Species composition and forest structure explain the temperature sensitivity patterns of productivity in temperate forests.

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Abstract. Rising temperatures due to climate change influence the wood production of forests. Observations discovered that some temperate forests increase their productivity, whereas others reduce their productivity. This study focus on how species composition and forest structure properties influences this temperature sensitivity of forest productivity. Further it investigates for which forests rising temperatures increase productivity strongest. We describe forest structure by leaf area index , forest height and tree height heterogeneity. Species composition is described by a functional diversity index (Rao's Q) and optimal species distribution (Ω_{AWP}). Ω_{AWP} quantifies how well species are distributed within the forest structure regarding with the given environmental conditions of each single tree. We analyzed 370,170 forest stands, which were generated with 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). The scenarios differ in mean annual temperature and annual temperature amplitude. Temperature sensitivity of forest productivity is quantified as relative change of productivity due to a 1°C temperature rise in mean annual temperature or rather annual temperature amplitude. Increasing Ω_{AWP} influences positively both temperature sensitivity indices of forest, whereas forest height shows a bell-shaped relationship with both indices. Further, we reveal that there are forests in each successional stage, which are positively affected by temperature rise. For such forests, large Ω_{AWP}-values are important. In case of young forest, low functional diversity and small tree height heterogeneity support a positive effect of temperature on forest productivity. During later successional stages, higher species diversity and larger tree height heterogeneity is an advantage. This study highlights that forest structure and species composition are both relevant to understand the temperature sensitivity of forest productivity.

1 Introduction

Climate change alters forest growth by modifying the photosynthesis and respiration rates of trees (Cao and Woodward, 1998; Barber et al., 2000; Luo, 2007; Peñuelas and Filella, 2009). Changes in forest productivity have been observed in past decades all over the world (Nemani et al., 2003; Boisvenue and Running, 2006; Seddon et al., 2016). These observations have stimulated discussions about whether forest management strategies can be adapted to reduce forest vulnerability to climate change, to

support recovery after extreme events and to compensate for anthropogenic CO_2-emissions (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Bonan, 2008).

Forest productivity is influenced by several factors. Temperature can strongly alter forest productivity, in addition to other climate variables such as CO_2-fertilization or nitrogen deposition (Barford et al., 2001; De Vries et al., 2006, 2009; Solberg
5 et al., 2009; Keenan et al., 2013). Temperature modifies the 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). In the temperate biome, positive effects as well as negative effects on forest productivity (Bontemps et al., 2010; Delpierre et al., 2009; Pan et al., 2013; McMahon et al., 2010, e.g.) have been found (Barber et al., 2000; Jump et al., 2006; Charru et al., 2010, e.g.). However, it remains unclear why forests react differently to temperature change.

10 In addition to the influence of climate, forest productivity is also affected by internal forest properties. These properties can be grouped into two types: those properties which describe forest structure, and those which describe the species composition (Fig. 1). For instance, changes in productivity can result from changes in basal area (Vilà et al., 2013), in leaf area index (Asner et al., 2003) or in the heterogeneity of tree heights within a forest (Bohn and Huth, 2017). Furthermore, forest productivity often increases with the increasing number of species (Zhang et al., 2012; Vilà et al., 2007).

15 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 forest (McMahon et al., 2010; Bontemps et al., 2010, e.g.) and Morin et al. (2014) showed that higher diversity buffer the effect of inter-annual variability on forest productivity. However, these studies include only a few forest properties and rarely include both properties of both types, species composition and forest structure. Hence, it remains unclear, how forest properties
20 influence forest productivity change due to temperature rise and which forests will benefit from rising temperatures.

As far as we know, there is no data set available, which covers forests, differing in structure and diversity, under almost identical climatic conditions. Even if a larger number of forest stands would be available, it would be difficult to manipulate for instance temperature while keeping all other climate variables constant. An alternative option to field data analysis is offered by forest simulation models. Such models are able to estimate forest productivity under different climate conditions (Lasch
25 et al., 2005; Bohn et al., 2014, e.g.). For instance, Reyer et al. (2014) investigated the effect of climatic change on forests by simulating 30 years into the future for 135 inventoried forest stands. There are also model-based studies, which systematically nalyzed 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 have been not included in these analyses.

In this study we therefore propose a new simulation-based approach. First, we generate a huge number of forest stands
30 covering various forest structures and species composition (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. These senarios differ in the mean annual temperature (MAT) and the intra-annual temperature amplitude (Q95). We aim to analyze (i) how productivity of forest stands (AWP) is influenced by increasing temperature (MAT) and (ii) by increasing intra-annual temperature amplitude? Furthermore, we address the question (iii) which forest stands will benefit most from rising temperatures?
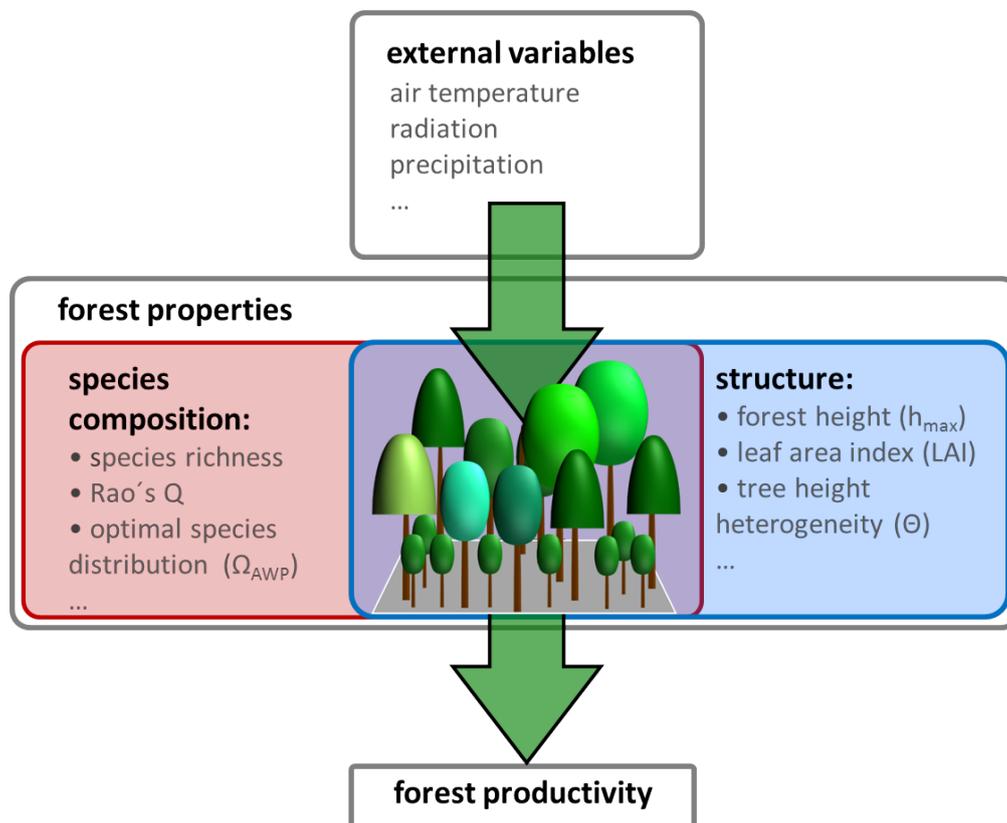
Figure 1. Overview of drivers influencing forest productivity. External variables in this study are temperature, radiation, and precipitation. Forest properties are divided into two groups: species composition properties (e.g., the Rao's Q as a measure of functional diversity and optimal species distribution Ω_{AWP}) and forest structure properties (e.g., forest height, leaf area index and tree height heterogeneity).

