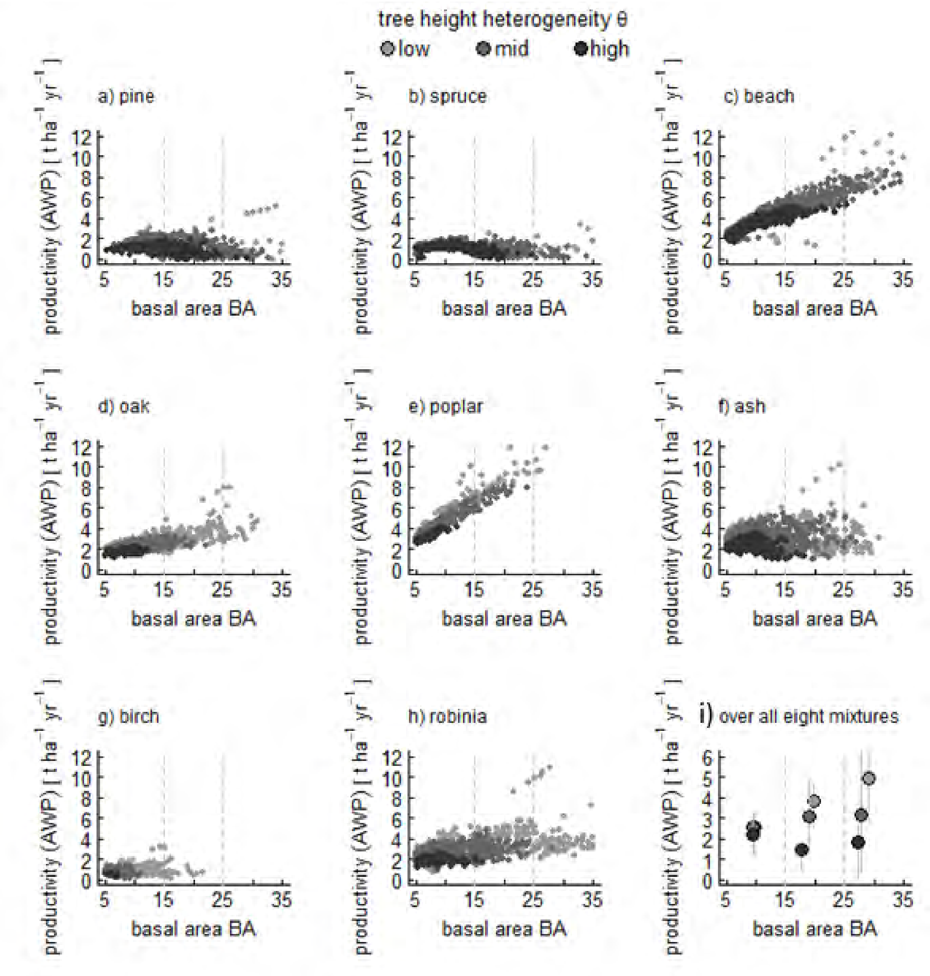


Figure D.3: Analysis of the structure-productivity relationship of monocultures (a-h); every dot represent one forest stand. Darker greys indicate higher height heterogeneity classes. AWP_N values over all eight monocultures (i) with IQR as grey stripes.

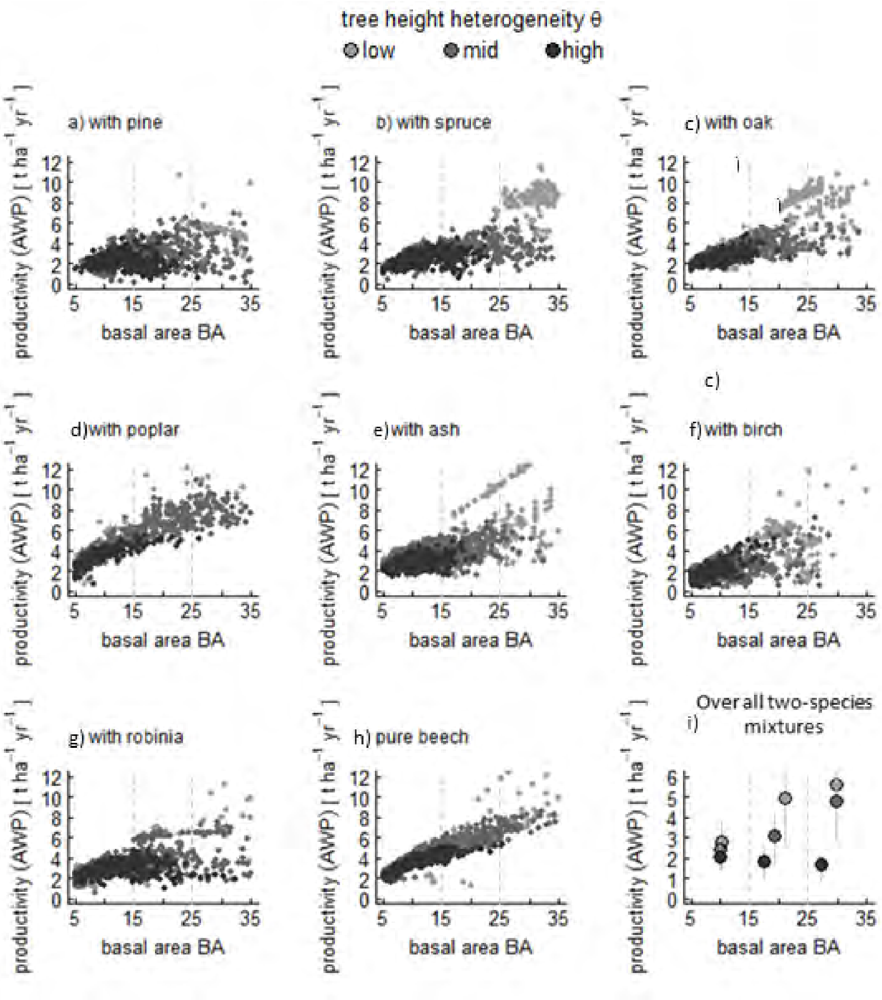


Figure D.4: Analysis of the structure-productivity relationship of two-species-mixtures with beech (a-g) and beech monoculture (h); every dot represent one forest stand. Darker greys indicate higher height heterogeneity classes. (i) AWP_N over all seven two-species mixtures with IQR as grey stripes.

