Reviewer 1 (Christopher Reyer)

Compared to the announced text changes in our reply in the interactive discussion we slightly changed several text fragments to improve readability, English and grammar (especially in the three new sections: 4.2 Implications for forest management, 4.3 Implications for global vegetation modelling and the new Conclusion).. We mark major changes in our reply in purple.

Comments of reviewer 1 in blue, reply in black.

I am sorry for being late. The manuscript uses an innovative modelling approach to assess the temperature sensitivity of above ground wood production. It is generally well written but there are quite a number of minor fixed that still need to be carried out.

Thank you very much for your detailed and helpful comments. We will include your recommendations carefully.

I have two major concerns that can be addressed in a thorough minor revision: 1) I think your "climate scenarios" are actually rather a "climate sensitivity test". Even though many things can be scenarios in the wider sense in the narrow sense, a scenario usually refers to an internally consistent projection while your scenarios systematically explore change temperature but do not adjust precip and radiation accordingly. This may lead to physically inconsistent "climates" because under a given temperature pathway it might be impossible to get a certain precip or radiation behavior.

Thanks for this comment. We agree. We will replace “climate scenarios” by “climate sensitivity test” or “climate time series” depending on the context. For instance, P1L9: For each stand we estimate annual above-ground wood production and perform a climate sensitivity analysis analysis based on 320 different climate time series (of one year length).

Related to that, you should possibly also discuss that your approach basically ignores transient responses and time lags longer than a year that influence forests. So i think this "sensitivity test" aspect should be carved out more clearly. The title actually is fine but some of the other sections give the impression this is rather a scenario study.

This is a good point. Thank you. We will replace the sentences between P15L12 and P15L15 with the following text:

…This RCP scenario predicts only small changes of annual precipitation levels for many temperate regions. Hence, our approach focuses only on the effect of temperature change on wood production. For instance, we do not simulate the effect of changing CO_2 in combination with an increase of temperature. This might be critical for analysis of strong temperature changes (e.g. RCP 8.5), which will result in an increase of droughts and changes in the annual temperature cycles. Such more complex scenarios should be analyzed in future studies. Further, we neglect the effect of time lags (e.g. the bud building in the autumn in the previous year). However, it is possible to enlarge the used time series to analyze the behavior of the forest over longer time periods and study not only productivity, but also effects on regeneration or mortality.

2) I think, even though referring to central European, temperate forests, you are not putting enough emphasis on the interpretation of the results from a forest management perspective. However, your target variable "above ground wood production" as well as the stand densities, species choices etc. are subject to forest management and species mixing etc. are important *elements of EU silvicultural strategies. I think the discussion of the influence of forest management on your results and their implications for forest management should be strengthened.*

We agree that our result might be important for forest management strategies. We therefore will add a new section "4.2. Implications for forest management" in the Discussion section ~~(see Appendix R 2).~~

Thank you for these detailed smaller points.

P1L1: Either "Observational studies discovered that" or "Observations show that..."

P1L4: "increase productivity the most"

P1L8: "cover a wide range of possible"

We will reformulate the phrases.

P1L6: unclear: "within the forest structure" ==> don't you simply mean "within the forest given the environmental conditions of each..."?

We will write: … how well species are distributed over the different forest layers regarding…

P1L11 and also L14: "increasing OmegaAWP" it sounds weird that an optimum can be increased or have "large values". Maybe I am too picky and I do not have a good alternative... maybe ask a native speaker...

We will introduce a new term for Ω_{AWP}: "species distribution index" but keep the acronym Ω_{AWP}.

P1L15: "heterogenity is associated with a positive"

We will reformulate the sentence, following your suggestion.

P1L14-16: This sounds like quite a contradiction: for young forests low diversity and low height spread make the forest react positively to temperature while for older forests this is not the case. Could you add one sentence of explanation here and discuss potential implications for forest management in the discussion? This would mean foresters should go for even aged, mono-species stands during establishment and then bring in other species later? or keep the canopy closed with one species while having other species in the undergrowth for some time?

We recommend paying attention to young forests with low diversity and even-aged structure. A mixture of climax species should be planted below the main canopy. Later those climax species will replace the pioneer species in the canopy and build the mature forest with heterogeneous tree sizes.

We will add a new section regarding the implications on forest management (4.2. Implications for forest management).

P1L19: I have the feeling you are using "forest growth", "wood production" and "forest productivity" interchangeably. While this can be correct in some instances I wonder whether all the references you cite here actually refer to forest growth or rather productivity.}

We will focus on (above-ground) wood production in the whole manuscript. Barber et al. 2000 analyzed the change in radial growth of white spruce under climate change. We will replace the references of Cao and Woodard 1998 (as it refers more to carbon fluxes of ecosystem in general and not explicit wood production) by Reyer et al. 2013.

The other two refer to the effect of climate change on photosynthesis or respiration of trees (Luo 2007) or plants (Penuelas and Filella 2009).

P1L21-P2L2: I think this sentence is imprecise. the observed changes in productivity are not the primary reason for discussing the compensation of co2. it is rather the overall high carbon stocks and sequestration rates (even without changes) that matter for this discussion. I see what you want to say but I think it is a bit too condensed here....

We will reformulate the sentences:

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). The carbon stock of forests and their role as carbon sink are therefore changing. These findings stimulated discussions about whether forest management strategies can be adapted to reduce forest vulnerability to climate change, to support recovery after extreme events and foster the carbon sink function of forests.

P2L3-9: I think this section should also mention the influence of other factors, at least briefly... Especially since you say that "productivity is influenced by several factors" in the first sentence of this paragraph...

We will add the following sentences: … in addition to other climate variables (Barford et al. 2001). For instance, increasing CO_2 increases water use efficiency of forests (Keenan et al. 2013), which could compensate negative effects of climate change on European forest growth ~~(whereas, with constant CO_2 at 350ppm, forest growth declines on several sites due to climate change –~~ (Reyer et al. 2014). Another important often investigated process is the fertilization effect of nitrogen (De Vries et al., 2006, 2009). For instance due to depositions in the second half of the last century, wood production had increased in European forests (Solberg et al. 2009). In case of temperature change, photosynthesis, respiration and growth rates are modified…

P2L18/19: “rarely include properties related to both species composition . . .

P2L22: “forests stands were available, it would”

P2L23.: “option to such field experiments is”

P2L26: "simulating 30 year time slices of a range of different future climates for 135..."

P2L27: “analyzed”

P2L29: “a large number”

P2L30: "species compositions"

Figure 1: I would delete the "..." in each box as your study does not cover more climate variables nor more stand structural or composition related variables. In the caption, I would precise: "overview of drivers influencing forest forest productivity in this study" and also clearly state that only temperature is varied in a "temperature sensitivity analysis" or so.

P3L3: "2017). The forest factory generates 370,170...and allows to estimate"

We will realize all these suggestions. Thank you.

P4L2: How to get from the 15 stem size distributions and 256 mixtures to the 370,170 stands?

The forest factory creates forest patches which are based on 15 different stem size distributions and 256 species mixtures. 100 forests patches of each combination are built (in total 15*256*100 = 384,000 forests). In a few cases not all species of the mixture could be placed within a patch by the algorithm, so these forests are rejected. We end up with 370,170 forest stands.

We will reformulate section 2.2 of the Method section to clarify these points.

P4L3/4: At some point you should give the latin names of the species to allow international readers to check which species you mean...

Good point. We will add the Latin names in the section 2.2.

P4L6: I wonder how you can actually represent complex mixtures on a 400m^2 plot. This could be covered by one large beech tree? I think you need to discuss the implications of choosing this patch size. Or do you upscale to the ha or so?

Within an area of 400m² the trees compete for light as large trees shade the smaller ones. This is the typical plot size used in forest gap models. You are right, a very large tree could cover such a plot but below its crown there is space for smaller trees of other species. However, there are indeed a few combinations of species mixtures and stem size distribution that could not be represented within a plot because of limited space. Thus, these forests do not exist in the collection of forests generated by the forest factory.

We will reformulate the text in section 2.2. to clarifying these points.

P4L6: "space limits"

We will reformulate the text.

P4L8: You should discuss in detail why you think the year 2007 in Hainich is representtative of temperate climatic conditions! I think you make two dangerous assumptions: 1) Hainich is somehow representative for "temperate climates" (it certainly is but only to a certain degree and 2) the 2007 climate is somehow representative of the overall Hainich climate

We agree. We use this year as an example of a temperate climate. (In principle, it is possible to use climate data of every other location). We will reformulate the text in section 2.2.

P4L11-22: This is from FORMIND, right? You could say that

We will add the following sentence at the beginning of the paragraph: The calculation of wood production of trees is based on algorithms of the model FORMIND (Fischer et al. 2016,).

P4L10: "2.2 Forest productivity . . . ''

P4L15: "by the photosynthesis-limiting . . . ''

We will use your suggestions.

P4L17/18: I read this as if Rm was both maintenance respiration and allocation to non-woody tissues?

This is correct.

P4L23: I would introduce a new subheading here about the "climate sensitivity"

We will add it.

P4L25: "separated" The methods description should be in the past tense

We will change the tense.

`\emph{\color{blue}`*Figure2: You should explain once more all the variables shown on t he plots in the caption, AWP and MAT are not explained currently.*

Good point. We will modify the caption of Figure 2.

P5L1: unclear: do you include co2 and nitrogen in the model but keep them constant or are they not included at all? You should discuss that co2 will matter in a 2 $^{\circC$ warmer world . . .

They are not included at all. We will modify the sentence. See also the reply to your first major comment above.

P6L6: Do you have any reference or argumentation to support using BA as a proxy for LAI? I could imagine this only works until canopy closure?

In the forest factory dataset LAI and basal area correlate quite well (R^2=0.74). A high correlation between leaf area and basal area (R^2>0.92) has been found for instance also by Levi and Jarvis 1999.

P6L13: "maximum forest height"

We will replace the phrase.

P7L1-2: Is “10.2015” the right citation format?

No. We will correct the citation format to “2015”.

P7L5: Why Gaussian? Any deeper reasons or simply because it is the default?

It is the default setting. We will modify the sentence: … assuming a Gaussian error structure (default setting).

P7L8: the heading is unclear. “benefit the most” ==>from what?

We will add: … the most from increasing temperatures.

P7L18-19: I wonder if the mean is the appropriate measure here given that the distributions are so skewed (figure b1)?

Figure B1 shows the distribution of the SI values. The shown SI values do not represent mean values; they are the slope of linear models, which relate temperature changes with AWP changes divided by the average AWP of the forest (see equation 2, 3 & 4).

We will modify the sentence: We than quantified the changes in productivity due to changes in MAT (SI_{MAT}) and Q95 (SI_{Q95}).

P7L28: This has to be carefully discussed. It seems to be obvious that the species choice will have the strongest influence.

Thanks for this point. We will modify the sentences at P11 L16ff: … If species are unfavourably distributed within the forest (low Ω_{AWP}), the AWP of the forest is low. Note, Ω_{AWP} is the ratio between current AWP and the highest possible AWP of the forest which can be reached due to shuffling of species identities. If AWP is low the forest will suffer from increasing temperatures, which results in negative slopes (ΔAWP / ΔT). These values are than divided by low AWP values (Equation 4), which results in large negative values of SI_{MAT} and SI_{Q95}. (See Appendix B5).

Figure 3: maybe explain somewhere (can be in the main text) how to interpret the scale from 0-1 of the $Omega_{AWP}$.

We will add an explanation in the caption of figure 3.

P8L12: “analysed how”

We will reformulate the phrases.

P8L12: Maybe recap here that AWP is your expression of productivity.

We will replace forest productivity by (above-ground) wood production. See also reply to your comment P1 L19.

P9L1: “specific value combination of forest properties” ==> rephrase

We will write: …with a specific set of forest properties which…

P9L5/6 & 12-14: Certainly analyzing all possible combinations of species and structures etc as done in the Forest Factory approach is valuable but this approach will also generate a huge number of stands which are highly unrealistic and that will never be found in reality. So the discussion could be more balanced here highlighting that you also produce quite a lot of “non-sense” forests as well.