2 Method

To analyse the effect of temperature on the productivity of forest stands, we apply the "forest factory" model approach (Bohn and Huth, 2017). With this approach, we generate 370,170 different forest stands (see section 2.1) and estimate the above ground wood production (AWP) under various climate scenarios (see section 2.2). The 320 scenarios differ in mean annual

5 temperature (MAT) and annual temperature amplitude (Q95). Finally, we calculate the forest stand-specific sensitivity of productivity against temperature change (SI_{MAT} and SI_{Q95}) as the relative change of forest productivity per temperature change of 1 °C (see section 2.2). To relate these sensitivities to forest structure and species composition, we characterize every forest stand with five properties (see section 2.3). We analyse the influence of the five forest properties on temperature sensitivity using boosted regression trees (see section 2.4). Finally, we analyse which combination of forest properties results in the highest

10 sensitivity values for different successional stages (see section 2.5).

2.1 The forest factory approach

The forest factory combines 15 different stem size distributions with 256 species mixtures. The stem size distributions cover a gradient from young to old and disturbed to undisturbed forests. Species mixtures include all possible combinations of pine, spruce, beech, oak, ash, poplar, birch and robinia. The species parameter set and algorithms of the FORMIND-model version

5   for temperate forests are used in the forest factory (Bohn et al., 2014; Fischer et al., 2016).

The forest factory generates forest stands with a size of $400\,\mathrm{m^{-2}}$ using the following rules: (i) space limit the maximal number of trees and (ii) every tree must have a positive productivity under a typical temperate climate. For a typical temperate climate, we employ a climate time series from the year 2007, measured at Hainich National Park, central Germany. Bohn and Huth (2017) presented a detailed description and discussion of the forest factory.

10 ## 2.2 The forest productivity under temperature variation

The productivity (AWP) of a single tree is calculated as the difference between climate driven respiration rates and photosynthesis. The photosynthesis rate (P_{tree}) results from the crown size, self-shading within the crown and available light at the top of the tree. The available light depends on the radiation above the canopy, reduced by the shading of larger trees within the forest stand. Furthermore, productivity can be limited due to air temperature and available soil water, which is expressed by

15 photosynthesis-limiting factor ϕ for each tree (Gutiérrez, 2010; Fischer, 2013; Bohn et al., 2014). Available soil water within the stand results from precipitation, interception, evapotranspiration of trees and run-off.

One part of the photosynthesis production of a tree (P_{tree}) is allocated to its maintenance respiration (and to non-wood tissues; R_m). R_m depends on tree biomass and temperature ψ (Piao et al., 2010). The remaining organic carbon is transformed into newly grown above-ground wood (AWP_{tree}) and a proportional growth respiration (r_g).

20 $$AWP_{tree} = (\phi P_{tree} - \psi R_m)(1 - r_g) \qquad (1)$$

AWP_{tree} is summed over all trees to obtain the productivity of the forest stand - AWP (for a more detailed description of growth processes, see Bohn et al. (2014); Bohn and Huth (2017)).

To generate a set of 320 annual climate scenarios, we selected daily climate measurements of the Hainich station in central Germany between the years 2000 and 2004. This time series includes mean daily radiation, precipitation and air tempera-

25 ture (see Appendix A1; Fig. A1)). We separate these time series into five distinct time series of one-year length. First, we increase/decrease the mean annual temperature of each year by adding/subtracting $0.5\,^{\circ}\mathrm{C}$ steps between $-1.5\,^{\circ}\mathrm{C}$ and $+2\,^{\circ}\mathrm{C}$. 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 % and +16 %. We end up with five climate scenario sets of one-year length that differ in precipitation and radiation. Each set includes 64 time series, which differ only in temperature (see Appendix A1 , Fig. A2).

30 Temperature change is quantified using two indices: (i) mean annual temperature (MAT) and (ii) annual temperature amplitude (Q95), which describes the 95% inter-quantile range of all daily temperature values of a given year. We exclude the effects of
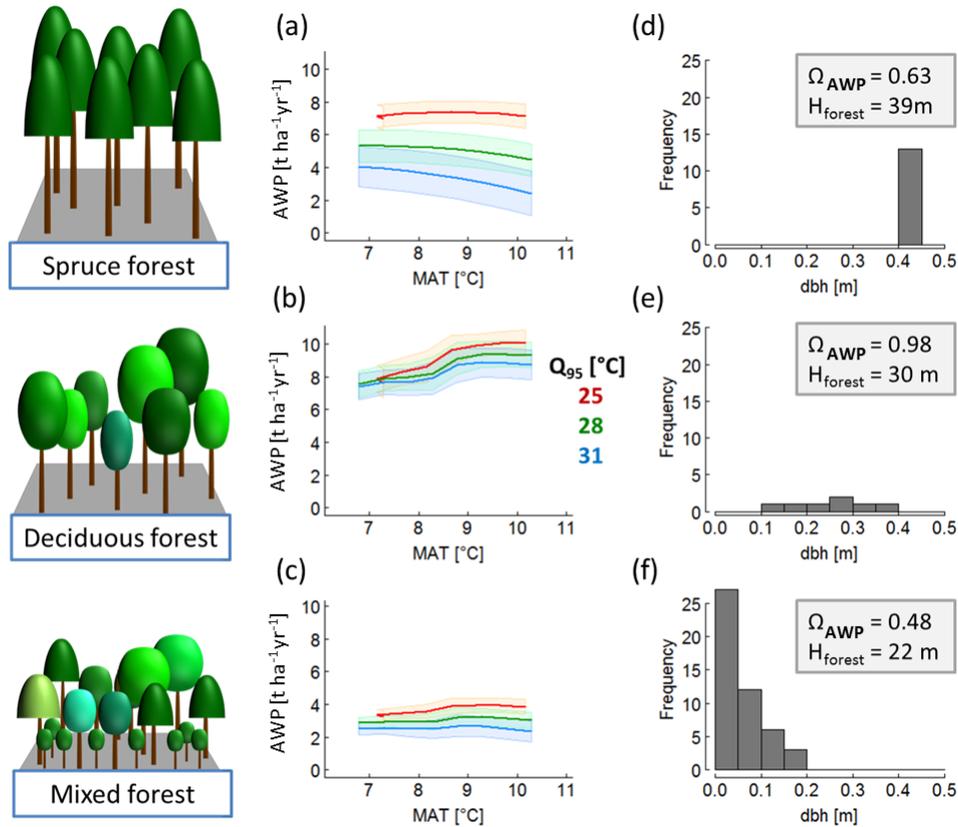
Figure 2. Overview of drivers influencing forest productivity. External variables in this study are temperature, radiation, and precipitation. Forest properties are divided into two groups: species composition properties (e.g., the Rao's Q as a measure of functional diversity and optimal species distribution Ω_{AWP}) and forest structure properties (e.g., forest height, leaf area index and tree height heterogeneity).