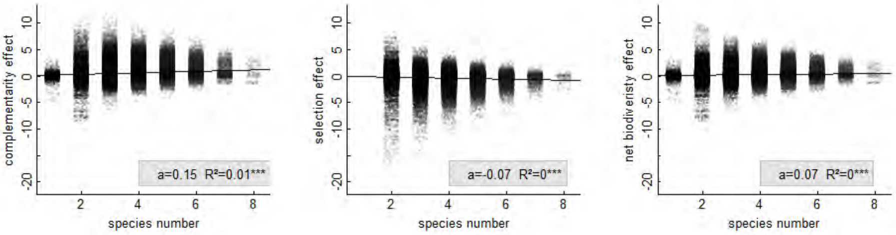


Figure D.5: Additive partitioning. a) complementarity; b) selection; c) net biodiversity effect. Line is a linear model with a as slope. Stars indicate significance of the model: *** indicates a p-value <0.001. Every dot represents one forest stand.

D.4 ADDITIVE PARTITIONING ANALYSIS

Based on the concept of Loreau and Hector (2001) we perform additional partitioning analysis. As the forest factory does not include information about age we use as monocultures the average of those monocultures which show a similar forest structure. The structure indices (BA, Θ) are z-transformed so that both have a mean of 0 and a standard deviation of 1. We select the 10 nearest monocultures using Euclidean distance (95% of the structural distances between monocultures and the mixtures are below 0.22 in the z-transformed structure and the average distance is 0.08). The overall analysis of the forest stands shows that both complementarity and selection mechanisms have low potential to explain the variance of the forest productivity (figure D.5). This finding does not change if we use relative abundances (in terms of biomass or basal area) for the calculation of the expected yield.The analysis of the nine different forest structure classes shows also hardly any correlation between selection/complementarity and forest productivity.

D.5 EXAMPLE OF THE APPLICATION OF STRUCTURE OPTIMALITY MECHANISM

We analyse the relationship between diversity and the three indices of the structure-optimality-mechanism (figure D.6) by calculating the coefficient of determination for all structure classes. The correlation between species number and optimal species distribution (Ω_{AWP}) or forest structure indices are on average much higher than the correlation found in the additive partitioning analysis (figure D.7) and reach an R^2 of up to 0.25. Please note that a high correlation between species number and one index does not automatically result in a strong correlation of that in-

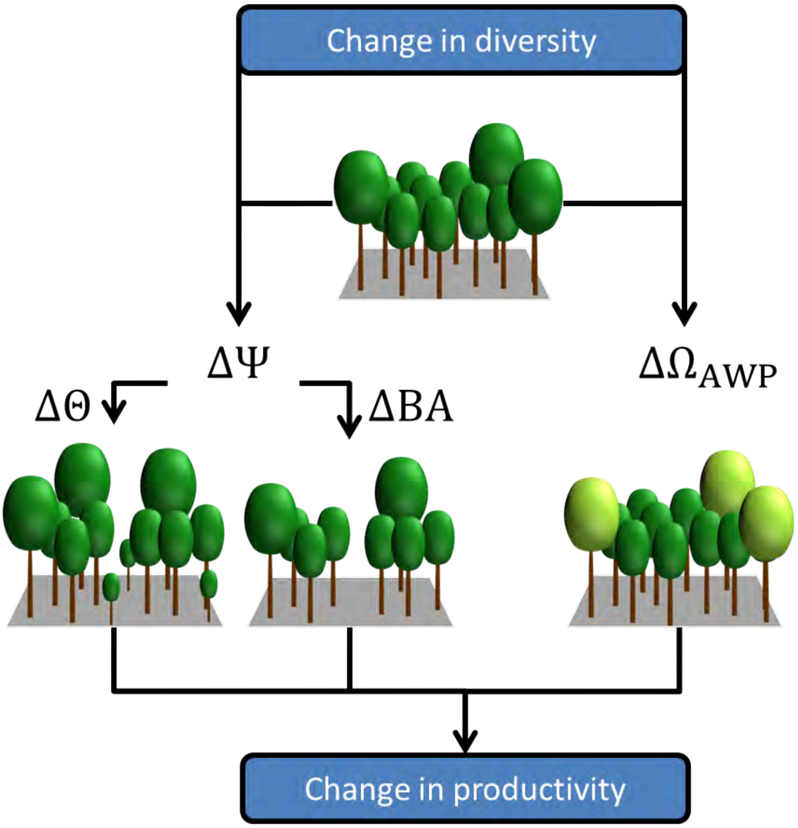


Figure D.6: Concept of the structure-optimality-mechanism, which convert a change in diversity into a change of productivity. A change in tree diversity between two forests result in a change of forest structure Φ and/or Ω_{AWP}. The change in forest structure splits into a change of tree height heterogeneity θ and/or in a change of basal area (BA).

dex with the productivity. For instance, in the forest structure class with high basal areas and low tree height heterogeneity species number correlate quite well with structure indices (figure D.8 a & b) but it correlates weak with Ω_{AWP} (figure D.8 c).However, Ω_{AWP} is the main driver of productivity in this structure class (figure D.8 f).

D.6 ANALYSIS OF FOREST STANDS WITH EQUAL ABUNDANCES OF SPECIES

To quantify, how strong unequal abundances of species due to rule 3 influence the results we repeat the analysis with a subsample of the forest factory data set. This data set includes only those forest stands which have a functional evenness greater than 0.9 (Laliberté and Legen-