This is an important point of the forest factory approach.

All forest patches could exist in reality, as every tree has a positive productivity and enough space for its crown. It is not possible that “non-sense” forests are generated as the used method prevents that a light demanding species occurs below a closed canopy or that forests are overcrowded. We will revise the text to makes this clearer.

P9L10: “FORMIND”

We will replace the phrase.

P10L2-3: This sentence needs to be rewritten for clarity

We will remove this sentence.

P10L11: RCP2.6

We will correct this.

P10L15-28: I had the feeling this section needs to be rewritten for clarity and logical connection to the preceding sections.

Thanks for this comment. We will reformulate the section in the following way:

To characterize the annual cycles of temperature we select two variables: mean annual temperature (MAT) and inter annual temperature amplitude (Q95). Both variables can be varied independently. In case of higher MAT we observe an elongation of the vegetation period. This leads to higher forest productivity, if other resources are sufficiently available (Luo, 2007). This explains why SI_{MAT is often positive. However, warmer summer temperatures can also lead to a decline in wood production due to an increase in respiration. In case of increasing Q95, more days with extreme temperatures will occur in a year. Thus, an increase of one $^{\circ}^C{-1}$ of Q95 will increase respiration more strongly compared to an increase of one $^{\circ} C^{-1}$ of MAT. Hence, the increase of Q95 has normally negative effects on the productivity (negative SI values).

P11L3-12: Also here maybe some rewriting is needed to better link the paragraph to the rest of the discussion.

We will modify the two paragraphs of section 4.2.

P13L5: I find the conclusions too short and too close to the results. The conclusion in my view should clarify: Why do your results matter? What do we learn?

We will extent the conclusion and include implications of our study for future forest modelling and forest management.

P13L12: I find the supporting material organized in a complicated way. Can you not provide the text plus the associated figures and then another piece of text etc. The online material is not meant to be read as one text but one should find things quickly.

We will rearrange the text and figures as suggested.

Figure A2: I am pretty sure you are showing the annual precipitation sum and not the ''mean" here.

Correct. We will revise the sentence.

P15L4/5: I do not understand this: it seems mean (1.5%) is outside of the interquartile range?

The unit is \%${\circ}C{-1}$. This means that on average forest increase their productivity by one \% if temperature increases by ${\circ}C$. The interquantile range of 95\% (Q95) is used only to quantify the interannual temperature variability.

We will modify the sentences to make this clearer:

Figure A3: hec should be ha}

P16l5: "the first plot" ==>not very precise. Do you mean plot 3a)? Then also include small letters in the plots!

We will follow your suggestions.

P16L6: I would always refer to Ω_{AWP} and not introduce any other terms such as suitability etc. it is getting too complicated . . .

We will modify text and figure.

Figure A4: To me it looks like You are overestimating SI_{MAT} quite systematically but you never really discuss this?

Good point. It is quite difficult to evaluate the theoretical analysis by using field data, as a huge number of similar forest plots are needed, which cover a temperature gradient. In case of the German forest inventory only a few forest plots can be used for such an analysis. For spruce and beach monocultures we were able to select enough similar plots. Further, these inventory plots provide no direct measurements of climate or LAI, which would be needed for an appropriate evaluation. We therefore used altitude as proxy for temperature (although other environmental variables like precipitation or soil attributes could change as well with altitude) and basal area as proxy for LAI. The reason for the overestimates of SI_{MAT} is not clear, but might be a result of the differences between SI_{MAT}-calculations based on field data and the calculation of SI_{MAT} based on the forest factory approach.

We will add some sentences regarding this point to the Appendix.

P17L6: sentence misses a verb

We will revise the sentence.

Figure b3: I wonder why there are so distinct patterns of values with y=0 and also x=-100 in panel a and y=-8 (or so) and x=-100. Is this an artifact?

The vertical dots occur as all forests with SI values smaller than -100\% ${\circ}C{-1}$ where set to -100\% ${\circ}C{-1}$ for this graphic. To be consistent, we will remove them, also as they were removed for the final analysis, which is presented in the paper. See page 6, line 4 of the manuscript: …*In our analysis we exclude all forests stands for which AWP is negative if the temperature rises by 1* ${\circ}C{-1}$ *(2\% of all stands).*

I assume the horizontal structure is an artifact of the boosted regression tree algorithm. We will reformulate the corresponding sentences.

P18L2: “in some simulated”

P18L7: “we calculate a mean . . . ’’

Figure B5: panel “b)” is missing the “b)”

We will reformulate these phrases and add the “b)”.

Figure B6: The layout of this figure makes it very hard to see which color overlays the other . . . so do most “brownish” species rather follow the green line or the dark blue for the left-side of the bell-shaped lines in panel a)?

We will revise the figure based on a modified color-palette and enlarge the graphic.

Figure B7: Is nowhere referred to in the text. What is the unit of the y-axis?

It will be referred in the text and the text will be reformulated and we will revise the figure.

Figure B8: The SI_{MAT} values are so small, is that correct?

We forgot conversion into \% (multiplication by 100, as done in all the other graphics). We will also add the unit to the y-axes.

Reviewer 2 (anonymus)

Compared to the announced text changes in our reply in the interactive discussion we slightly changed several text fragments to improve readability, English and grammar (especially in the three new sections: 4.2 Implications for forest management, 4.3 Implications for global vegetation modelling and the new Conclusion). We mark major changes in our reply in purple.

The authors use an individual-based forest modelling approach to isolate the effect of five forest structure (LAI, maximum stand height, and canopy stratification) and composition (functional diversity and its optimal distribution) parameters on the overall sensitivity of simulated wood production to increasing mean annual temperature and seasonal amplitude in a European temperate setting. The model is integrated hundred of times over a single year and forest stand using synthetic climate scenarios with perturbed temperature to simulate an ensemble of productivities for thousands of stands with a range of initial conditions of structure and composition, representative of different stand development stages. This synthetic dataset, broadly consistent with ecological rules observed in the real world, is then analysed using a statistical regression method in order to quantify the relative effect of the five structural and compositional parameters on the simulated temperature sensitivity of forest productivity. Their results indicate that an index of optimal species distribution of the trees in a forest stand – the ratio of actual productivity of a forest stand to the maximum productivity achieved by changing only the species of the trees whilst keeping the same stand structure – explains ? 88% of the temperature sensitivity of forest productivity simulated by the model.

Among the remaining four parameters, forest height (a proxy of stand development stage) is the most important variable in explaining the rest of the fractional variance of temperature sensitivities. Thus the authors conclude that the sensitivity of plant productivity in temperate forests to changes in temperature is driven by forest structure and species diversity. I believe that the main scientific finding is of interest for the wider biogeosciences communities.

The overall modelling experiment seems appropriated to disentangle the relative importance of forest structure and composition properties on patterns of temperature sensitivity of temperate forest productivity in the model world. However, the manuscript is very difficult to follow at times and the discussion of the main findings is simply too thin. I recommend major revisions in order to improve (i) the readability and English of the manuscript and (ii) to better discuss the underlying mechanisms and implications of the findings for the wider ecological theory.

Thank you very much for your review. We will revise our manuscript carefully including your recommendations.

We will enhance the readability and we will send the revised manuscript to native speakers to improve the English and the grammar.

We further will add two new sections discussing the implications of our results for forest management and global vegetation modelling (see new section 4.2 and 4.3) and enlarge the conclusion ~~(see appendix R3)~~. Finally, we will carefully revise the Discussion including more details of the underlying mechanisms (Please note that some sections of the former discussion are now in section 3.1).

SPECIFIC COMMENTS

Regarding the first point above, I have the following comments:

-Introduction

It is informative but the English and grammar need revision.

As explained above, we will revise the manuscript regarding English and grammar using the help of a native speaker.

-Method

This section tends to be redundant with the opening paragraph and appendices. I recommend reorganizing it and make it more concise. It is not clear how the stands at different stages of development were initialised. Were the structure, composition and development stage randomly generated or did you apply some spin-up? This has implications for the realised productivity when computing the ?_AWP index. Why exactly 370,170 stands?

We did not perform any spin-off. Trees are "planted" with a certain size derived from the stem size distribution considering that each tree of a forest has a positive productivity and enough space for its crown. The forest factory creates forests, which are based on 15 different stem size distributions and 256 species mixtures. 100 forest patches with a size of 400m² of each combination were built (in total 384,000). To generate these 100 forests of each combination, we randomly selected a tree from a stem size distribution, assigned a species and checked if the tree has enough space and a positive productivity. In a few cases not all species of the mixture could be placed within a forest by the algorithm, so we rejected such forests. We end up with 370,170 forest stands. We will reformulate the text in 2.2 of the Methods section.

In Line 28 of page 4 it is said "We end up with five climate scenario sets of one-year length that differ in precipitation and radiation." But since these scenarios are derived from five different real years, they should also differ in absolute temperature values? As I understand it, within each synthetic scenario, radiation and precipitation are the same and only temperature changes at the specified steps. Among the five scenarios, the absolute values of all variables should be different. Please explain better this part to the reader.

Thanks for mentioning this point. The absolute temperature values differ between the 5 time series. We will explain this point in more detail.

In Fig. 2, what does the shading in the middle panels mean? The meaning of H_forest is not explained in the caption.

Thanks for mentioning this point. The shading represents the standard deviation obtained from the analysis of five different time series (with the same modification of MAT and Q95). We will rewrite the text and explain H_{forest}.

-Results and Discussion

I found many passages in these sections very difficult to follow. There are result statements with no reference to the figures or tables that leave the reader guessing the corresponding figures. The results section is rather short and most of *the discussion is still results.}*

We will move figure 5 und 6 (and the corresponding text) from the Discussion into the Result section. We further will expand the Discussion by two new sections, which will discuss the implications for forest management and vegetation modelling (see 4.2 Implications for forest management and 4.3 Implications for global vegetation modelling). Finally we will carefully revise the results and discussion to improve the text and link the statements with the corresponding figures.

Figure B1 shows a long negative tail in the distribution of the obtained sensitivities. The authors focus exclusively on the positive sensitivities and neglect negative values, despite declaring in the introduction that responses can be both positive and negative. Why the simulated sensitivities are so asymmetrical and the negative values are not discussed?

We will explain the large negative values and the long negative tail of the sensitivity values in more detail. However, we don´t know the reason for the asymmetric distribution. In addition, we will modify figure 5 and replace forest C by an old-growth forest with negative SI-values.

In the discussion I miss a more complete explanation of the underlying ecophysiological and metabolic mechanisms (e.g„ Figs 5 and 6). Also, there is no discussion of the potential limitations of the model and the modelling experiments performed here. For instance, autotrophic respiration seems to be a critical factor affecting the response of net productivity to changes in temperature in the model. How well is this process represented in the model version used? Would you get the same result if you account for uncertainties in parameterisation of this process?

Thanks for mentioning these points. The forest factory is based on the well-established and often applied forest gap model FORMIND. The parametrization was used and discussed in several previous studies (Bohn et al 2014, Bohn et al 2017, Rödig et al. 2017). We will make this clearer in the Method section. We further will enlarge the section “4.1. The study-design” and enlarge the explanations in the Appendix discussing photosynthesis and respiration rates of single trees (Figure B7). In general, the parameters with the highest uncertainty within the FORMIND-model are establishment and mortality, which are not used in this study.

Finally, what are the implications of the main finding for the wider ecosystem and climate modelling communities that usually rely on global models that have no explicit forest structure? Any recommendation?

This is a good point. Thank you. We will add a new section, which discusses the implication of our analysis on global vegetation modelling (see 4.3 Implications for global vegetation modelling).

-Conclusion Rather brief. Here the authors could wrap-up the wider implications of their main findings.

We will extend the conclusions to include implications of our study for future forest modelling and forest management. (See also ~~Appendix R3 :~~ new conclusion).

-Figures

The figures are excellent but the captions are not sufficiently informative. Please improve the captions.