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 2 (a-c) shows the above-ground wood production (AWP) for different annual temperatures for three different forest stands.

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

$$AWP = \alpha x_{MAT} + \beta x_{Q95} + \gamma x_{year} + \epsilon \qquad (2)$$

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

$$SI_{MAT} = \frac{\alpha}{AWP} \qquad (3)$$

$$SI_{Q95} = \frac{\beta}{AWP} \qquad (4)$$

In our analysis we exclude all forests stands for which AWP is negative if the temperature rises by 1 °C (2% of all stands).

5 We also determine the sensitivity of forests against temperature change using the German forest inventory to validate our results. However, the inventory does not include LAI measurements. We therefore assume the basal area as a proxy for LAI, and we select subsamples of forests stands with similar structure (basal area, tree height heterogeneity, forest height, and same species mixtures). In addition, we use elevation as a 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 did we find

10 enough data to calculate SI_{MAT}-values for several forest structures (see Appendix A3, Fig. A3 & A4). The correlation of the sensitivity values based on field data and simulation data was quite high ($R^2 = 0.65$).

2.3 Five forest properties to describe forest stands

We use 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

15 of the tree heights.

  To describe species composition, we use 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, for details see Appendix A2). Ω_{AWP} analyses the optimal location of species within the forest structure. Ω_{AWP} is defined as the ratio of the forest's productivity to the maximum possible productivity of the forest without changing tree sizes or number. Hence, the maximum

20 productivity can be obtained by varying only the species identities of trees in the forest stand. We change the assigned species of each tree until we find the optimal species for each individual tree and its specific environmental condition (Bohn and Huth, 2017). All five indices are nearly uncorrelated for the investigated forest stands (Appendix A2 Table A1).

2.4 Boosted regression trees

We applied boosted regression trees (BRT) to quantify the influence of the five forest properties on SI_{MAT} and SI_{Q95}. BRT

25 is a machine learning algorithm using multiple decision (or regression) trees. It is able to address 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 on (SI_{MAT} or SI_{Q95}) to multiple predictors (θ, h_{max}, LAI, Rao's Q, and Ω_{AWP}). To omit an over-fitting regarding maximal forest height, we classify forest stands into 18 classes (H_{max}). Each class has a width of 2 metres, starting with 4 to six metres and finishing with 36 to 38 metres. The BRT try an iterative process to minimize the squared error between

30 predicted SI values and those of the data set. Hereby, part of the data is used for a 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 in the R-package gbm 2.1.1 (Ridgeway, 10.2015).

We used a quarter of the data (randomly sampled) for the machine learning procedure. To get the best model, we vary 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 interactions depth

5 (1, 3 and 5) and the cross-validation (3-, 6- and 9-fold) assuming a Gaussian error structure. The best fitted BRT 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 a 3-foldcross validation. These two models were used for all further analyses. The remaining 75% of the data are used to validate the fitted BRT algorithm.

2.5 Finding the forest stands for different successional stages that benefit the most

Here, we assume forest height as a proxy for the successional stage of a forest. In every height class, (H_{max}) we select those

10 5% of forests that show the highest sensitivity values (SI_{MAT} and SI_{Q95}). We removed the forest height classes between 10 and 14 metres, as they only contain a few forests (15). For all other classes, we analyse the relationship between H_{max} and the forest properties (Ω_{AWP}, Rao's Q, LAI and θ).

3 Result

We analysed the sensitivity of productivity (AWP) against temperature for forest stands that differ in forest properties (optimal

15 species distribution (Ω_{AWP}), functional diversity (Rao's Q), tree height heterogeneity (θ), and forest height class (H_{max}) and LAI). The annual above-ground wood production (AWP) was estimated for each forest stand using 320 different climate scenarios. We than quantified the changes in productivity due to the changes in mean annual temperature (SI_{MAT}) and amplitude of inter-annual temperature (SI_{Q95}). For the analysed forest stands, the average SI_{MAT} is 1.5 % °C $^{-1}$ and the average SI_{Q95} is -5.4 % °C $^{-1}$ (see also the frequency distribution in Appendix B1, Fig. B1).

20 With a boosted regression tree algorithm, we analysed how the five forest properties influence the temperature sensitivity of forests. To validate the fitted BRT algorithm, we compare SI-values, which are not used for the fitting, with the SI-value predicted by the BRT algorithm (Fig. 3). The sensitivities against mean annual temperature change (SI_{MAT}) correlate very well (R^2 of 0.84) and show a low RMSE of ± 2.9 % °C $^{-1}$ (see Appendix B2 Fig. B3).The RMSE even decreases to ± 1.5 % °C $^{-1}$ if a subset of the forest stands is analysed that shows SI_{MAT} values larger than -5 % °C $^{-1}$ (90% of the data). The accuracy

25 of the sensitivities against temperature amplitude change (SI_{Q95}) was even slightly better. In addition, a subset that includes SI_{Q95}-values larger than -15 % °C $^{-1}$ (93% of the data) shows a RMSE of only ± 1.1 % °C $^{-1}$ (see Appendix B2 Fig. B4).

According to BRT analysis, Ω_{AWP} is the most relevant forest property to explain temperature sensitivities (relative influence of 87 % for SI_{MAT} and 89% for SI_{Q95}; see also Appendix B2, Fig. B2). However, the influence of Ω_{AWP} on temperature sensitivity flattens out for high Ω_{AWP} levels (Fig. 4). The second relevant forest property is forest height (H_{max}). Forest with

30 heights between 25 and 30 m benefit the most from increasing mean annual temperatures. The other three properties (LAI, Rao's Q, and θ) have a low influence on SI_{MAT}.
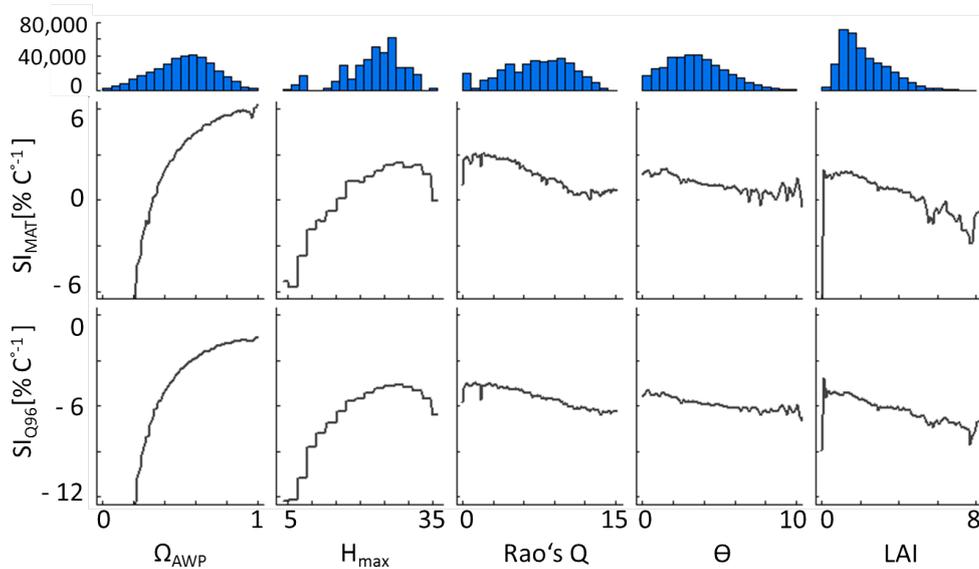
Figure 3. Partial dependency plots of the five forest properties Ω_{AWP} (optimal species distribution), forest height class h_{max}, Rao's Q (functional diversity), θ (tree height heterogeneity) and LAI (leaf area index) for SI_{MAT} (sensitivity against changes in the mean annual temperature) and SI_{Q95} (sensitivity against changes in the annual temperature amplitude). Histograms show the frequency of forest property values in the analysed data set.