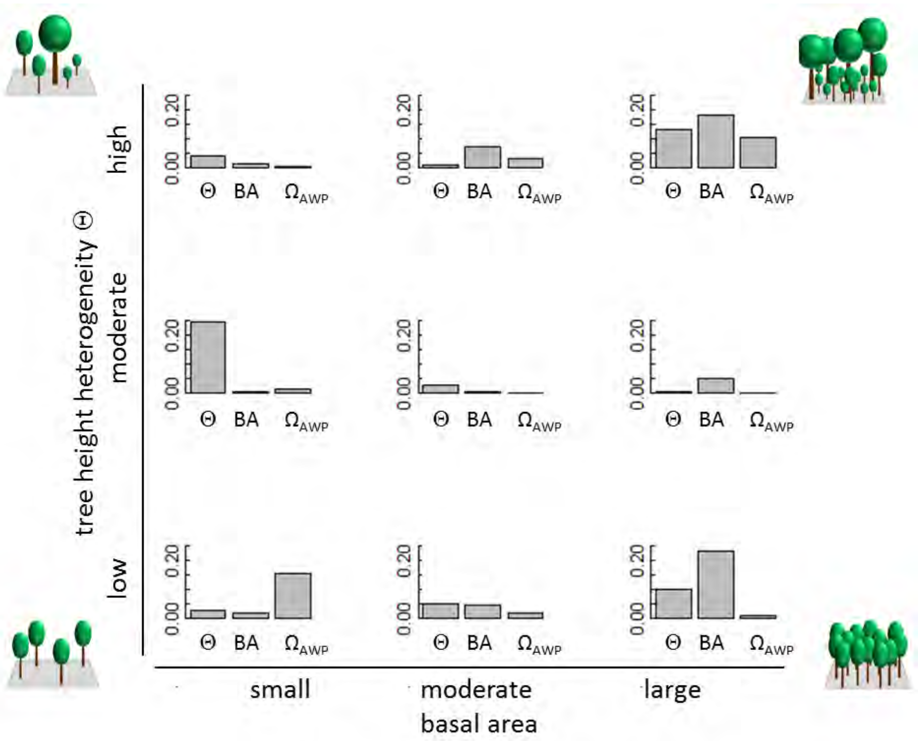


Figure D.7: Coefficient of determination (R^2) between number of species and the indices of the structure-optimality-mechanism for the nine structure classes.

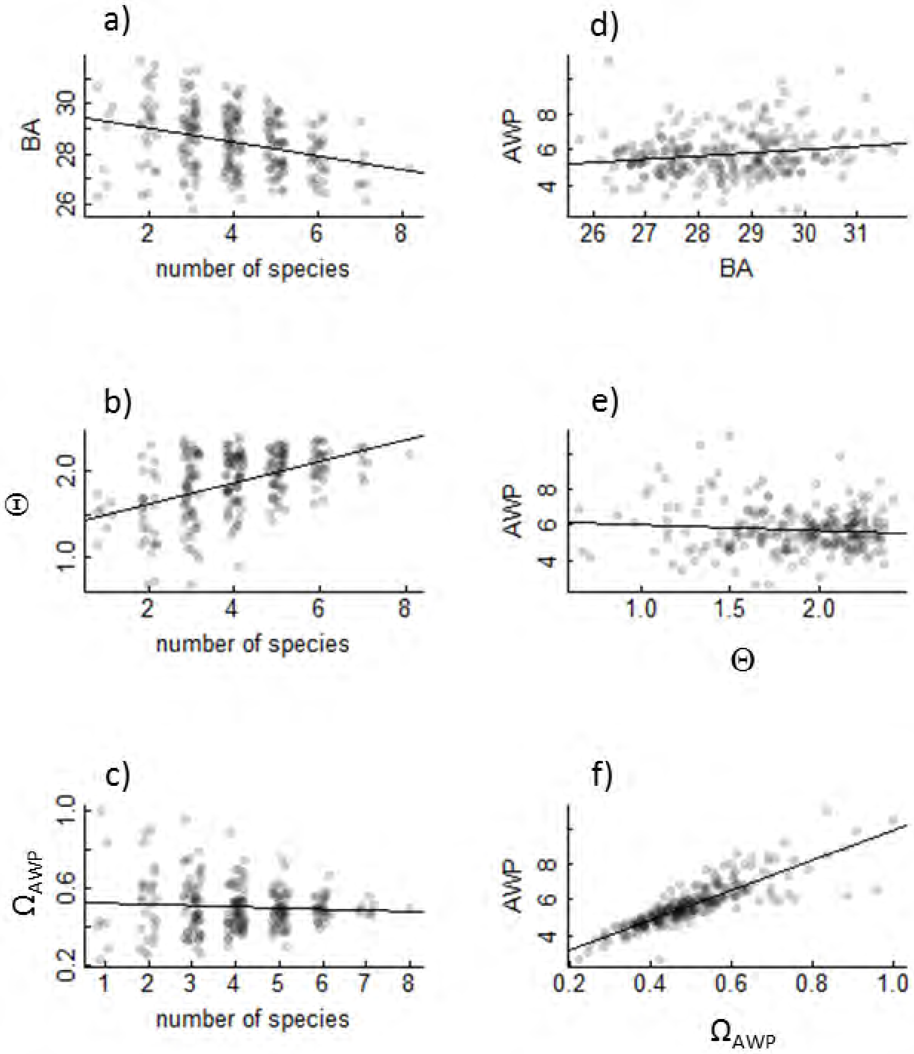


Figure D.8: Relationship between number of species and forest structure indices (Ω_{AWP} and BA) as well as optimality (Ω_{AWP}) for forest stands with high basal area and low tree height heterogeneity (a, b, c). Relationship between forest structure indices (Ω_{AWP} and BA) and optimality (Ω_{AWP}) with forest productivity (AWP) (d, e, f). Every dot represents one forest stand. Black line shows a fitted linear model.

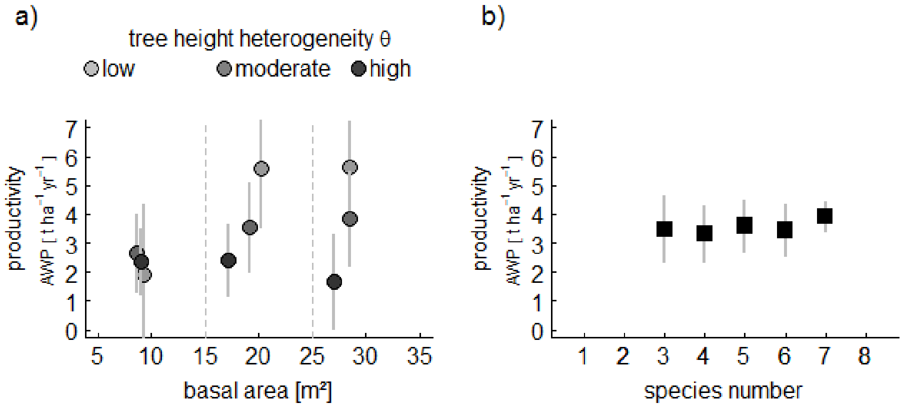


Figure D.9: Analysis of mean productivity (aboveground wood production) of those forest stands, which show a functional evenness greater than 0.9. a) Mean productivity of the nine structure classes: small, moderate and large basal area BA (5-15 m^2 hectare-1; 15-25 m^2 hectare-1; 25-35 m^2 hectare-1) and low, moderate, and high tree height heterogeneity Θ (0.5-2.5 m; 2.5-4.5 m; 4.5-6.5 m); b) Mean productivity depending on the numbers of species in a forest stand. Grey bars denote the mean standard deviation.

dre, 2010). Note that the calculation of functional evenness requires at least 3 different species. The analysis of the subsample shows a quite similar pattern as the analysis including all forest stands (figure D.8). Only forest stands with high basal area and high tree height heterogeneity show lower productivities.