We will revise the captions.

Fig 3 could be merged with Fig B2. The latter is important to understand the overall result.

We will do this.

-English and grammar.

There are many grammar errors and typos through the text. Please revise English and correct typos.

We will send the revised manuscript to an language expert to improve the English and grammar.

List of major changes

- Revised section 2.2 forest factory approach
- Revision of most captions of the figures
- Revision of former section 4.2 The influence of forest structure on temperature sensitivity - now section 3.1.1.
- Revision of former section 4.3 The effect of species composition on temperature sensitivity - now 3.1.2
- Extention of the discussion of the study design (section 4.1)
- Two new sections 4.2 Implications for forest management and 4.3 Implications for global vegetation modelling
- Revision of the conclusion.

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 [c1]show that some temperate forests increase their productivity, whereas others reduce their productivity. This study focus on how species composition and forest structure properties influences [c2]the temperature sensitivity of [c3]above-ground wood production (AWP). It further investigates, which forests will [c4]increase in their productivity the most with rising temperatures. 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 [c5]species distribution index (Ω_{AWP}). Ω_{AWP} quantifies [c6]how well species are distributed over the different forest layers regarding AWP. [c7]. We analyzed 370,170 forest stands, generated with a forest gap model. These forest stands [c8]cover a wide range of possible forest types. [c9]For each stand we estimate annual above-ground wood production and perform a climate sensitivity test based on 320 different climate time series (of one year length). The scenarios differ in mean annual temperature and annual temperature amplitude. Temperature sensitivity of [c10]wood production 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 that 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 [c11]heterogeneity is associated with a positive effect of temperature on [c12]wood production. During later successional stages, higher species diversity and larger tree height heterogeneity is an advantage.[c13]To archieve

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[c1] ~~discovered~~
[c2] ~~this~~
[c3] ~~forest productivity~~
[c4] ~~rising temperatures increase productivity strongest~~
[c5] ~~optimal species distribution~~
[c6] ~~how well species are distributed within the forest structure regarding~~
[c7] ~~with the given environmental conditions of each single tree~~
[c8] ~~cover a large number of possible~~
[c9] ~~For each forest stand we estimate annual above-ground wood production under 320 climate scenarios (of one year length)~~
[c10] ~~forest productivity~~
[c11] ~~heterogeneity support~~
[c12] ~~forest productivity~~
[c13] *Text added.*

such a development, one could plant below the closed canopy of even-aged, pioneer trees a climx-species-rich understory that will build the the canopy of the mature forest. This study highlights that forest structure and species composition are both relevant [c14]in understanding the temperature sensitivity of [c15]wood production.

Copyright statement. TEXT

1 Introduction

Climate change alters [c1]wood production by modifying [c2]the rates of photosynthesis and respiration rates of trees (Barber et al., 2000; Luo, 2007; Peñuelas and Filella, 2009; Reyer et al., 2014). 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). [c3]The carbon stock of forests and their role as carbon sink are therefore changing. These [c4]findings 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 [c5]foster the carbon sink function of forests (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Bonan, 2008).

[c6]Wood production is influenced by several factors [c7], such as CO_2 fertilization, nitrogen deposition, precipitation, and temperature. (Barford et al., 2001)[c8]. [c9] For instance, rising CO2 increases water use efficiency of forests (Keenan et al., 2013) [c10], which could compensate negative effects of climate change on European forest growth (whereas, with constant CO_2 at 350ppm, forest growth declines on several sites due to climate change - see Reyer et al. 2014). Another important process is the fertilization (De Vries et al., 2006, 2009)[c11]. Due to depositions of nitrogen in the second half of the last century wood production had increased in European forests (Solberg et al., 2009). However, 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). In the temperate biome, positive effects on [c12]wood production (Bontemps et al., 2010; Delpierre et al., 2009; Pan et al., 2013; McMahon et al., 2010, e.g.) as well as negative ones 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.

[c14] ~~to understand~~
[c15] ~~forest productivity~~
[c1] ~~forest growth~~
[c2] *Text added.*
[c3] *Text added.*
[c4] ~~observations~~
[c5] ~~to compensate for anthropogenic CO2-emissions~~
[c6] ~~Forest productivity~~
[c7] ~~Temperature can strongly alter forest productivity, in addition to other climate variables~~
[c8] ~~such as CO_2-fertilization or nitrogen deposition~~
[c9] *Text added.*
[c10] *Text added.*
[c11] *Text added.*
[c12] ~~forest productivity~~

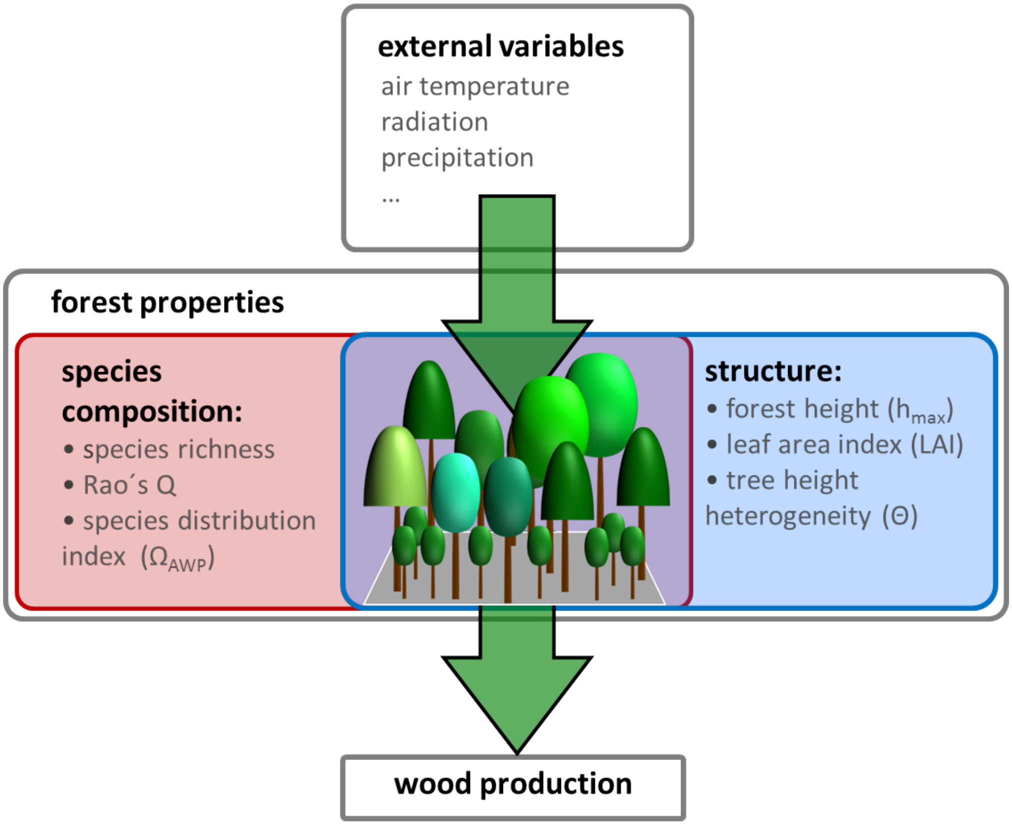


Figure 1. Overview of drivers influencing [c15]wood production. External variables in this study are temperature, radiation, and precipitation. Forest properties are divided into two groups: species composition properties (e.g., the Rao's Q as a measure of functional diversity and [c16]species distribution index Ω_{AWP}) and forest structure properties (e.g., forest height, leaf area index and tree height heterogeneity).

In addition to the influence of climate variables, [c13]wood production is also affected by internal forest properties. These properties can be grouped into two types: properties which describe forest structure, and those which describe 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, [c14]wood production often increases with the increasing number of species (Zhang et al., 2012; Vilà et al., 2007).

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 [c1]wood production 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 [c2]wood production. However, these studies include only a few forest properties and rarely

[c13] ~~forest productivity~~
[c14] ~~forest productivity~~
[c1] ~~forest productivity~~
[c2] ~~forest productivity~~

include [c3]properties related to both species composition and forest structure. Hence, it [c4]is unclear, how [c5]these forest properties influence [c6]wood production change due to temperature rise and which forests will benefit from rising temperatures.

As far as we know, there is no data set available[c1] that covers forests, differing in structure and diversity, under almost identical climatic conditions. Even if a larger number of forest stands [c2]were available, it would be difficult to manipulate for instance temperature while keeping all other climate variables constant. An alternative option to [c3]such field experiments analysis is offered by forest simulation models. Such models are able to estimate [c4]wood production under different climate conditions (Lasch 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 [c5]year time slices of a range of different future climates for 135 inventoried forest stands. There are also model-based studies, which systematically analyzed 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 [c6]large number of forest stands covering various forest structures and species composition[c7]s (for up to eight temperate tree species). Annual above-ground wood production (AWP) is then calculated for all forest stands based on climate [c8]time series. These [c9]time series 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) [c10]of which forest stands will benefit most from rising temperatures.

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). [c11]The forest factory generates 370,170 different forest stands (see section 2.1) and [c12]allows the estimat[c13]ion of above ground wood production (AWP) under various climate [c14]time series (see section 2.2). The 320 scenarios differ

[c3] ~~both properties of both types,~~

[c4] ~~remains~~

[c5] *Text added.*

[c6] ~~forest productivity~~

[c1] ~~, which~~

[c2] ~~would be~~

[c3] ~~field data~~

[c4] ~~forest productivity~~

[c5] ~~years into the future for~~

[c6] ~~huge~~

[c7] *Text added.*

[c8] ~~scenarios~~

[c9] ~~senarios~~

[c10] *Text added.*

[c11] ~~With this approach, we generate~~

[c12] *Text added.*

[c13] ~~e the~~

[c14] ~~scenarios~~

in mean annual 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 [c15]wood production 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 2.4). We analyse the influence of the five forest properties on temperature sensitivity using boosted regression trees (see section 2.5). Finally, we analyse which combination of forest properties results in the highest sensitivity values for different successional stages (see section 2.6).

2.1 The forest factory approach

The forest factory [c1] creates forest patches which is based on 15 different stem size distributions [c2]and 256 species mixtures.[c3]100 forests patches of each combination are built.

The stem size distributions cover a gradient from young to old and disturbed to undisturbed forests. Species mixtures include all possible combinations of [c4] *Pinus sylvestris*, *Picea abies*, *Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*, *Populus x canadensis*, *Betula pendula* and *Robinia pseudostuga*. [c5]We use the species parameter set and algorithms of the FORMIND-model version for temperate forests [c6] within the forest factory (Bohn et al., 2014; Fischer et al., 2016). [c7]To generate forest patches, we randomly choose trees from the stem size distribution, assign a species identity and plant them within a patch of 400m^2[c8]size.

[c9]To place a tree within a patch the following rules must be meet: (i) [c10]there must be available enough space for crowns of every tree (ii) every tree [c11]in the forest must have a positive productivity under [c12]its environmental conditions (light, temperature, water). [c13]We use climate time series of the year 2007, measured at Hainich National Park, central Germany. We assume this time series as a typical example for a temperate year (in principle it possible to use climate data of every other location). In contrast to an artificially generated climate this climate is perfectly physically consistent (regarding light, air temperature and precipitation).

[c14]In a few cases not all species of the mixture could be placed within a patch by the algorithm, so we rejected such forests. We end up with 370,100 forest stands. For more details regarding the forest factory see Bohn and Huth (2017).

[c15] ~~forest productivity~~
[c1] ~~combines~~
[c2] ~~with~~
[c3] *Text added.*
[c4] ~~pine, spruce, beech, oak, ash, poplar, birch and robinia~~
[c5] ~~The~~
[c6] ~~are used~~
[c7] *Text added.*
[c8] *Text added.*
[c9] ~~The forest factory generates forest stands with a size of 400m2 using the following rules:~~
[c10] ~~space limit the maximal number of trees and~~
[c11] *Text added.*
[c12] ~~a typical temperate climate~~
[c13] ~~For a typical temperate climate, we employ a climate time series from the year 2007, measured at Hainich National Park in central Germany. presented a detailed description and discussion of the forest factory.~~
[c14] *Text added.*

2.2 The wood production

[c1]The calculation of above-ground wood production (AWP) of trees is based on algorithms of the model FORMIND (Bohn et al., 2014; Fischer et al., 2016). The [c2]wood production of a single tree is calculated as the difference between climate variables 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 [c3]the 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).