Both sensitivity indices show similar relationships to the five forest properties. However, an increase in annual temperature amplitude always reduces productivity, whereas increasing mean annual temperature can result in a positive effect on forest productivity. To detect those stands that benefit the most from increasing temperature, we select the 5% of forest stands that showed the highest SI_{MAT}-values in each forest height class (Fig. 4). In all forests classes, we found forest stands that would benefit from increasing temperatures. The analysis of their forest properties reveals that the Ω_{AWP} levels were always high. Young forests (low forest height), which have a positive temperature sensitivity, show low functional diversity and low tree height heterogeneity (θ). For older forests (of intermediate and high forest height) with positive temperature sensitivity, we found an intermediate level of functional 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 B3 Fig. B5).

4 Discussion

In this study, we analyse of how temperature changes affect forest productivity (AWP) and quantify the effect of five different forest properties on this relationship. The change of forest productivity (AWP) was investigated for 370,170 forest stands under 320 different climate scenarios. Our analysis shows a high influence of Ω_{AWP} and H_{max} on the temperature sensitivity of AWP.
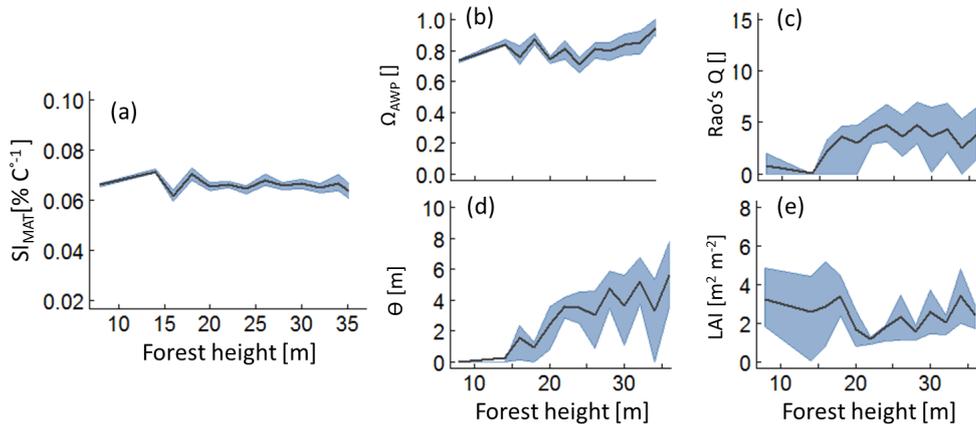
Figure 4. Analysis of those forests, which show the highest 5% of the SI-values de- pending of forest height. Lines indicate mean values of the subsamples and the grey band indicates the inter quartile range. Figure a) shows temperature sensitivity of pro- ductivity against forest height, analysing only 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 quantiles functional diversity).

Further, for all successional stages of forests, we detect some forests with a specific value combination of forest properties, which benefit from temperature rise. This specific combination varies with forest height.

4.1 The study design

In this theoretical study, we present a new approach to investigate the effects of climate change (here temperature) on forest
5   productivity (AWP). This approach extends field observation and long-term model simulations, as it allows the analysis of forests, which already exist but also which might exist in the future due to management changes and/or disturbances. In the case of field observations, it is 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 are altered at the same time (see also Appendix A3). Process-based models are one option to analyse such relationships and separate these effects. The simulation of forest productivity with the
10 FORMIDN-model in temperate forests has been successfully compared to Eddy flux sites Rödig et al. (2017), 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 various forests stands that can be analysed. The dataset includes forest stands that often occur in temperate forests (even-aged spruce, pine and beech stands). However, it also includes hypothetical ones that could occur through alternative forest management or disturbances (fire, bark beetles, etc.). Hence, our
15 data set of forest stands covers a much larger variety of forest property combinations compared to long term forest simulations with the focus on natural forests in their equilibrium state (Morin et al., 2011, e.g.) or on monocultures (Reyer et al., 2014,

e.g.). However, it would be possible to reconstruct a forest succession based on the forest factory by selecting forest stands in an 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; Reyer 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

5   uncertainty and omit path dependencies by including only those processes that 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 inputs but only analysing the effect of one variable might lead to incorrect interpretations of its effect. For example, temperature and radiation often correlate, and both might increase productivity. Therefore, in this study, we only vary one variable in all 5 scenarios. This guarantees no relationships between the target

10   climate variable and the remaining climate variables. As an increase in global mean temperature of 1.5 °C to 2 °C can hardly be avoided, even under the RCP 2.5 climate scenarios IPCC (2013), this study focuses on temperature change. This scenario predicts only a small change of annual precipitation levels for many areas of the temperate biome. However, other scenarios, which result in a stronger climate change, predict an increase in droughts and changes in annual temperature cycles. Such a more complex scenario should be analysed in future studies.

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

The temperature sensitivity values obtained here are in the same range as that found for temperate ecosystems in heating

20   experiments (Lu et al., 2013, $4.4 \pm 2.2 \% \, °C^{-1}$). Within the 16 analysed studies reviewed by Lu et al. (2013), the experimental plots show almost identical environmental conditions (soil, radiation, and precipitation) and species composition. To heat the plots, greenhouses or infrared heaters were used. Another study, based on natural forest stands in New Zeeland, found an AWP increase between 5 and 20 % $°C^{-1}$ for forest, assuming no change in forest structure and species composition Coomes et al. (2014). The analysed plots were spread all over New Zeeland, and warmer temperatures coincide with higher radiation

25   Mackintosh (2016). Hence, the analysed temperature effect also includes the influence of radiation. In our setting, however, the influence of temperature is independent from radiation Lu et al. (2013, as in). 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 A3 Fig. A3 & A4).