D.7 THE INFLUENCE OF MEAN TREE HEIGHT AND TREE HEIGHT HETEROGENEITY ON PRODUCTIVITY

Different indices were developed to describe forest structure (Pommerening, 2002). We tested also the effect of mean tree height by replacing basal area in the analysis (figure D.10). We observed similar patterns compared to the original analysis.

D.8 DIVERSITY-PRODUCTIVITY-RELATIONSHIPS COVERING ONLY ONE FOREST STRUCTURE CLASS

Beside the comparison between the forest stands of the forest factory with analysis of large data set, which based on forest inventories and cover several forest structure classes, subsamples of the forest factory can be compared with small datasets which belong only to one forest structure class.

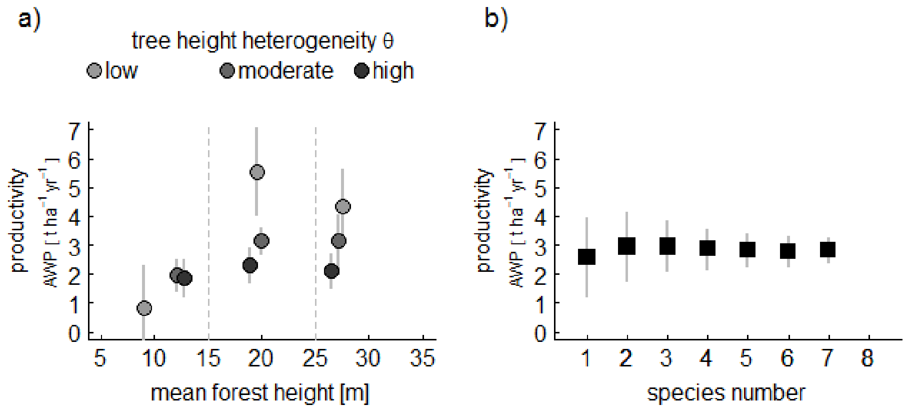


Figure D.10: Analysis of mean productivity (aboveground wood production) of those forest stands. a) Mean productivity of the nine structure classes: small, moderate and large mean tree height (5-15 m; 15-25 m; 25-35 m) and low, moderate, and high tree height heterogeneity θ(0.5-2.5 m; 2.5-4.5 m; 4.5-6.5 m); b) Mean productivity depending on the numbers of species in a forest stand. Grey bars denote the mean standard deviation.

D.8.1 *Positive diversity-productivity relationship*

Many studies have analysed forest productivity in two or three species mixture experiments (e.g. Edgar and Burk, 2001; Chen and Klinka, 2003; Amoroso and Turnblom, 2006; Pretzsch et al., 2010). For instance, Edgar and Burk (2001) analysed pure aspen stands and stands with admixtures of other species. The analysed forest stands are described by a top canopy height of 25 m, a high basal area and a medium Θ. For the analysed forest stands an increase of basal area with diversity was found (basal area increase of 30%). Beside a positive structure mechanism figure D.7), the optimality-mechanism might also support the positive effect: In the monocultures larger aspen trees shade some smaller ones. In the mixture, smaller trees belong mostly to more shade-tolerant species and aspen only occur in the top layer which should result in an increase in $(\Omega_{AWP}$. Thus, the positive effect of diversity on productivity results from positive correlation between diversity and structure as well as $(\Omega_{AWP}$. This change in both forest properties (structure and (Ω_{AWP}) is then responsible for the increase in productivity (figure D.7). In other studies sometimes a separation over height of the species is described (e.g. Pretzsch et al., 2010) or a change in forest structure can be related to the observed productivity (e.g. Chen and Klinka, 2003; Amoroso and Turnblom, 2006).

D.8.2 *Negative diversity-productivity relationship*

A decreasing relationship between diversity and productivity was found by Jacob et al. (2010) in the Hainich forest (Germany). They analysed nine forest plots which all show high basal areas, high tree height heterogeneity and cover an area of 50x50 meter. The plots contain only deciduous tree species (more than six) whereby the monocultures are dominated by beech (abundance = 96%). For the corresponding forest stands of the forest factory (same structure class only deciduous trees) (n = 16) a negative relationship between Shannon-diversity and productivity can be observed which fits to the field observations. Our analysis of the structure-optimality-mechanisms reveals a strong effect of (Ω_{AWP} (R^2 = 0.91) and no effect of structure (R^2=0.01). Thus, the negative relationship can be explained by the fact that beech is the most productive species for all sizes of trees in such a forest (figure 10, area A). The low diverse forests in the study are dominated by beech resulting in the maximal productivity (high (Ω_{AWP}). If beech trees are replaced by trees of other species (due to an increase in diversity) the productivity have to decrease. In this example diversity has a negative effect on (Ω_{AWP}, while structural effects can be neglected (figure 13). The result is a negative diversity-productivity-relationship. This negative effect also occurs if we include also evergreen species (spruce and pine).

E

ADDITIONAL INFORMATION REGARDING METHODS AND VALIDATION OF CHAPTER 4

E.1 CLIMATE DATA

The generation of the 320 climate scenarios, are based on measured climate time series of the eddy-flux station Hainich in central Germany (Knohl et al., 2003) for the years 2000-2004 (figure E.1). Mean annual temperature of these five years does not correlate with the annual precipitation sum, nor with the mean annual radiation (figure E.2). Radiation and precipitation within these years correlate quite well (Pearson's r =0.73).