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

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)).

2.3 climate sensitivity

To generate a set of 320 annual climate [c4]time series, 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 temperature (see Appendix A1; Fig. A1)). We separated these time series into five distinct time series of one-year length. First, we increase or decrease the mean annual temperature of each year by adding or subtracting 0.5 °C steps between -1.5 °C and +2 °C. Second, we change the amplitude of the annual temperature cycle for these time series [c5]variation of each year. [c6]To do so, we modify the standard deviation of each year by 4% steps between -12 % and +16 %. We end up with five [c7]sets of climate times series (of one-year length) that differ in [c8]temperature, precipitation and radiation. Each [c9]of these five sets includes 64 time series, which differ only in temperature (see Appendix A1 , Fig. A2). 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

[c1] *Text added.*
[c2] ~~productivity (AWP)~~
[c3] *Text added.*
[c4] ~~scenarios~~
[c5] *Text added.*
[c6] ~~by modifying~~
[c7] ~~climate scenario sets~~
[c8] *Text added.*
[c9] *Text added.*

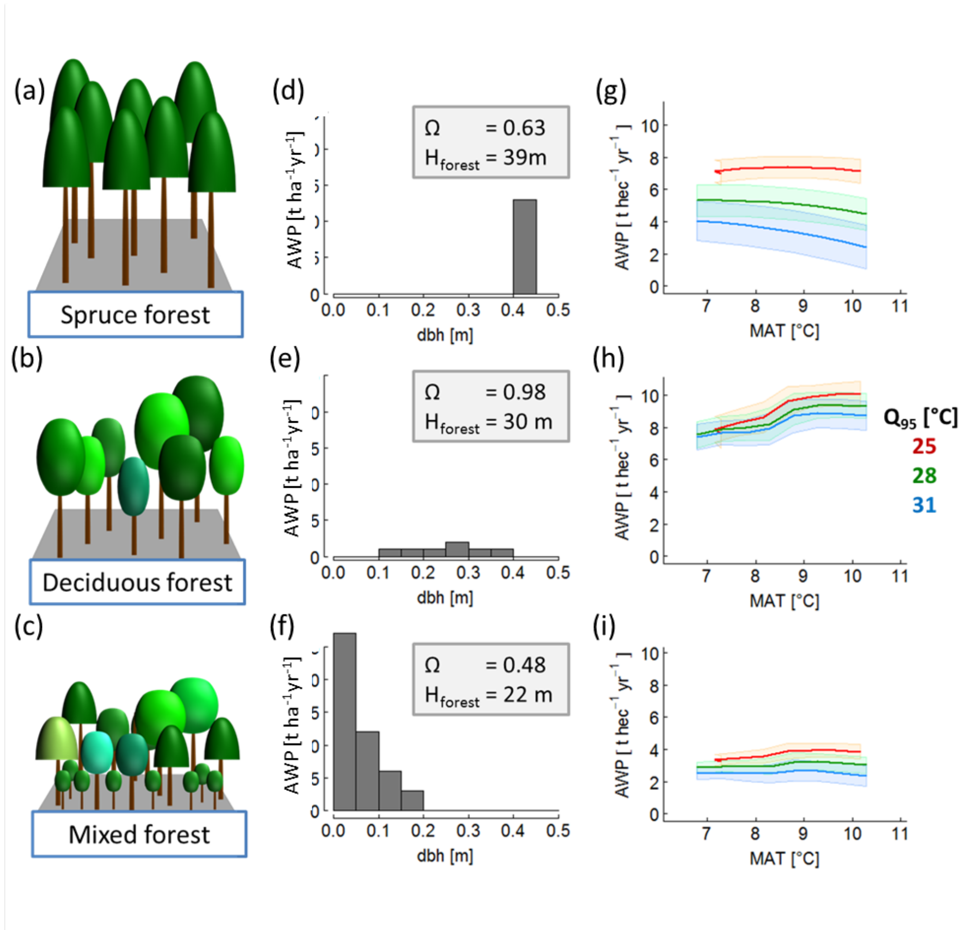


Figure 2. Overview of [c1]forest properties and resulting temperature sensitivity of above-ground wood production (AWP) of three exemplary forests: a) old even-aged spruce forest; b) mature deciduous forest; c) a quite young mixed species forest. [c2]The middle panel (subfigures d, e & f) shows the corresponding stem size distributions and inform about the forest height (the highest tree) and species distribution indexΩ_{AWP}[c3](which quantifies, how suitable a species distributed with in the forest structure regarding AWP). [c4] [c5]Each forest is treated with 320 climate time series: The last panel shows the AWP as a a function of mean annual temperature (MAT). The colours indicate different inter-annual amplitudes of the temperature (Q95) of the used time series. (The coloured bands show the standard deviation due to the variability of the five different time series, which exist for each combination of MAT and Q95).

daily temperature values of a given year. We [c10]do not model 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 [c11]wood production. Figure 2 (a-c) shows the above-ground wood production (AWP) for different annual temperatures for three different forest stands.

[c10] ~~exclude~~
[c11] ~~forest productivity~~

We analysed the sensitivity of every forest stand [c6]to temperature change by following the approach of Piao et al. (2010). For every forest stand, a general linear model is fitted relating [c7]wood production and the two temperature indices MAT and Q95, as well as the nuisance parameter year.

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

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

$$SI_{MAT} = \frac{\alpha}{AWP} \tag{3}$$

$$SI_{Q95} = \frac{\beta}{AWP} \tag{4}$$

In our analysis we exclude all forests stands for which AWP [c1]turns negative if the temperature rises by 1 °C ([c2]This occures in 2% of all stands).

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 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).

2.4 Five forest properties to describe forest stands

We use three indices to describe the forest structure: leaf area index (LAI), [c3]maximum 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.

To describe species composition, we use Rao's Q and [c4]species distribution index (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 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

[c6] ~~against~~
[c7] ~~forest productivity~~
[c1] ~~is~~
[c2] *Text added.*
[c3] ~~maximal~~
[c4] ~~optimal species distribution~~

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).

2.5 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 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 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, 2015). This BRT-analysis was performed in the R-package gbm 2.1.1 (Ridgeway, 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 (1, 3 and 5) and the cross-validation (3-, 6- and 9-fold) assuming a Gaussian error structure [c1](the default setting). 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.

2.6 Finding the forest stands for different successional stages that benefit the most increasing temperatures

Here, we assume forest height as a proxy for the successional stage of a forest. In every height class, (H_{max}) we select those 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 ([c2]species distribution index (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

[c1] *Text added.*
[c2] ~~optimal species distribution~~

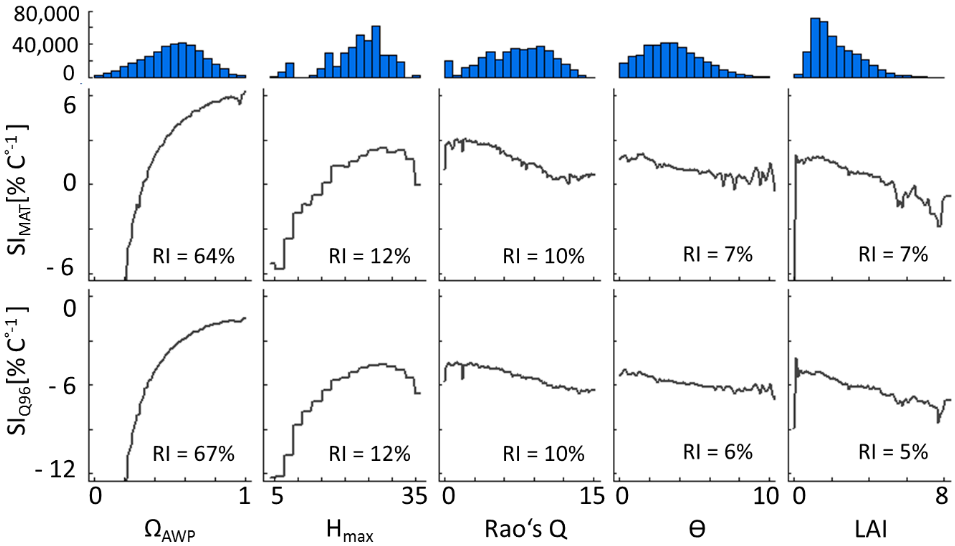


Figure 3. Partial dependency plots of the five forest properties Ω_{AWP} ([c1]species distribution index), forest height class h_{max}, Rao's Q (functional diversity), θ (tree height heterogeneity) and LAI (leaf area index) for SI_{MAT} (sensitivity against changes inthe mean annual temperature) and SI_{Q95} (sensitivity against changes in the annual temperature amplitude). [c2]Relative importance (RI) compares the influence of different input variables on the variability of a target variable. Histograms show the frequency of forest property values in the analysed data set. [c3]Note, a Ω_{AWP} is the ratio of the current AWP of a forest and the highest possible AWP optained by shuffling ony species identies without changing the forest structure.

[c3]time series. We than quantified the changes in productivity due to [c4] changes in [c5]MAT (SI_{MAT}) and [c6]Q95 (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).

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 $\pm$ 2.9 % °C $^{-1}$ (see Appendix B2 Fig. B3).The RMSE even decreases to $\pm$ 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 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 $\pm$ 1.1 % °C $^{-1}$ (see Appendix B2 Fig. B4).

[c3] ~~scenarios~~
[c4] ~~the~~
[c5] ~~mean annual temperature~~
[c6] ~~amplitude of inter-annual temperature~~

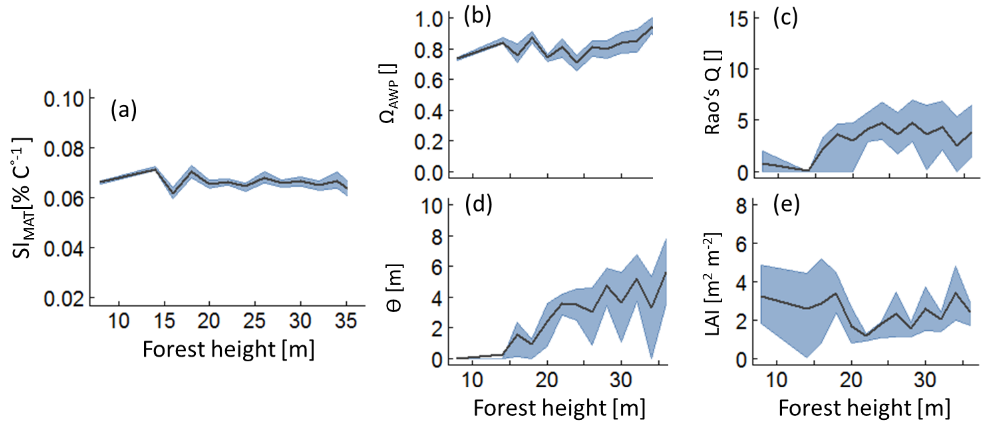


Figure 4. Analysis of those forests that show the highest 5% of the SI-values depending of forest height. Lines indicate mean values of the [c1]forest subsamples [c2]which includes the best 5% regarding SI_{MAT} [c3]of each hight class. [c4]The grey band indicates the inter quartile range. Figure a) shows temperature sensitivity of above-ground wood production [c5]over forest height, analysing only the best [c6]the forest subsample. b) to d) shows the change of the remaining forest properties within the [c7]forest subsamples (Ω_{AWP} = optimal species distribution; θ = tree height heterogeneity; LAI = leaf area index; Rao s Q quantiles functional diversity).

data set. 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 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}.