4.2   The influence of forest structure on temperature sensitivity

30   Forest structure affects productivity in two ways. First, it determines the available light for each single tree and second, the size of trees influences photosynthesis and respiration rates. Hence, based on the height of a tree and its available light, it is possible to calculate its SI-values (for a detailed discussion of these calculations, see Appendix B4). For instance, in a forest of even-aged trees, all trees have the same height and receive full light (e.g., forest C in Fig. 5). Such even-aged forests show a
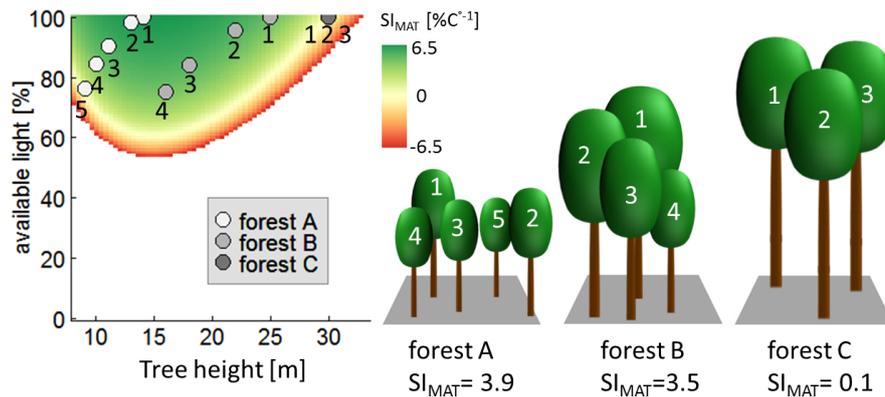
Figure 5. Analysis of SI_{MAT} values of single trees within three different forests. The diagram shows the calculated the SI_{MAT} value of individual trees for every combination of tree height and available light. The dots indicate the different trees of the three forest examples, whereby the grey tone indicates the forest the tree belongs to, and the number indicates 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.

bell-shaped relationship between forest height and temperature sensitivity (Fig. 5 SI values for 100% available light depending on tree height). Even if trees receive less light, the bell-shaped curve persists (see also Fig. 3)

In a forest that consists of trees with different heights (but similar LAI as an even-aged forest), smaller trees receive less light due to shading. Two cases will be discussed: first, a case in which all trees have not reached the maximal SI-values (forest A, Fig. 5); and second, a case in which all trees are larger than their maximal SI-values (forest B, Fig. 5). In the case of forest A, trees in the shade of larger trees always have lower SI-values if they belong to the same species (see Appendix B4). Hence, the temperature sensitivity level of this forest is lower than the sensitivity of an even-aged forest, whose trees have the same size as the largest tree in forest A. In forest B, SI-values of the shaded trees can be similar (or even higher) than the SI-value of the largest trees in the forest. SI-values of tree 1 show similar values to trees 2, 3 and 4. This result is similar to (or even higher than) temperature sensitivity levels compared to an even-aged forest, which only consists of the largest trees. These general considerations explain the change from low levels of height heterogeneity in young forests to a more heterogeneous structure for the optimal forests analysis (see Fig. 4 d).

4.3 The effect of species composition on temperature sensitivity

In this study, we use the new index Ω_{AWP} called optimal species distribution (Bohn and Huth, 2017). Ω_{AWP} describes the ratio of the realized to the maximal possible productivity, which can be reached by shuffling species identities in the given forest stand. Its huge importance on forest temperature sensitivity might be illustrated by the following considerations: If species are
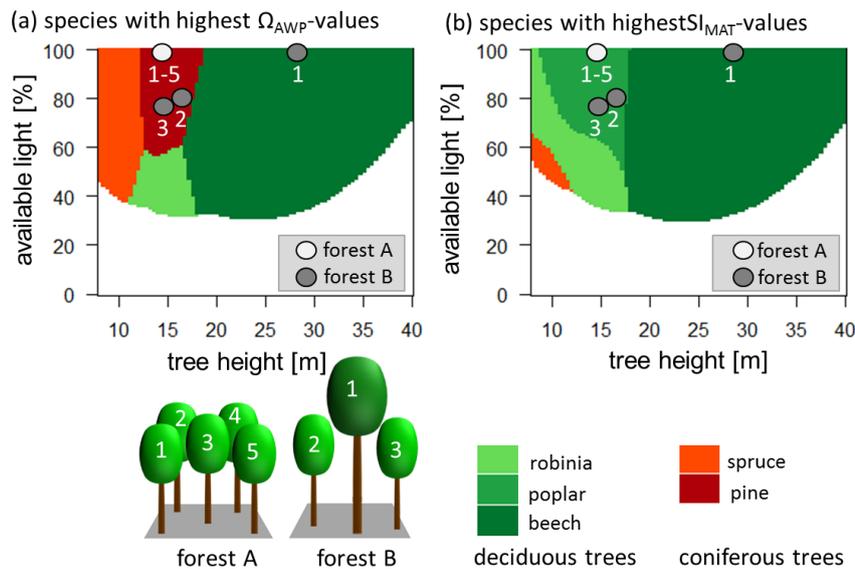
Figure 6. Graphic (a) shows which species shows the highest increase in productivity due to increasing temperatures at different heights under different light conditions. Graphic (b) shows which species shows the highest productivity at different heights und different light conditions. Red colours indicate coniferous trees, whereas green colours indicate deciduous trees. Darker colours indicate late successional species, whereas lighter colours indicate pioneers. The dots indicate the different trees of the two forest examples, whereby the grey tone indicates the forest the tree belongs to, and the number indicates the specific tree of that forest.

unfavourably distributed within the forest (low Ω_{AWP}), the AWP of the forest is low, and in consequence, the SI values are low as well (see Appendix B5).

Increasing functional diversity (Rao's Q) has a stabilizing effect (in the case of mean temperature sensitivity). This corresponds to results of Morin et al. (2014) and the theoretical consideration of Yachi and Loreau (1999). The analysis of the
5 single species can give additional insight into the mechanisms behind those species that benefit the most from temperature increase, which are deciduous trees under most conditions. This is reasonable as warmer regions host more deciduous species than needleleaf species. The highest functional diversity (Rao's Q) instead occurs in mixtures of deciduous and needleleaf trees (Appendix B5 Fig. B8). As only two needleleaf species are considered here in the species pool, low Rao's Q values are dominated by mixtures of deciduous trees. Such deciduous tree mixtures mostly benefit from temperature increases. In conse-
10 quence, mixtures with high Rao's Q values, which mostly include both functional types, react more poorly (Fig. 3; Appendix B5 Fig. B8).

We developed two diagrams that show the species with the highest temperature sensitivity and with the highest productivity for different conditions (light and height of a tree) (Fig. 6). Interestingly, the species with the highest productivity differ from the species that benefit most from rising temperatures in many cases. This has important consequences. The highest benefit due
15 to increasing temperatures shows forests with high but surprisingly not maximal Ω_{AWP} (Fig. 4). Additionally, deciduous trees

benefit more than coniferous trees from rising temperatures (Fig. 6, Appendix B5, Fig. B8). Hence, young forests should consist of deciduous trees (compare Fig. 5, forest A, and Fig. 6), although the highest productivity values are found for coniferous trees (Fig. 6; forest A). Forests including large trees obtain the highest sensitivity values if intermediate sized trees differ in their species identity from the largest trees (Fig. 6).

5   Conclusions

The temperature sensitivity of forest productivity is driven by forest structure and species diversity. Most relevant to the temperature-productivity-relationship are the optimal species distribution (Ω_{AWP}) and forest height. Forests that benefit most under temperature rise consist of deciduous tree species, whereby young forests show low and old forests show high tree height heterogeneity.