E.2 FOREST PROPERTIES

We use three forest properties to describe forest structure (tree height heterogeneity θ, forest height $H_{max}$and LAI) and two properties to describe species diversity (Rao´s Q describes functional diversity and Ω_{AWP} describes suitability). The calculation of Rao´s Q is based on 12 species-specific parameters which are relevant for productivity and the species abundance (based on crown area). None of the properties correlate (table 10).

E.3 VALIDATION WITH THE GERMAN FOREST INVENTORY

We analyse the influence of forest structure on temperature sensitivity within the German forest inventory. Tree height data are used to calculate forest height (h_{max}) and tree height heterogeneity (θ). We replace

Variables	Rao´s Q	θ	H_{max}	LAI
Ω_{AWP}	0	0.02	0	0.2
LAI	0	0.23	0.06	
H_{max}	0.01	0.2		
θ	0.02			

Table 10: Coefficient of Determination (R^2) between all used internal forest properties for 370,170 stands of the forest factory. θ= tree height heterogeneity; H_{max}= forest height; LAI = leaf area index; Ω_{AWP}= suitability

ADDITIONAL INFORMATION REGARDING METHODS AND VALIDATION OF CHAPTER 4

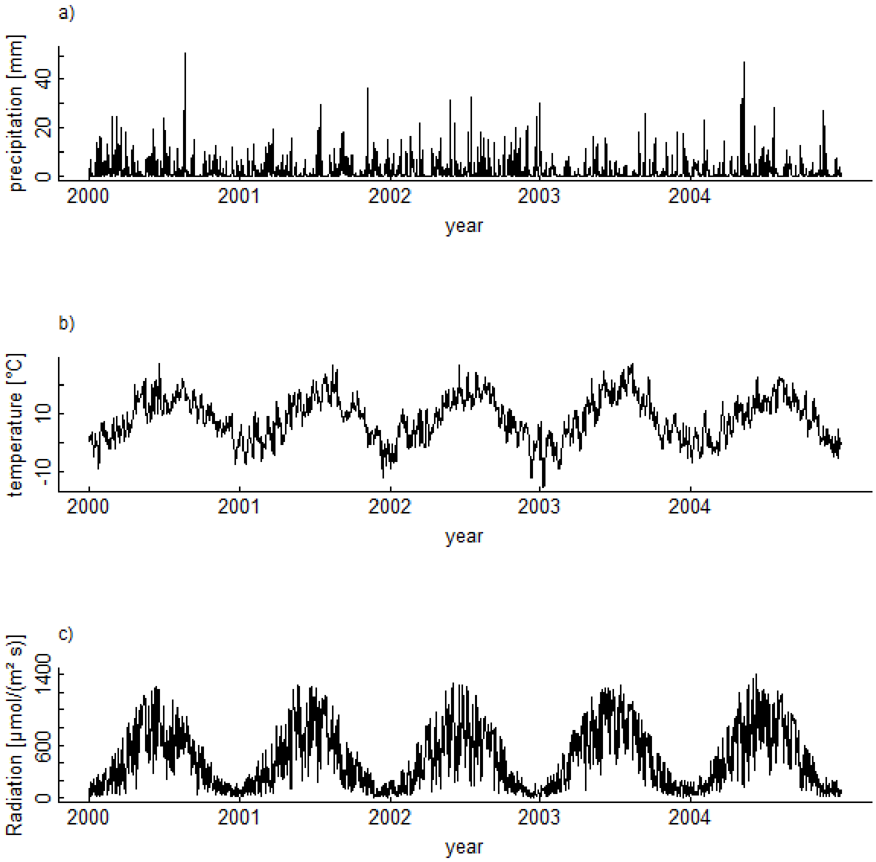


Figure E.1: The climate time series measured at FLUXNET-station Hainich from 2000 to 2004 which are used to generate the 320 climate scenarios: (a) daily precipitation [mm], (b) daily air temperature [°C], (c) daily incoming radiation [photoactive photon flux density ($\mu\mathrm{molm}^{-1}\mathrm{s}^{-1}$)].

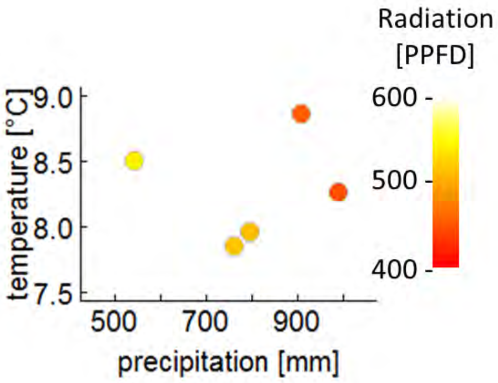


Figure E.2: Mean annual temperature, mean annual precipitation and mean annual radiation of the five climate series measured at Hainich station from 2000 to 2004.

LAI, which is not measured, by basal area (both properties correlate quite well in the forest factory data set; R^2=0.74). We analyzed forest stands of beech monocultures (deciduous species) and spruce monocultures (needle leaf species). The forest stands of each species were classified into six structure classes: three forest height classes which are based on the height of the largest tree in the forest stand (10-15 m, 20-25m and 30-35 m), and two classes representing different tree height heterogeneities (0-1 and >1.6 m). We analyse only plots that are located on flat terrain (sloped at less than 15 %) and have a maximum dbh of 0.5 meters (which results in a total plot area of 400 m^2). We fit a linear model to the data of every class using basal area and elevation as input variables to predict above-ground wood productivity (AWP).