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 [c8]wood production. 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. [c9]Analysing 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

[c8] ~~forest productivity~~
[c9] ~~The analysis~~

change their character between young and intermediate forest heights. We obtain similar simulation patterns for SI_{Q95} (Appendix B3 Fig. B5).

3.1 Understanding the patterns

3.1.1 The influence of forest structure on temperature sensitivity

Forest structure affects [c1]wood production of the single trees in two ways. First, it determines the available light for each single tree and second, the size of trees influences photosynthesis and respiration rates [c2](Fig. B6). 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).

[c3]In [c4]even-aged forest[c5]s [c6], all trees have the same height and receive full light (e.g., [c7] Fig. 5[c8], forest C). Such forests show a bell-shaped relationship between forest height and temperature sensitivity (Fig. 5 SI values for 100% available light depending on tree height). [c9]

[c13]In case of a forest consisting of trees with different heights [c14]smaller trees receive less light due to shading. Note that, even if trees reveive less light, the bell-shaped relationship between tree height and productivity persists (Fig. 5). Two cases will be discussed [c15](assuming identical LAI as forest C, Fig. 5 [c16]). [c17]In the first case all trees have not yet reached their maximal SI-values (Fig. 5, forest A,); and [c18]in the second case all trees [c19]already passed their maximal SI-values (Fig. 5, forest B). 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 (Fig. 5,[c20] tree 1). Hence, if maximal SI-Values are not reached, increasing height heterogeneity decreases SI-values of a forest.

[c1] ~~productivity~~
[c2] *Text added.*
[c3] ~~For instance, i~~
[c4] *Text added.*
[c5] *Text added.*
[c6] ~~of even-aged trees~~
[c7] ~~forest C in~~
[c8] *Text added.*
[c9] ~~Even if trees receive less light, the bell-shaped curve persists (see also Fig. 3)~~
[c13] ~~In a forest that consists~~
[c14] ~~(but similar LAI as an even-aged forest), smaller trees receive less light due to shading.~~
[c15] *Text added.*
[c16] *Text added.*
[c17] ~~first, a case in which~~
[c18] ~~second, a case in which~~
[c19] ~~are larger than~~
[c20] *Text added.*

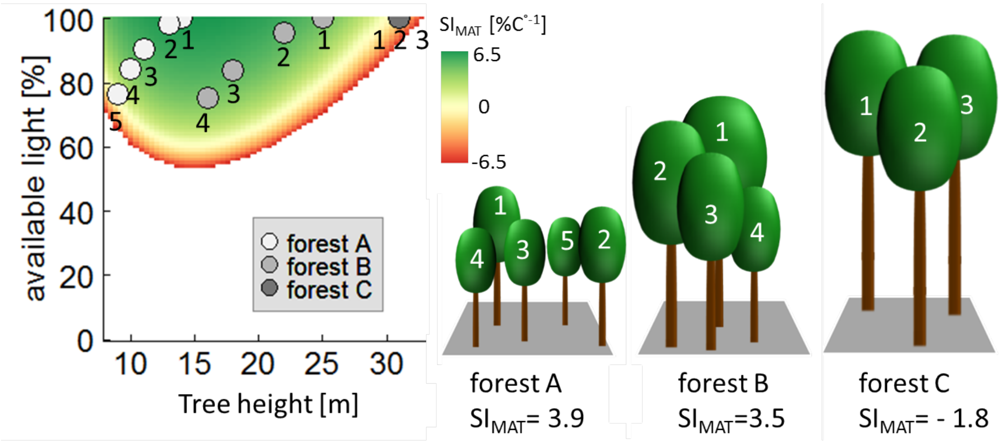


Figure 5. Analysis of SI_{MAT} values of single trees within three different forests. The diagram shows the calculated SI_{MAT} value of individual trees for every combination of tree height and available light [c10](for pinus sylvestris between SI_{MAT} [c11]-levels of 6.5 and - 6.5; other species show similar patterns). The dots indicate the different trees of the three forest examples [c12]The white dots belong to trees with the corresponding number of forest A, gray dots belong to the trees of forest B and dark gray dots belong to forest C. 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.

In forest B [c21](Fig. 5), SI-values of the shaded trees can be similar (or even higher) than the SI-value of the largest trees in the forest [c22](SI-values of tree 1 show similar levels as tree 2, 3 and 4 in forest B, Fig. 5). [c23]Hence, if maximal SI-values are passed, increasing tree height heterogeneity results in similar [c24] (or even [c25]more positive) temperature sensitivity levels compared to an even-aged forest [c26] trees [c27](an even-aged forest consisting only of trees similar to tree 1 of forest B in Fig. 5). These general considerations explain the change from low levels of height heterogeneity in young forests to a more heterogeneous structure [c1]in the analysis of those forests, which will benefit from increasing temperature (see Fig. 4 d).

3.1.2 The effect of species composition on temperature sensitivity

In this study, we use the new index Ω_{AWP} called [c2]species distribution index (Bohn and Huth, 2017). Ω_{AWP} [c3] is the ratio between current AWP and the highest possible AWP of the forest which can be reached due to shuffling of species identities. Its huge importance on forest temperature sensitivity might be illustrated by the following considerations: If species are

[c21] *Text added.*
[c22] *Text added.*
[c23] ~~SI-values of tree 1 show similar values to trees 2, 3 and 4. This~~
[c24] ~~to~~
[c25] ~~higher than~~
[c26] ~~which only consists of the largest~~
[c27] *Text added.*
[c1] ~~for the optimal forests analysis~~
[c2] ~~optimal species distribution~~
[c3] ~~describes the ratio of the realized to the maximal possible productivity, which can be reached by shuffling species identities in the given forest stand~~

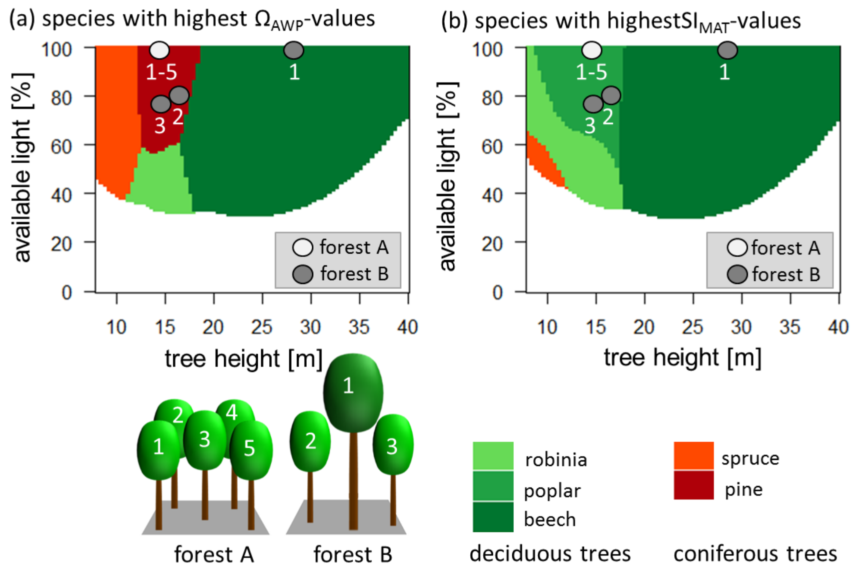


Figure 6. Graphic (a) shows which species [c1]have the highest productivity (Ω_{AWP} [c2] value of 1) under the current climate for different heights and different light conditions. Graphic (b) shows which species shows the highest [c3]increase of productivity due to rising temperatures for different 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[c4](A and B). The white dots belong to trees with the corresponding number of forest A. Note, that all trees have the same height and the same light, so all five dots are at the same place in the diagram. Gray dots belong to the corresponding trees with the same number of forest B.

unfavourably distributed within the forest (low Ω_{AWP}), the AWP of the forest is low [c4]. If AWP is low the forest will suffer from increasing temperatures, which results in negative slopes (ΔAWP / ΔT). These values are than divided by low AWP values (Equation 4), which results in large negative values of SI_{MAT} and SI_{Q95}. (See Appendix B5).

Increasing functional diversity (Rao's Q) [c5]stabilizes the forests' sensitivity to temperature. This corresponds to results of Morin et al. (2014) and the theoretical consideration of Yachi and Loreau (1999). The analysis of the 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 needle-leaf species. The highest functional diversity (Rao's Q) instead occurs in mixtures of deciduous and needle-leaf trees (Appendix B5 Fig. B7). As only two needle-leaf 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 consequence, mixtures with high Rao's Q values which mostly include both functional types react more poorly (Fig. 3; Appendix B5 Fig. B7).

[c4] ~~and in consequence, the SI values are low as well (see Appendix)~~

[c5] ~~has a stabilizing effect (in the case of mean temperature sensitivity)~~

We developed two diagrams that show the species with the highest temperature sensitivity and with the highest productivity for different conditions (available 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 to increasing temperatures obtain forests with high but not maximal Ω_{AWP} (Fig. 4). Additionally, deciduous trees benefit more than coniferous trees from rising temperatures (Fig. 6, Appendix B5, Fig. B7). 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).

4 Discussion

In this study, we analyse how temperature changes affect [c1]above-ground wood production (AWP) and quantify the effect of five different forest properties on this relationship. The change of [c2] AWP was investigated for 370,170 forest stands under 320 different climate [c3]time series. Our analysis shows a high influence of Ω_{AWP} and H_{max} on the temperature sensitivity of AWP. Further, for all successional stages of forests, we detect some forests with a specific [c4]set 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 [c5]climate sensitivity analysis ([c6]regarding temperature) on [c7] 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.[c8]Our approach includes only forest stands in which every tree in a forest has a positive productivity and enough space for its crown. Hence it is impossible for instance, that light demanding species grow below a closed canopy or forests are overcrowded. However, the data set include also a few very unusual stands structures or species combinations, which can not emerge in a natural system, but may result from disturbances or managment. 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 [c9]AWP with the FORMIND-model in temperate forests has been successfully compared to Eddy flux sites Rödig et al. (2017b), the national German forest inventory (Bohn and Huth, 2017), and European yield tables Bohn et al. (2014).

[c1] ~~forest productivity~~
[c2] ~~forest productivity~~
[c3] ~~scenarios~~
[c4] ~~value combination~~
[c5] ~~approach to investigate the effects of climate change~~
[c6] ~~here~~
[c7] ~~forest productivity~~
[c8] *Text added.*
[c9] ~~forest productivity~~

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 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.). [c10] 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 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 [c11]sets of time series. This guarantees no relationships between the target 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.[c1]6 climate scenarios IPCC (2013), this study focuses on temperature change. [c2]This RCP scenario predicts only small changes of annual precipitation levels for temperate regions. Hence, our approach focuses only impacts of change in temperature. However, this might be critical for analysis of strong temperature changes (e.g. RCP 8.5), which will result in an increase of droughts and changes in the annual temperature cycles and a strong change in CO_2. Such more complex scenarios should be analyzed in future studies. Further, we neglect the effect of time lags (e.g. bud building in the previous year). However, it is possible to extent the used time series to analyze the behaviour of the forest over longer time periods and study not only productivity, but also effects on regeneration or mortality.

[c3]To characterize the annual cycles of temperature we used two variables: mean annual temperature (MAT) and inter annual temperature amplitude (Q95). Both variables can be varied independently. In case of higher MAT we observe an elongation of the vegetation period. This leads to higher forest productivity (if other resources are not limiting (Luo, 2007) [c4]and explains why SI_{MAT} is often positive. However, warmer summer temperatures can also lead to a decline in wood production due to an increase in respiration. In case of increasing Q95, more days with extreme temperatures will occur in a year. Thus, an increase

[c10] ~~However, it would be possible to reconstruct a forest succession based on three forest factory by selecting forest stands in an appropriate order.~~

[c11] ~~scenarios~~

[c1] ~~5~~

[c2] ~~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.~~

[c3] ~~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 citep Luo et al. 2007. On the other hand, high temperatures increase respiration citep Piao et al. 2010 , resulting in higher respiration rates, especially in years with high intra-annual temperature amplitude (whereby MAT could stay constant).~~

[c4] *Text added.*

of 1 $°C^{-1}$ of Q95 will increase respiration more strongly compared to an increase of 1 $°C^{-1}$ of MAT. Hence, the increase of Q95 has normally negative effects on the productivity (negative SI values).