Data availability. In the online supplement you find the a R-workspace which includes the dataset of the analysed forests "foreststands" and the calculated SI-values "SIValues".

Appendix A: Additional information regarding methods and validation

A1   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 (Fig. A1). Mean annual temperature of these five years does not correlate with the annual precipitation sum, nor with the mean annual radiation (Fig. A2). Radiation and precipitation within these years correlate quite well (Pearson's r =0.73).

A2   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 A1).

A3   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 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
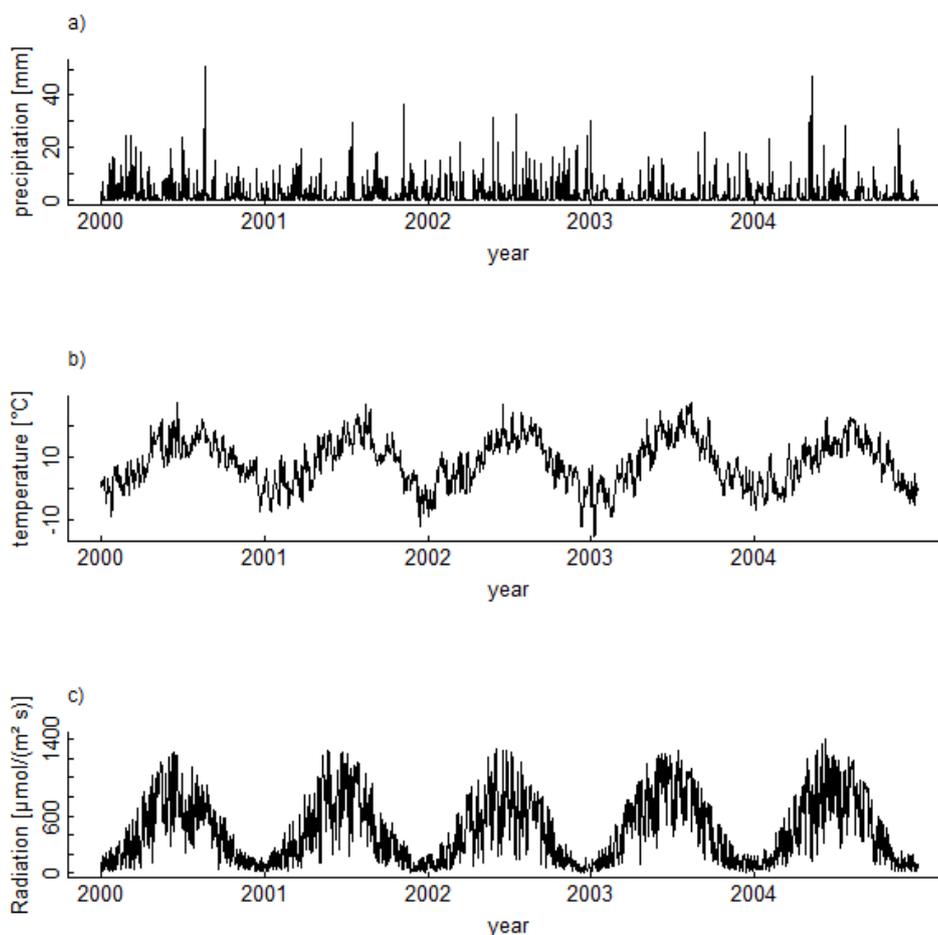
Figure A1. The climate time series measured at FLUXNET-station Hainich from 2000 to 2004 which are used to generate the 320 climate scenarios: (a) daily precipitation [mm], (b) daily air temperature [% °C $^{-1}$], (c) daily incoming radiation [photoactive photon flux density $\mu mol\,m^{-1}s^{-1}$].

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 m (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

5 above-ground wood productivity (AWP).
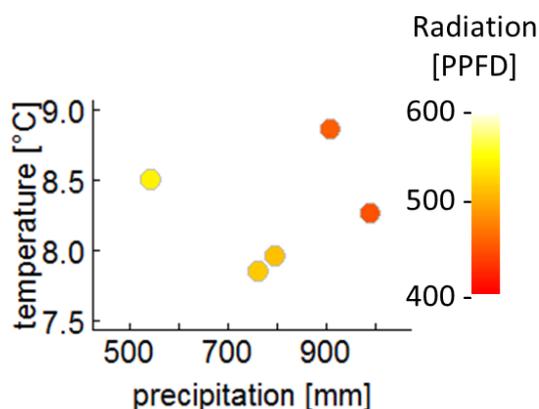
Figure A2. Mean annual temperature, mean annual precipitation and mean annual radiation of the five climate series measured at Hainich station from 2000 to 2004.

Table A1. 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}= optimal species distribution

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			

Appendix B

B1 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 SI_{MAT} and up to -0.5 % °C $^{-1}$ for SI_{Q95}(Fig. B1). The mean SI_{MAT} is 1.5 % °C $^{-1}$ and the interquartile range (iqr) ranges from 1.6 % °C $^{-1}$
5 to 5.2 % °C $^{-1}$. The mean $SI_{Q95}$is -5.4 % °C $^{-1}$ and the iqr ranges from -5.2 % °C $^{-1}$ to -2.2 % °C $^{-1}$.

B2 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 relation-
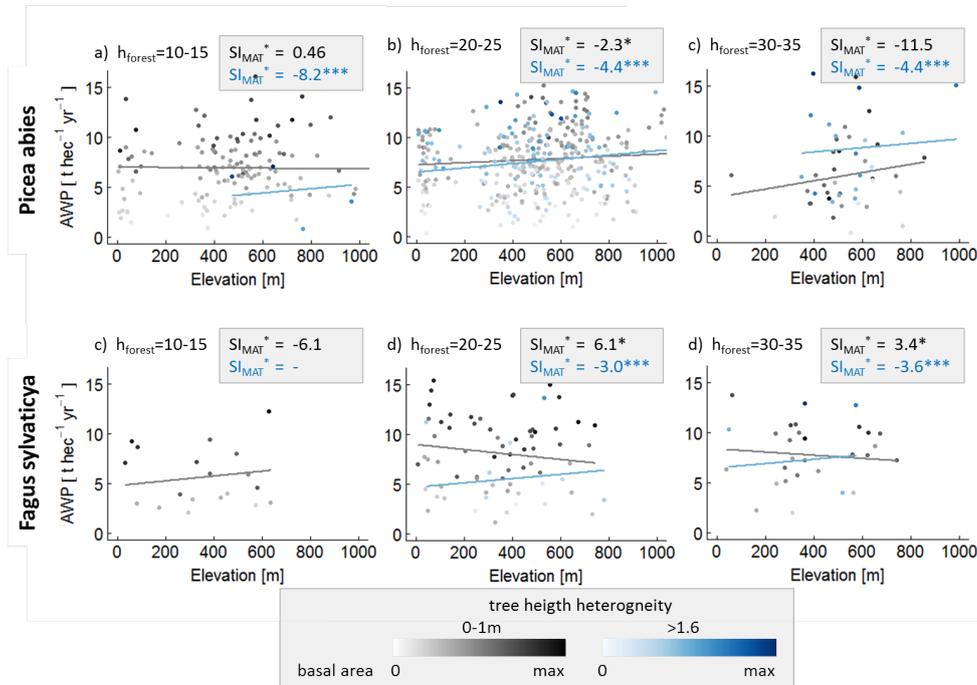
Figure A3. Analysis of the influence of forest structure on the relationship between elevation and above-ground wood production. Figure (a) - (c) are based on spruce monocultures and d)-e) are based on beech monocultures. For each species, forest stands are classified into three forest height classes 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^{-1} .

ship 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 (Fig. B2).