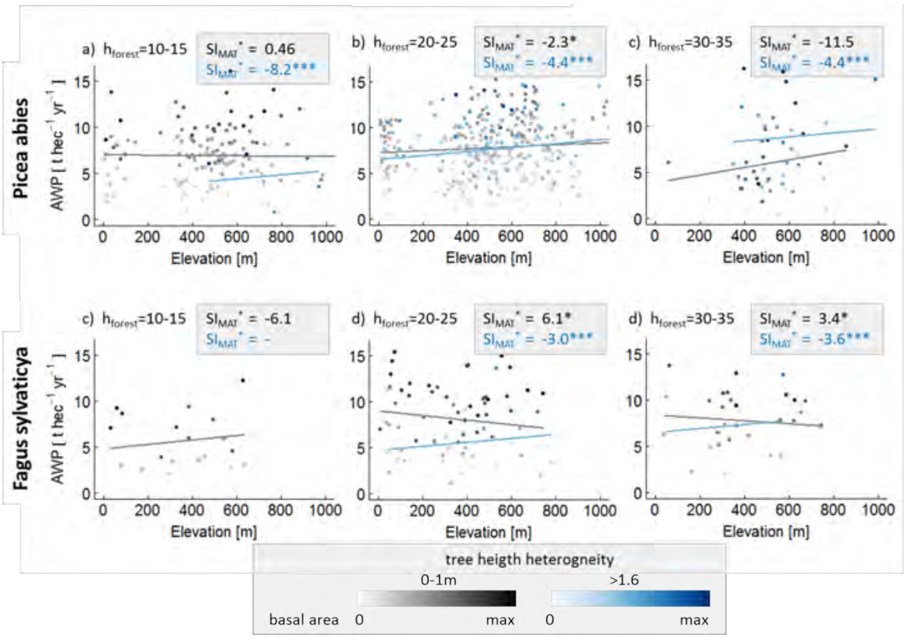


Figure E.3: Analysis of the influence of forest structure on the relationship between elevation and above-ground wood production. Figure a) – c) are based on spruce monocultures and d)-e) are based on beech monocultures. For each species, forest stands are classified into three forest height classes which are based on the largest tree (h_{max}) in a forest stand. These forest stand classes are additionally separated into two tree height heterogeneity classes (0-1 m in grey and >1.6 in blue). Intensities of the colours indicate the ration between basal area of the stand and maximal basal area found within one class. Lines show the results of the linear model with mean basal area. The amount of stars behind the SI-values indicates the significance of the slope within a linear model: (***) indicate a p-value below 0.001 and (*) indicates a p-value between 0.01 and 0.05. No star indicates p-values above 0.1. The unit of SI_{MAT}^{*} is $\% \, C^{\circ -1}$.

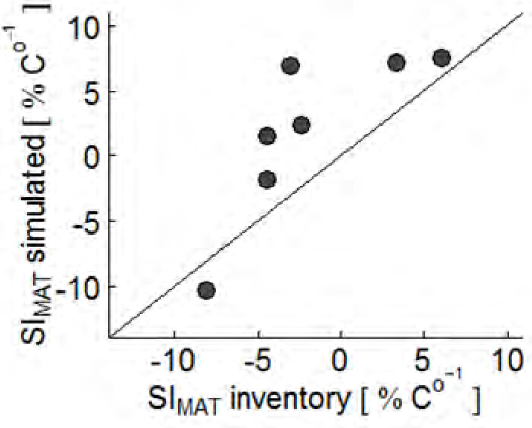


Figure E.4: SI$_{MAT}$*-values derived from the BWI-analysis vs. SI$_{MAT}$-values derived from corresponding forest types of the forest factory. Only field data with p-values smaller 0.05 are analysed.

F

ADDITIONAL INFORMATION REGARDING RESULTS AND DISCUSSION OF CHAPTER 4

F.1 FREQUENCY DISTRIBUTION OF SENSITIVITY VALUES

The analysed forest stands show a large range of temperature sensitivities levels, which reach up to 8.5% C°-1 for $\mathrm{SI}_{\mathrm{MAT}}$and up to -0.5% C°-1 for $\mathrm{SI}_{\mathrm{Q95}}$(figure F.1). The mean $\mathrm{SI}_{\mathrm{MAT}}$is 1.5% C°-1 and the interquartile range (iqr) ranges from 1.6% C°-1 to. 5.2% C°-1. The mean $\mathrm{SI}_{\mathrm{Q95}}$is -5.4% C°-1 and the iqr ranges from -5.2% C°-1 to –2.2% C°-1.

F.2 ANALYSIS WITH BOOSTED REGRESSION TREES

Boosted regression trees provide information about the underlying relationship between input variables (here forest properties) and output variables (here SI-values). Several technics were developed to visualize and interpret the high-dimensional relationship of input and target variables (Friedman, 2001). One of the most useful visualizations is the concept of relative importance which compares the influence of different input variables on the variability of a target variable (figure F.2).

Other commonly used visualization of the relationship of input and target variable are partial dependency plots (figure 18). These plots show the influence of an input variable on the target variable considering the influence of all input variables which have higher relative importance. In our study, the most important variable is Ω_{AWP}, hence the first plot shows the relationship between suitability and SI-values. The second relationship (forest height on SI-values) is based on the residuals of the first relationship (here between SI-values and Ω_{AWP}; Becker et al. (1996)). Although a collection of such plots can seldom provide a comprehensive analysis of the BRT, it can often produce helpful hints, especially if variables show very low correlations, as in this study.

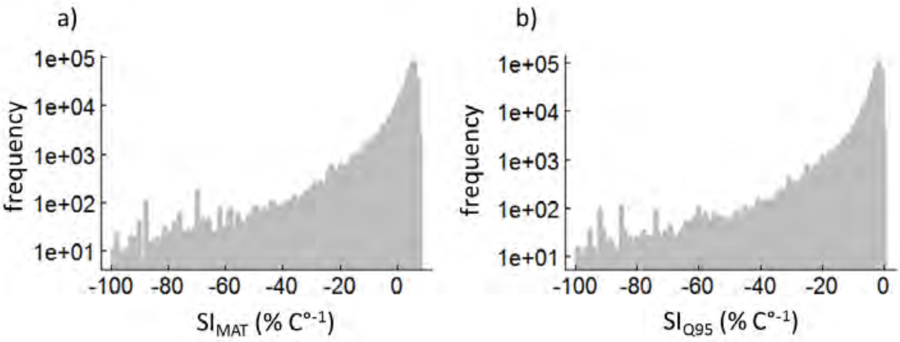


Figure F.1: Frequency distribution of SI_{MAT}-values (a) and SI_{Q95}-values (b) of all forest stands.

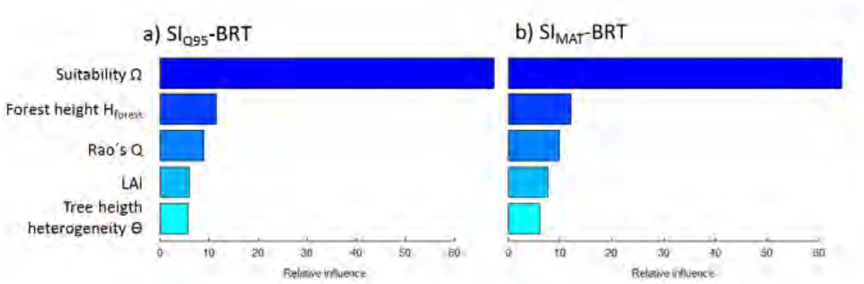


Figure F.2: Relative influence of the five forest properties on the variability of SI_{MAT}(a) and SI_{Q95}(b) within the two different boosted regression trees (BRT).