The temperature sensitivity values obtained here are in the same range as that found for temperate ecosystems in heating 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 Zealand, 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 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 Implications for forest management

[c1] Our findings might be relevant for future management strategies of temperate forests. Specifically, our new understanding of which species benefit most from rising temperatures (Fig 6), suggests possible strategies, e.g. replacing spruce monocultures with mixtures of deciduous trees. Further, based on the analysis of which forest structure benefits most from rising temperatures (Fig. 4, Fig 5, Fig 6), early stage even-aged forests should include mainly pioneer species. In the mature stage, we predict a positive effect of temperatures on wood production for a mixture of climax species including different tree sizes. These climax species could be planted below the canopy of the pioneer species in young forests. In our approach, we do not simulate the establishment of very young trees. However, during the conversion between these two forest types one big challenge might be the removal of the pioneer trees without damaging the young trees, which will build the mature forest.

4.3 Implications for global vegetation modelling

[c2] Most global vegetation models (DGVM) represent vegetation as fractional cover of different plant functional types within a grid cell (e.g. LPJ Sitch et al., 2003). [c3]Only a few global vegetation models include a more detailed representation of vegetation structure and functional diversity (Sato et al., 2007; Scheiter et al., 2013; Sakschewski et al., 2016). [c4]It would be interesting to perform the here presented analysis also with global vegetation models which include structure, to better understand the mechanisms driving the sensitivity of forest systems against climate change. Beside the global vegetation models, forest gap models, which have been restricted to local stands in the past are now able to simulate forest dynamics in regions or even entire continents (Seidl and Lexer, 2013; Rödig et al., 2017a). [c5]Studies using DGVMs or large scale forest gap models sim-

[c1] *Text added.*
[c2] *Text added.*
[c3] *Text added.*
[c4] *Text added.*
[c5] *Text added.*

ulate natural succession. Our analysis indicates that natural and managed (or disturbed) forest systems, which differ in forest structure, might react differently on climate change. Hence, we suggest considering forest structure in future analysis of global vegetation. Such information on forest structure might be derived from remote sensing.

5 Conclusions

[c1]The temperature sensitivity of wood production in temperate forests is influenced by forest structure and species diversity as our study showed. The species distribution index (Ω_{AWP}) and forest height seems to be the most important forest properties influencing temperature sensitivity.

Temperate forests that benefit most from temperature rise are those which consist of even-aged deciduous pioneer species in the case of young forests. Mature forests benefit most if tree height heterogeneity is large and the forest includes different deciduous climax species.

This study tries also to explain why certain forests types will decrease their productivityand others not. Our findings highlight the importance of forest structure for future studies investigating wood production under climate change.

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".

[c1] ~~The temperature sensitivity of above-ground wood production 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.~~

Appendix A: Additional information regarding methods and validation

A1 Climate data

The development of the 320 climate [c1]time series, is 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).

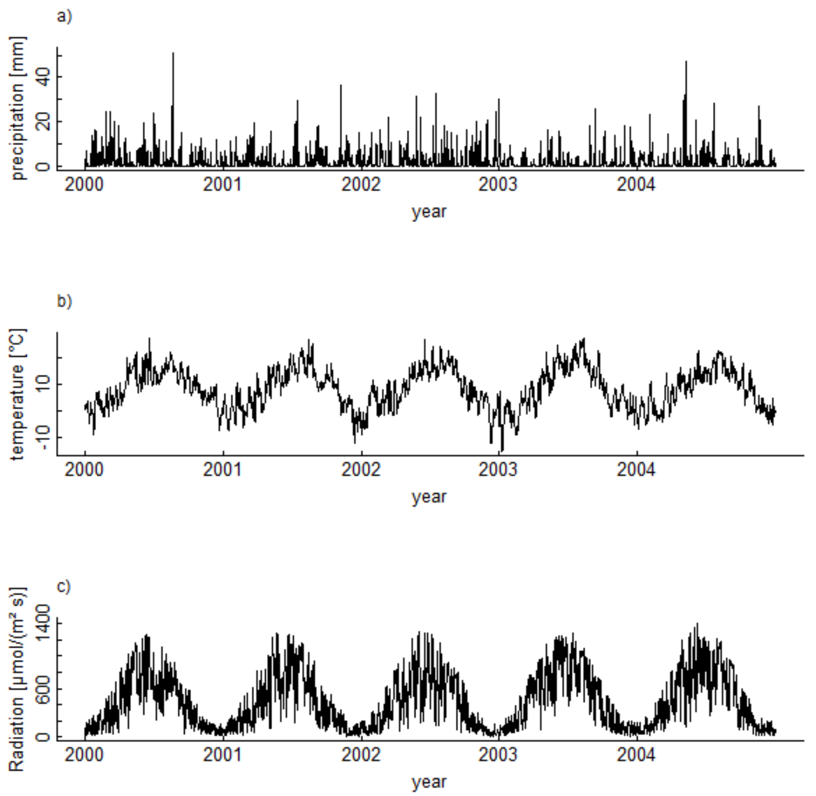


Figure A1. The climate time series measured at FLUXNET-station Hainich from 2000 to 2004 which are used to generate the 320 climate [c2]time series: (a) daily precipitation [mm], (b) daily air temperature [% °C $^{-1}$], (c) daily incoming radiation [photoactive photon flux density $\mu molm^{-1}s^{-1}$].

[c1] ~~scenarios~~

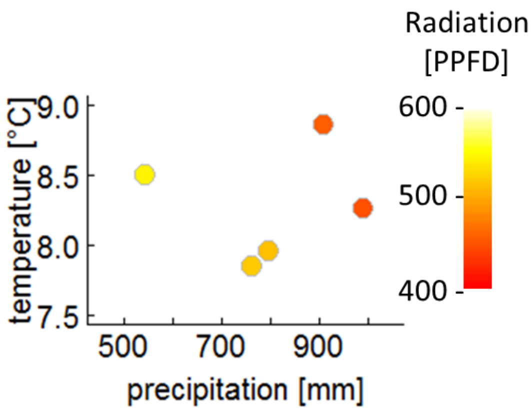


Figure A2. Mean annual temperature, [c3] annual precipitation [c4]sum and mean annual radiation of the five climate [c5]time series measured at Hainich station from 2000 to 2004.

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).

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} = [c1]species distribution index

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			

A3 Validation with the German forest inventory

We analyse the influence of forest structure on temperature sensitivity within the German forest inventory. We analyzed forest stands of beech monocultures and spruce monocultures. 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). 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 m). 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).

[c1]The comparison between the SI_{MAT}[c2]-estimation based on the German forest inventory with SI_{MAT}[c3] values of corresponding forests from the forest factory show a quite good agreement. However, the simulated SI_{MAT}[c4]-values of the forest factory slightly overestimate the sensitivity compared to the inventory-based values. The reason might be the difference in the methods as in case of the inventory we use basal area instead of LAI and altitude instead of temperature. Another reason could be, that in our approach the climate time series show relative high and regular precipitation. In the German forest inventory instead, warmer sites might exposed more often to water stress, which than reduces the SI-Values.

[c1] *Text added.*
[c2] *Text added.*
[c3] *Text added.*
[c4] *Text added.*

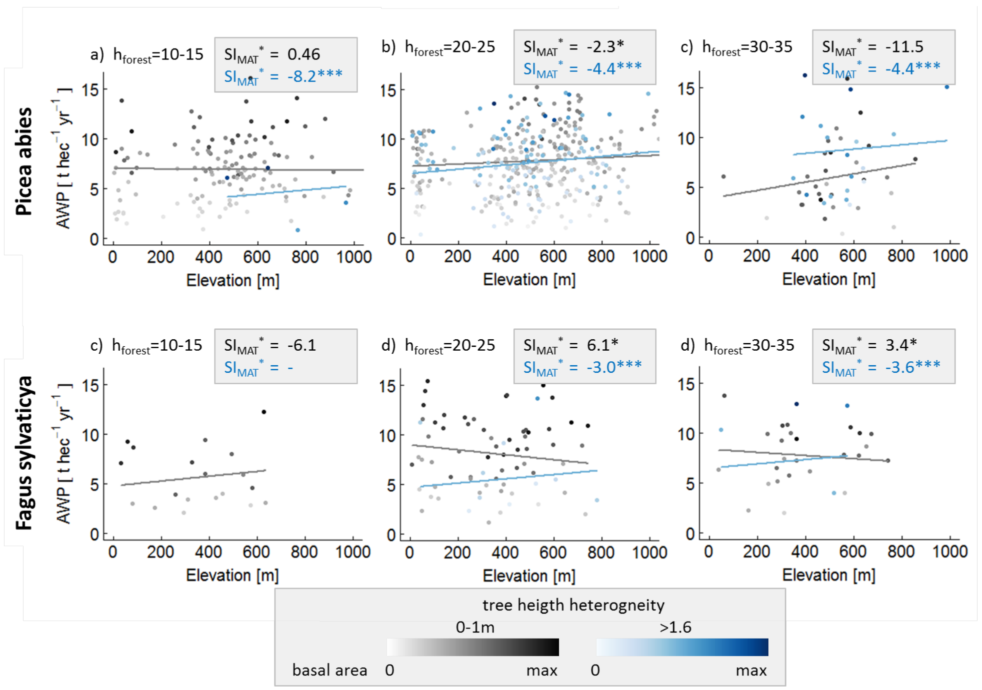


Figure A3. Analysis of the influence of forest structure on the relationship between elevation and above-ground wood production. Figure (a) - (c) are based on spruce monocultures and d)-e) are based on beech monocultures. For each species, forest stands are classified into three forest height classes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

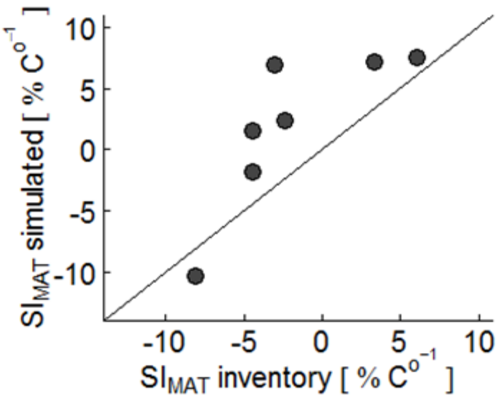


Figure A4. SI_{MAT}*-values derived from the BWI-analysis vs. SI_{MAT}-values derived from corresponding forest types of the forest factory. Only field data with p-values smaller 0.05 are analysed.

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 $^{-1}$ in case of SI_{MAT} (Fig. ref4Bf1a). [c1]This means that one forest increases it productivity by 8.5% due to an increase of the mean annual temperature by one $°C$. [c2]In case of the annual temperature amplitude, the best forest reduces its productivity by -0.5 $\% \, °C^{-1}$ (Fig. ref4Bf1b). The mean SI_{MAT} is 1.5 % °C $^{-1}$ and the interquartile range (iqr) ranges from 1.6 % °C $^{-1}$ 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 $^{-1}$.

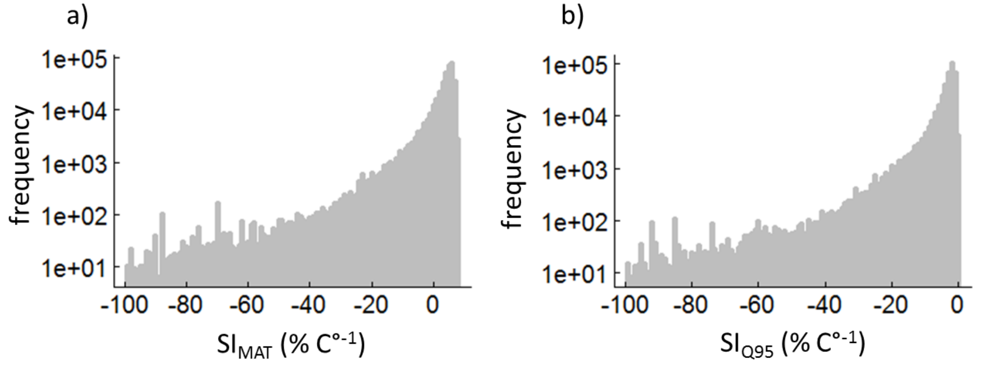


Figure B1. Frequency distribution of SI_{MAT}-values (a) and SI_{Q95}-values (b) of all forest stands.