Other commonly used visualization of the relationship of input and target variable are partial dependency plots (Fig. 3). 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.
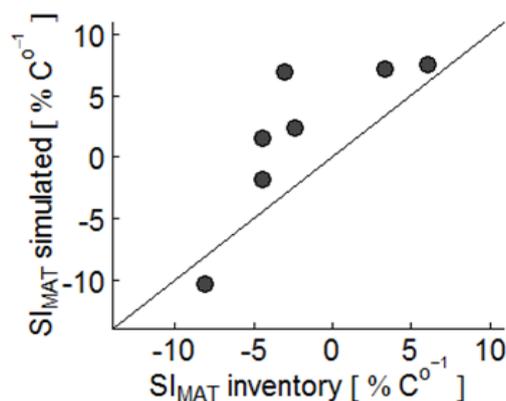
Figure A4. $SI_{MAT}*$-values derived from the BWI-analysis vs. SI_{MAT}-values derived from corresponding forest types of the forest factory. Only field data with p-values smaller 0.05 are analysed.
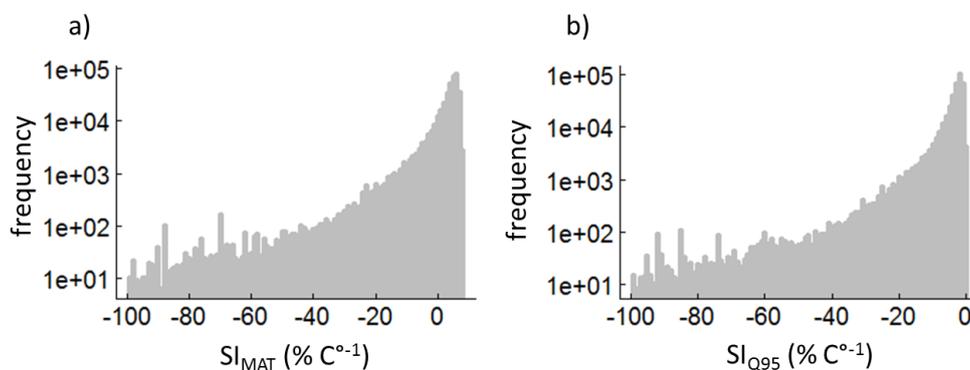
Figure B1. Frequency distribution of SI_{MAT}-values (a) and SI_{Q95}-values (b) of all forest stands.

B3   Forest stands properties with highest SI_{Q95} values over a forest height gradient

B4   SI-values of single trees

To understand the origin of the SI-values, we make the following considerations: An increase of 1 % °C $^{-1}$ always results in an increase of 8.6% of the respiration rate in the model (Fig. B6 b; Piao et al. (2010)). The positive effect of an temperature increase of 1 % °C $^{-1}$ on the photosynthesis rate varies between the years due to the assumed species-specific bell-shaped relationship (Fig. B6 a). In case of deciduous trees on the length of the vegetation period (e.g. Haxeltine and Prentice, 1996;
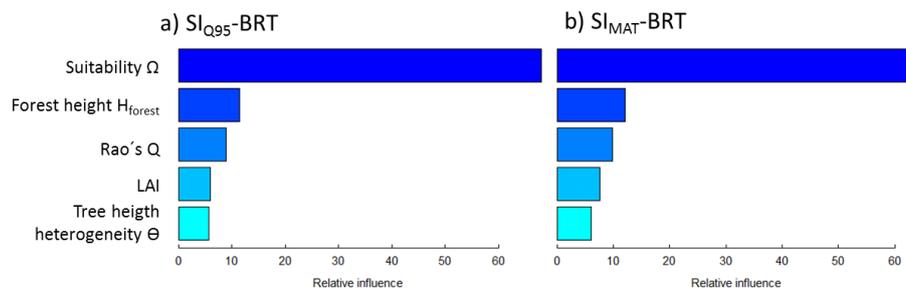
Figure B2. Relative influence of the five forest properties on the variability of SI_{MAT}(a) and SI_{Q95}(b) within the two different boosted regression trees (BRT).
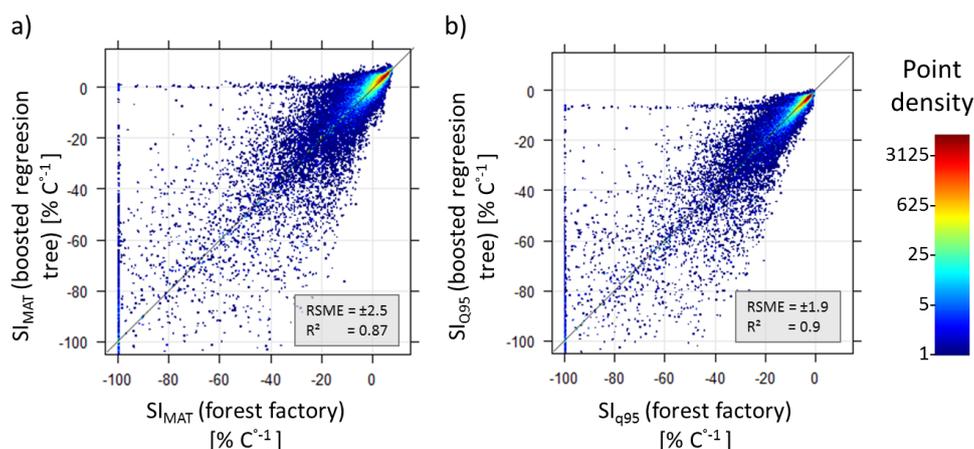
Figure B3. Comparisons of temperature sensitivity (SI_{MAT} and SI_{Q95}) based on Forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line.

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).