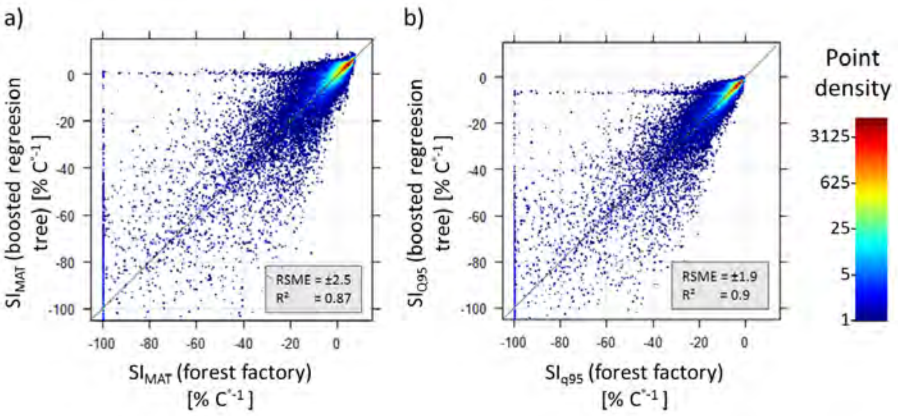


Figure F.3: Comparisons of temperature sensitivity ($SI_{MAT}$and SI_{Q95}) based on Forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line.

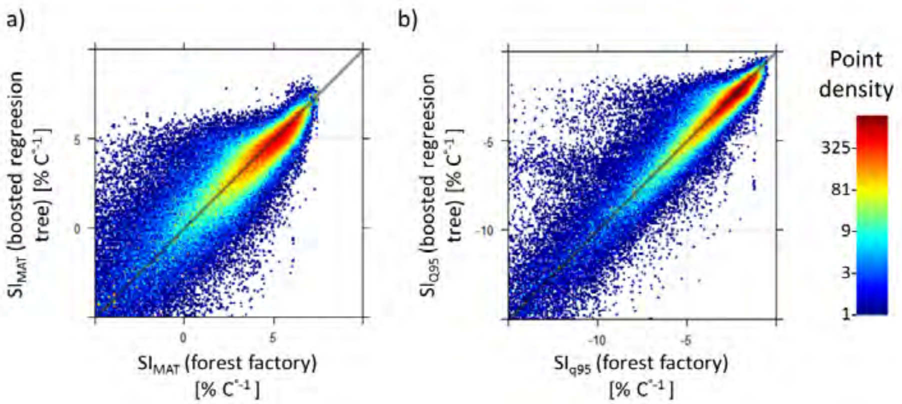


Figure F.4: Comparison of temperature sensitivity calculations ($SI_{MAT}$and SI_{Q95}) based on the forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line. a) Contains 90% of the forest factory data set and b) contains 93% of the forest factory data set.

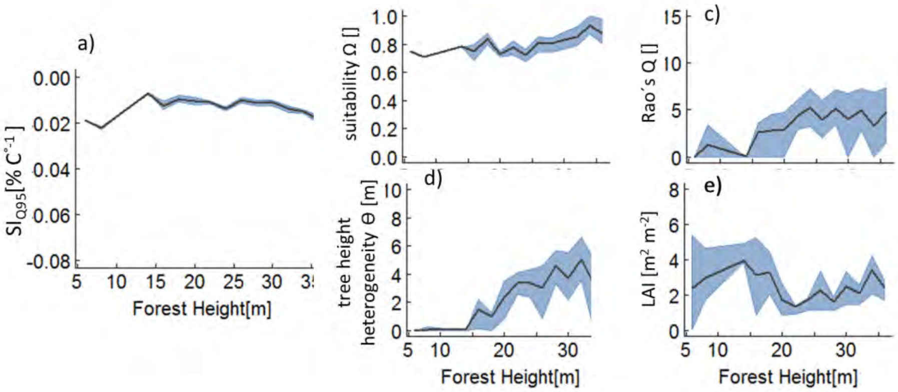


Figure F.5: Analysis of those forests which lie above the 95% percentile of SI_{MAT}, depending on forest height. Lines indicate mean values of the subsamples and the gray bands indicate the inter quartile range. Figure a) shows the temperature sensitivity of productivity against forest height, analysing only Values above the 95% percentile b) to d) shows the change of the remaining forest properties within the subsamples.

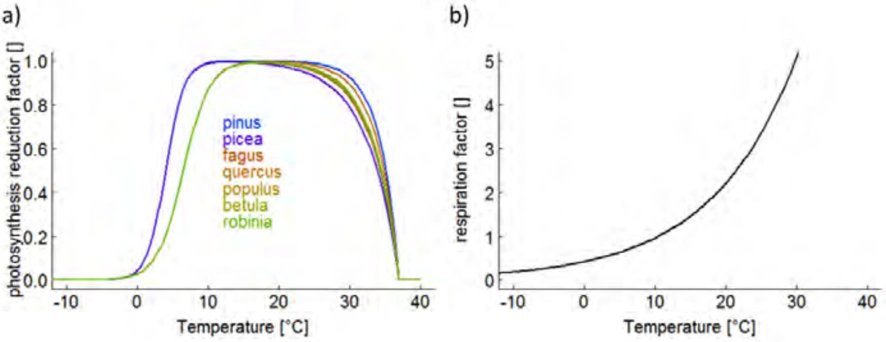


Figure F.6: a) Species-specific reduction factor of photosynthesis due to a change in air temperature. b) Species-unspecific correction factor for maintenance respiration due to a change in air temperature.