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 relationship of input and target variables (Friedman, 2001). [c3]. [c4]The comparisons between SI values of the forest factory and predicted SI values (based on the five properties as input), show a very high agreement (Fig. B2 & B3[c5]). The optained vertical patterns for SI_{Mat} [c6]= 0 and SI_{Q95} [c7]= -6 are probably artefacts of the boosted regression tree algorithm.

[c1] *Text added.*

[c2] ~~and up to~~

[c3] ~~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)~~

[c4] *Text added.*

[c5] *Text added.*

[c6] *Text added.*

[c7] *Text added.*

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.

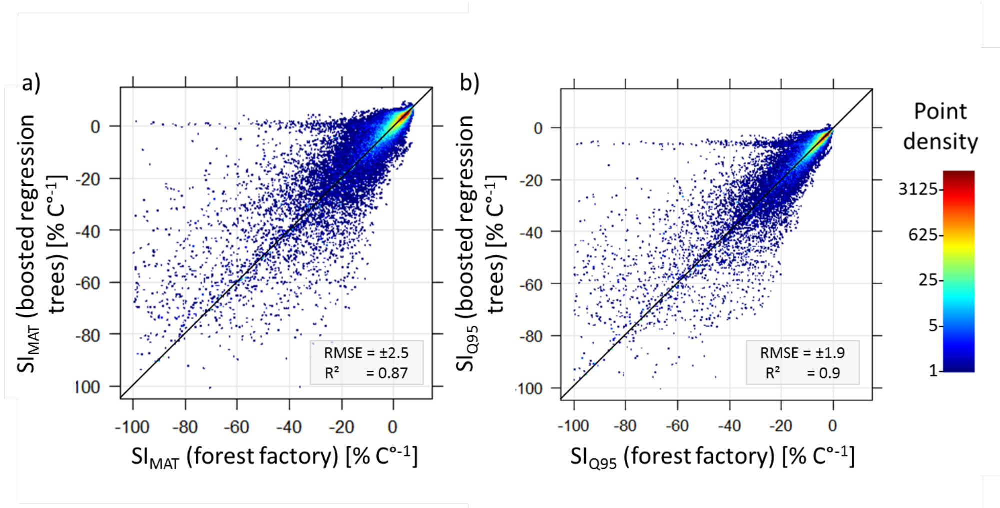


Figure B2. Comparisons of temperature sensitivity (SI_{MAT} and SI_{Q95}) based on Forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line.

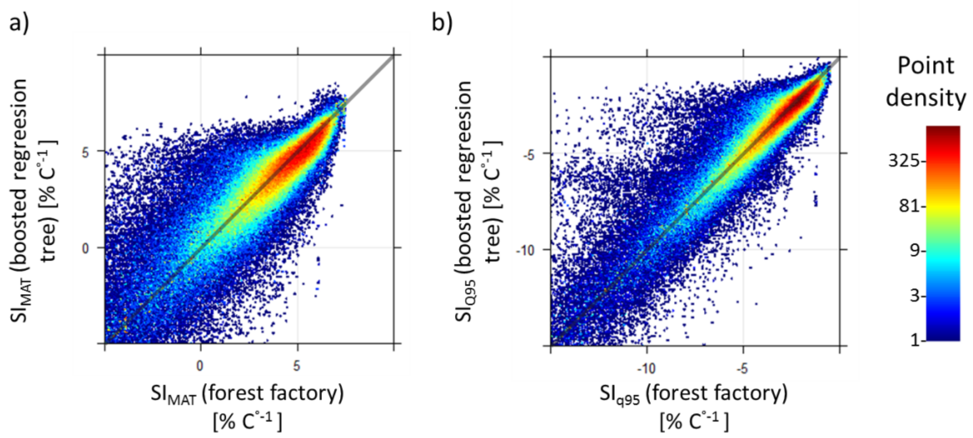


Figure B3. Comparison of temperature sensitivity calculations (SI_{MAT} and SI_{Q95}) based on the forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line. a) Contains 90% of the forest factory data set and b) contains 93% of the forest factory data set.

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

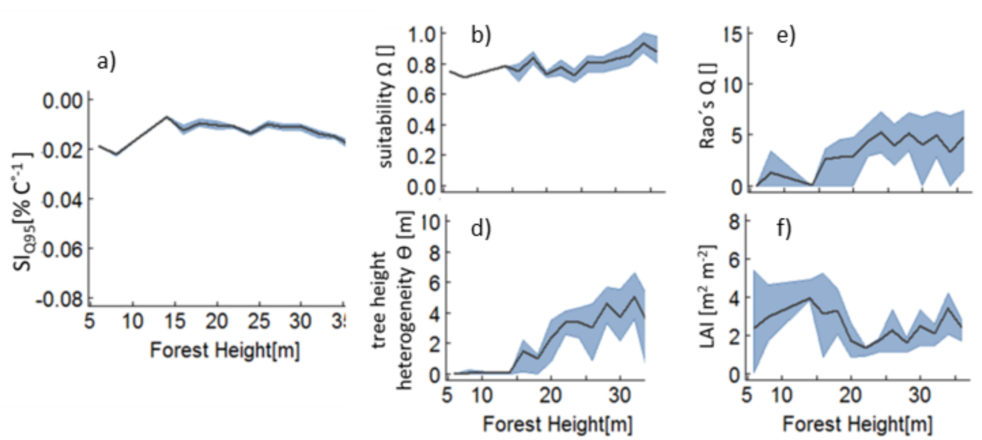
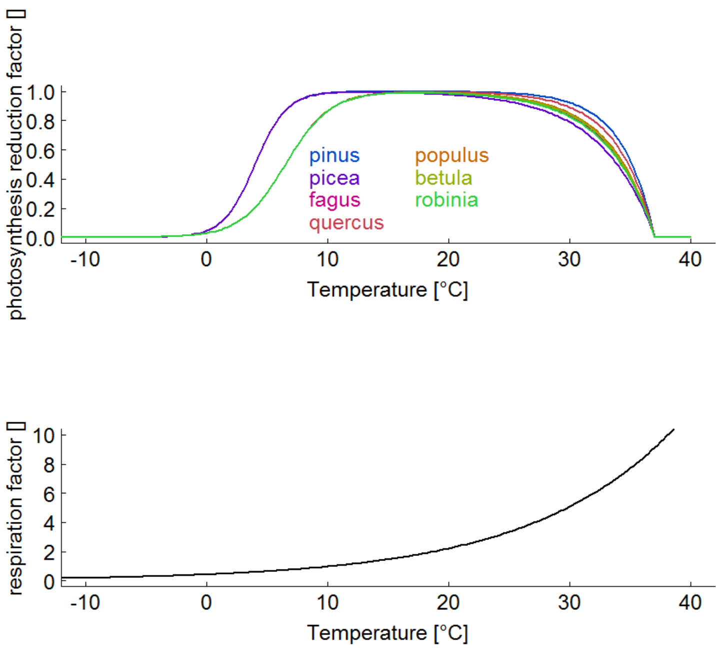


Figure B4. Analysis of those forests which lie above the 95% percentile of SI_{MAT}, depending on forest height. Lines indicate mean values of the subsamples and the gray bands indicate the inter quartile range. Figure a) shows the temperature sensitivity of productivity against forest height, analysing only Values above the 95% percentile b) to d) shows the change of the remaining forest properties within the subsamples.



h[!h!b]

Figure B5. 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.

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. B5 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. B5 a). In case of deciduous trees the length of the vegetation period [c1](leaf onset to fall) affects additionally the annual photoproduction (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[c2]; for instance, low ratio of maintenance respiration to photosynthesis (RMP) under full light in Fig. B6 b), the positive effect of temperature on photosynthesis causes an increase of AWP in [c3]some simulated years. If both rates show the same magnitude [c4](RMP under full light is closed to 1 in Fig. B6 b), higher temperatures increase respiration stronger than photoproduction (in most years)[c5], which result in a decrease of AWP.

[c1] *Text added.*
[c2] *Text added.*
[c3] ~~most~~
[c4] *Text added.*
[c5] *Text added.*

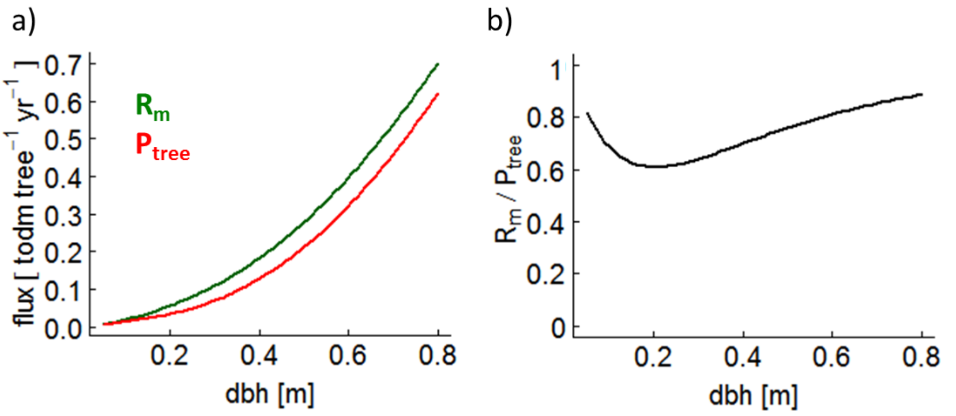


Figure B6. a) Photosynthesis (green) and maintenance respiration (red) rates of a single beech tree over stem diameter (dbh) under full light. b) The ratio between maintenance respiration and photosynthesis of the same beech tree.

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 [c1] calculate 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^{-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 (Fig. B7). Mixed forests with deciduous and needle leaf trees show lower values than the deciduous forests, but higher Rao's Q-values.

[c1] ~~build~~

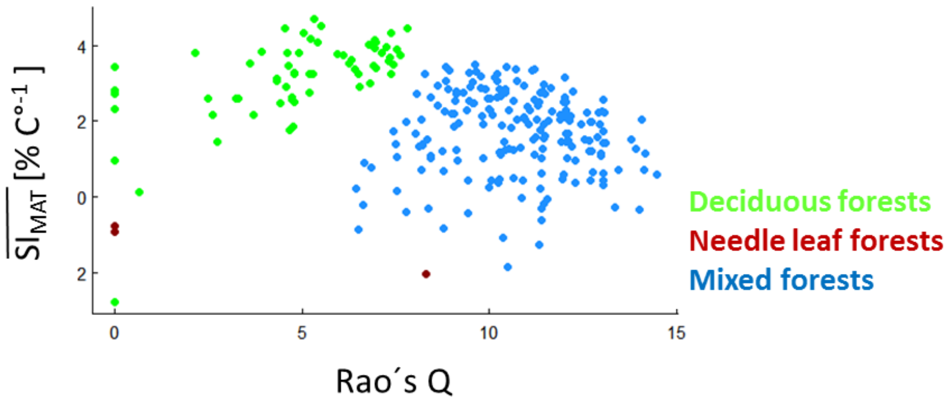


Figure B7. Rao's Q (with equal abundances) against $barSI_{MAT}$-values of all possible species mixtures (from the forest factory). The $barSI_{MAT}$-values are the average over all $SI_{h,l}$ values for all light-height combinations and with values larger than -7.5 % °C^{-1}. For mixtures, we assume 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.