5   **B5   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 5). 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 -7.5 % °C
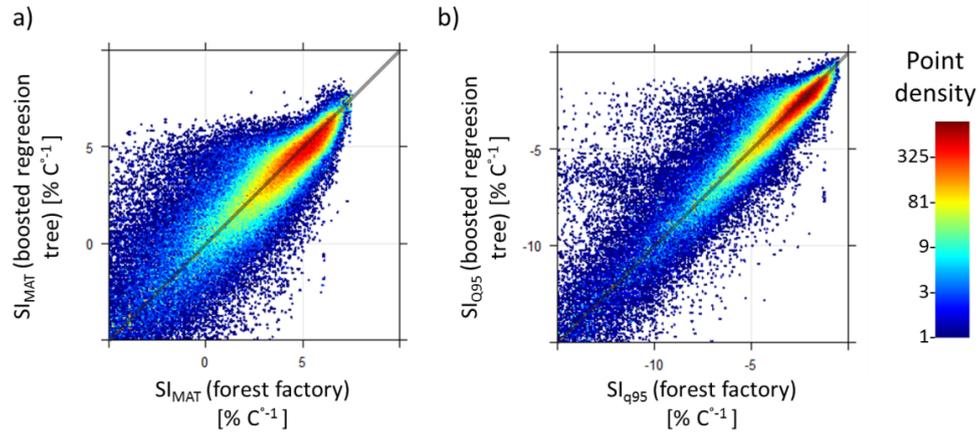
Figure B4. Comparison of temperature sensitivity calculations (SI_{MAT} and SI_{Q95}) based on the forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line. a) Contains 90% of the forest factory data set and b) contains 93% of the forest factory data set.
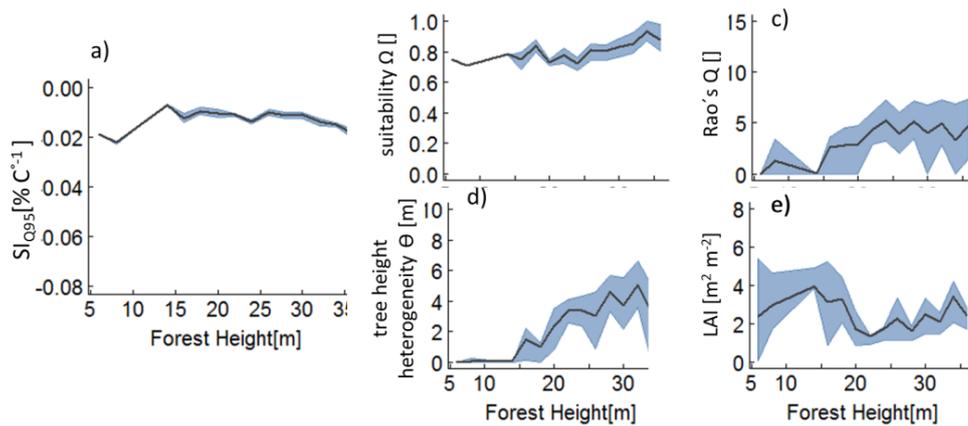
Figure B5. Analysis of those forests which lie above the 95% percentile of SI_{MAT}, depending on forest height. Lines indicate mean values of the subsamples and the gray bands indicate the inter quartile range. Figure a) shows the temperature sensitivity of productivity against forest height, analysing only Values above the 95% percentile b) to d) shows the change of the remaining forest properties within the subsamples.

$^{-1}$ ($bar\,SI_{MAT}$) and calculate the Rao's Q of the mixtures (based on equal abundances). The highest $bar\,SI_{MAT}$-values were found for deciduous forests (Fig. B8). Mixed forests with deciduous and needle leaf trees show lower values than the deciduous forests, but higher Rao's Q-values.
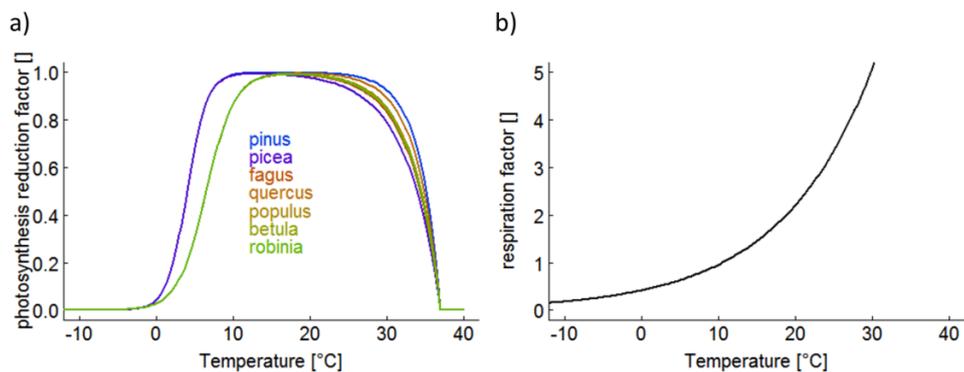
Figure B6. a) Species-specific reduction factor of photosynthesis due to a change in air temperature. b) Species-unspecific correction factor for maintenance respiration due to a change in air temperature.
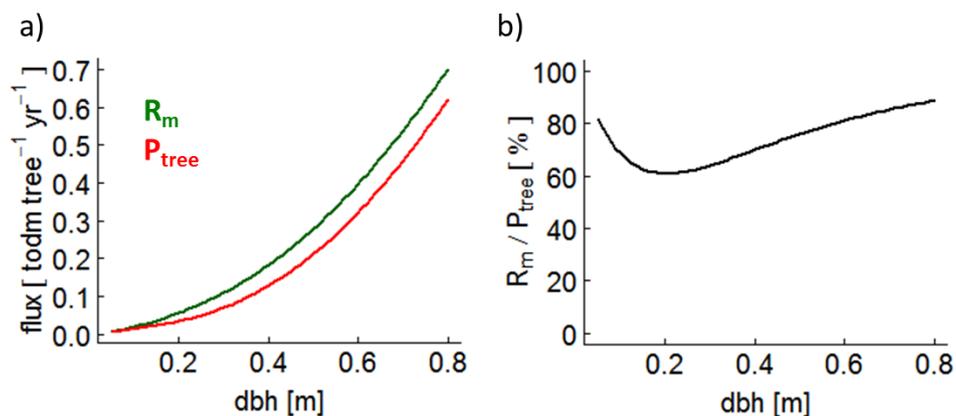
Figure B7. a) Photosynthesis (green) and maintenance respiration (red) rates of a single beech tree over stem diameter (dbh) under full light. b) The ratio between maintenance respiration and photosynthesis of the same beech tree.
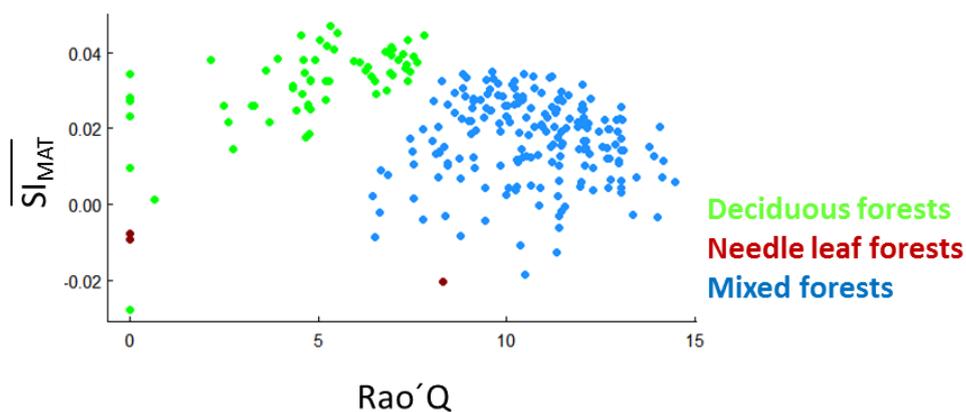
Figure B8. Rao's Q (with equal abundances) against $bar\,SI_{MAT}$-values of all possible species mixtures (from the forest factory). The $bar\,SI_{MAT}$-values are the average over all $SI_{h,l}$ values for all light-height combinations and with values larger than -7.5 % °C^{-1}. For mixtures, we assume 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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