F.3 FOREST STANDS PROPERTIES WITH HIGHEST SI_{Q95} VALUES OVER A FOREST HEIGHT GRADIENT

F.4 SI-VALUES OF SINGLE TREES

To understand the origin of the SI-values, we make the following considerations: An increase of 1°C always results in an increase of 8.6% of the respiration rate in the model (figure F.6 b; Piao et al. (2010)). The positive effect of an temperature increase of 1°C on the photosynthesis rate varies between the years due to the assumed species-specific bell-shaped relationship (figure F.6 a). In case of deciduous trees on the length of the vegetation period (e.g. Haxeltine and Prentice, 1996; Luo, 2007; Horn and Schulz, 2011; Gutiérrez and Huth, 2012; Sato et al., 2007). If the photosynthesis rate is much larger than the respiration rate (high AWP), the positive effect of temperature on photosynthesis causes an increase of AWP in most simulated years. If both rates show the same magnitude, higher temperatures increase respiration stronger than photosynthesis rates (in most years).

F.5 FUNCTIONAL DIVERSITY AND TEMPERATURE SENSITIVITY

To analyse the effect of functional diversity on temperature sensitivity, we first calculate the SI_{MAT}-values for every species depending on tree height and light availability (as done for pine trees in figure 21). Then, we build a mean SI_{MAT}-value for each species mixture for all light-height combinations ($SI_{h,l}$). Finally, we average all $SI_{h,l}$ which are larger than

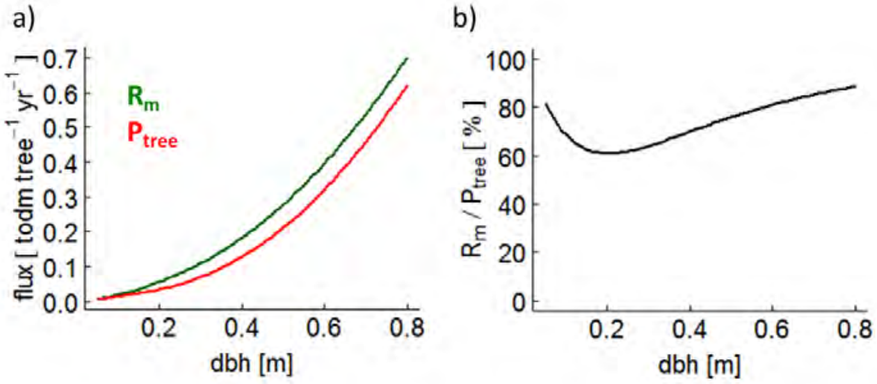


Figure F.7: a) Photosynthesis (green) and maintenance respiration (red) rates of a single beech tree over stem diameter (dbh) under full light. b) The ratio between maintenance respiration and photosynthesis of the same beech tree.

-7.5% C$^{\circ -1}$(barSI$_{MAT}$) and calculate the Rao´s Q of the mixtures (based on equal abundances). The highest barSI$_{MAT}$-values were found for deciduous forests (figure F.8). Mixed forests with deciduous and needle leaf trees show lower values than the deciduous forests, but higher Rao´s Q-values.

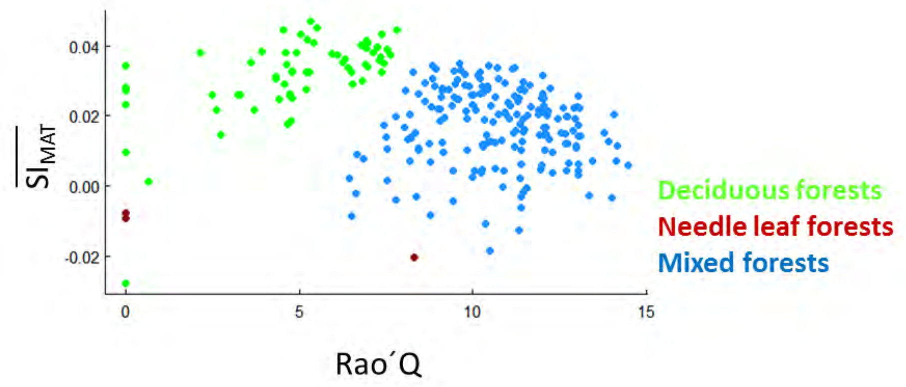


Figure F.8: Rao´s Q (with equal abundances) against $barSI_{MAT}$ –values of all possible species mixtures (from the forest factory). The $barSI_{MAT}$-values are the average over all $SI_{h,l}$ values for all light-height combinations and with values larger than -7.5% $C^{\circ -1}$. For mixtures, we assume equal abundances and calculate the mean over the $SI_{h,l}$ values of all species within the mixture. Green dots indicate forests that consist only of deciduous trees; red dots indicate forests that consist only of needle leaf trees; blue dots indicate forests that contain both tree types.

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FREQUENTLY USED ACRONYMS

symbol	description	unit
AWP	above-ground wood production	$t\ odm$
BA	basal area	m^2
dbh	stem diameter at breast hight	m
EVI	enhanced vegetation index	$-$
GPP	gross primary production	$-$
h_{max}	forest height	m
H_{max}	forest height class	m
LAI	leaf area index	m^2m^{-2}
m	metres	
MAT	mean annual temperature	$^\circ C$
NPP	nett primary production	
odm	organic dry matter	
P_{tree}	photosynthesis of a tree	odm
$PPFD$	photo active photon flux density	$\mu mol\ m^{-2}s-1$
$Q95$	intra-annual temperature amplitude	$^\circ C$
r_g	growth respiration	odm
R_m	maintenance respiration	odm
SI_{MAT}	temperature sensitivity to MAT	$\%\ C^{\circ -1}$
SI_{Q95}	temperature sensitivity to $Q95$	$\%\ C^{\circ -1}$
yr	year	
θ	tree height heterogeneity	m
Ω_{AWP}	optimal species distribution	$-$

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DECLARATION

Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

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Kapitel 1

- *Kommentare & Sprachliche Korrekturen* - Andreas Huth

Kapitel 2

- *Anteil an Idee, Konzept und Interpretation* - Andreas Huth, Karin Frank
- *Kommentare & Sprachliche Korrekturen* Andreas Huth

Kapitel 3

- *Anteil an Idee, Konzept und Interpretation* - Andreas Huth
- *Kommentare & Sprachliche Korrekturen* Andreas Huth

Kapitel 4

- *Anteil an Idee, Konzept und Interpretation* - Andreas Huth, Felix May
- *Kommentare & Sprachliche Korrekturen* Andreas Huth, Felix May

Kapitel 5

- *Kommentare & Sprachliche Korrekturen* - Andreas Huth

Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

, Dezember 2016

Friedrich J. Bohn, October 17, 2017