Author contributions. F.J.B. F.M. and A.H. conceived of the study. F.J.B. implemented and analysed the simulation model and wrote the first draft of the manuscript. A.H. and F.M contributed to the text. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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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 [c1]show that some temperate forests increase their productivity, whereas others reduce their productivity. This study focus on how species composition and forest structure properties influences [c2]the temperature sensitivity of [c3]above-ground wood production (AWP). It further investigates, which forests will [c4]increase in their productivity the most with rising temperatures. 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 [c5]species distribution index (Ω_{AWP}). Ω_{AWP} quantifies [c6]how well species are distributed over the different forest layers regarding AWP. [c7]. We analyzed 370,170 forest stands, generated with a forest gap model. These forest stands [c8]cover a wide range of possible forest types. [c9]For each stand we estimate annual above-ground wood production and perform a climate sensitivity test based on 320 different climate time series (of one year length). The scenarios differ in mean annual temperature and annual temperature amplitude. Temperature sensitivity of [c10]wood production 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 that 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 [c11]heterogeneity is associated with a positive effect of temperature on [c12]wood production. During later successional stages, higher species diversity and larger tree height heterogeneity is an advantage.[c13]To archieve

[c1] ~~discovered~~
[c2] ~~this~~
[c3] ~~forest productivity~~
[c4] ~~rising temperatures increase productivity strongest~~
[c5] ~~optimal species distribution~~
[c6] ~~how well species are distributed within the forest structure regarding~~
[c7] ~~with the given environmental conditions of each single tree~~
[c8] ~~cover a large number of possible~~
[c9] ~~For each forest stand we estimate annual above-ground wood production under 320 climate scenarios (of one year length)~~
[c10] ~~forest productivity~~
[c11] ~~heterogeneity support~~
[c12] ~~forest productivity~~
[c13] *Text added.*

such a development, one could plant below the closed canopy of even-aged, pioneer trees a climx-species-rich understory that will build the the canopy of the mature forest. This study highlights that forest structure and species composition are both relevant [c14]in understanding the temperature sensitivity of [c15]wood production.

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1 Introduction

Climate change alters [c1]wood production by modifying [c2]the rates of photosynthesis and respiration rates of trees (Barber et al., 2000; Luo, 2007; Peñuelas and Filella, 2009; Reyer et al., 2014). 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). [c3]The carbon stock of forests and their role as carbon sink are therefore changing. These [c4]findings 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 [c5]foster the carbon sink function of forests (Spittlehouse and Stewart, 2004; Spittlehouse, 2005; Bonan, 2008).

[c6]Wood production is influenced by several factors [c7], such as CO_2 fertilization, nitrogen deposition, precipitation, and temperature. (Barford et al., 2001)[c8]. [c9] For instance, rising CO2 increases water use efficiency of forests (Keenan et al., 2013) [c10], which could compensate negative effects of climate change on European forest growth (whereas, with constant CO_2 at 350ppm, forest growth declines on several sites due to climate change - see Reyer et al. 2014). Another important process is the fertilization (De Vries et al., 2006, 2009)[c11]. Due to depositions of nitrogen in the second half of the last century wood production had increased in European forests (Solberg et al., 2009). However, 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). In the temperate biome, positive effects on [c12]wood production (Bontemps et al., 2010; Delpierre et al., 2009; Pan et al., 2013; McMahon et al., 2010, e.g.) as well as negative ones 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.

[c14] ~~to understand~~

[c15] ~~forest productivity~~

[c1] ~~forest growth~~

[c2] *Text added.*

[c3] *Text added.*

[c4] ~~observations~~

[c5] ~~to compensate for anthropogenic CO2-emissions~~

[c6] ~~Forest productivity~~

[c7] ~~Temperature can strongly alter forest productivity, in addition to other climate variables~~

[c8] ~~such as CO_2-fertilization or nitrogen deposition~~

[c9] *Text added.*

[c10] *Text added.*

[c11] *Text added.*

[c12] ~~forest productivity~~

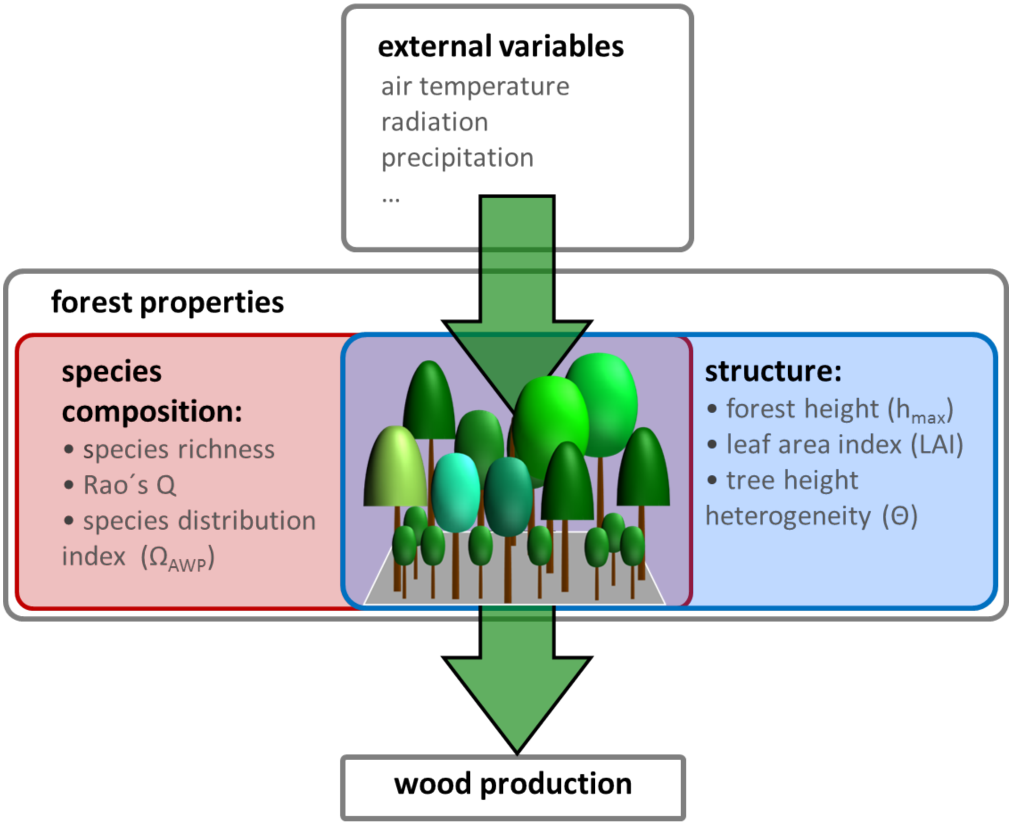


Figure 1. Overview of drivers influencing [c15]wood production. External variables in this study are temperature, radiation, and precipitation. Forest properties are divided into two groups: species composition properties (e.g., the Rao's Q as a measure of functional diversity and [c16]species distribution index Ω_{AWP}) and forest structure properties (e.g., forest height, leaf area index and tree height heterogeneity).

In addition to the influence of climate variables, [c13]wood production is also affected by internal forest properties. These properties can be grouped into two types: properties which describe forest structure, and those which describe 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, [c14]wood production often increases with the increasing number of species (Zhang et al., 2012; Vilà et al., 2007).

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 [c1]wood production 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 [c2]wood production. However, these studies include only a few forest properties and rarely

[c13] ~~forest productivity~~
[c14] ~~forest productivity~~
[c1] ~~forest productivity~~
[c2] ~~forest productivity~~

include [c3]properties related to both species composition and forest structure. Hence, it [c4]is unclear, how [c5]these forest properties influence [c6]wood production change due to temperature rise and which forests will benefit from rising temperatures.

As far as we know, there is no data set available[c1] that covers forests, differing in structure and diversity, under almost identical climatic conditions. Even if a larger number of forest stands [c2]were available, it would be difficult to manipulate for instance temperature while keeping all other climate variables constant. An alternative option to [c3]such field experiments analysis is offered by forest simulation models. Such models are able to estimate [c4]wood production under different climate conditions (Lasch 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 [c5]year time slices of a range of different future climates for 135 inventoried forest stands. There are also model-based studies, which systematically analyzed 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 [c6]large number of forest stands covering various forest structures and species composition[c7]s (for up to eight temperate tree species). Annual above-ground wood production (AWP) is then calculated for all forest stands based on climate [c8]time series. These [c9]time series 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) [c10]of which forest stands will benefit most from rising temperatures.

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). [c11]The forest factory generates 370,170 different forest stands (see section 2.1) and [c12]allows the estimat[c13]ion of above ground wood production (AWP) under various climate [c14]time series (see section 2.2). The 320 scenarios differ

[c3] ~~both properties of both types,~~
[c4] ~~remains~~
[c5] *Text added.*
[c6] ~~forest productivity~~
[c1] ~~, which~~
[c2] ~~would be~~
[c3] ~~field data~~
[c4] ~~forest productivity~~
[c5] ~~years into the future for~~
[c6] ~~huge~~
[c7] *Text added.*
[c8] ~~scenarios~~
[c9] ~~senarios~~
[c10] *Text added.*
[c11] ~~With this approach, we generate~~
[c12] *Text added.*
[c13] ~~e the~~
[c14] ~~scenarios~~

in mean annual 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 [c15]wood production 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 2.4). We analyse the influence of the five forest properties on temperature sensitivity using boosted regression trees (see section 2.5). Finally, we analyse which combination of forest properties results in the highest sensitivity values for different successional stages (see section 2.6).

2.1 The forest factory approach

The forest factory [c1] creates forest patches which is based on 15 different stem size distributions [c2]and 256 species mixtures.[c3]100 forests patches of each combination are built.

The stem size distributions cover a gradient from young to old and disturbed to undisturbed forests. Species mixtures include all possible combinations of [c4] *Pinus sylvestris*, *Picea abies*, *Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*, *Populus x canadensis*, *Betula pendula* and *Robinia pseudostuga*. [c5]We use the species parameter set and algorithms of the FORMIND-model version for temperate forests [c6] within the forest factory (Bohn et al., 2014; Fischer et al., 2016). [c7]To generate forest patches, we randomly choose trees from the stem size distribution, assign a species identity and plant them within a patch of $400m^2$[c8]size.

[c9]To place a tree within a patch the following rules must be meet: (i) [c10]there must be available enough space for crowns of every tree (ii) every tree [c11]in the forest must have a positive productivity under [c12]its environmental conditions (light, temperature, water). [c13]We use climate time series of the year 2007, measured at Hainich National Park, central Germany. We assume this time series as a typical example for a temperate year (in principle it possible to use climate data of every other location). In contrast to an artificially generated climate this climate is perfectly physically consistent (regarding light, air temperature and precipitation).

[c14]In a few cases not all species of the mixture could be placed within a patch by the algorithm, so we rejected such forests. We end up with 370,100 forest stands. For more details regarding the forest factory see Bohn and Huth (2017).

[c15] ~~forest productivity~~

[c1] ~~combines~~

[c2] ~~with~~

[c3] *Text added.*

[c4] ~~pine, spruce, beech, oak, ash, poplar, birch and robinia~~

[c5] ~~The~~

[c6] ~~are used~~

[c7] *Text added.*

[c8] *Text added.*

[c9] ~~The forest factory generates forest stands with a size of 400m2 using the following rules:~~

[c10] ~~space limit the maximal number of trees and~~

[c11] *Text added.*

[c12] ~~a typical temperate climate~~

[c13] ~~For a typical temperate climate, we employ a climate time series from the year 2007, measured at Hainich National Park in central Germany. presented a detailed description and discussion of the forest factory.~~

[c14] *Text added.*

2.2 The wood production

[c1]The calculation of above-ground wood production (AWP) of trees is based on algorithms of the model FORMIND (Bohn et al., 2014; Fischer et al., 2016). The [c2]wood production of a single tree is calculated as the difference between climate variables 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 [c3]the 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).

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

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)).

2.3 climate sensitivity

To generate a set of 320 annual climate [c4]time series, 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 temperature (see Appendix A1; Fig. A1)). We separated these time series into five distinct time series of one-year length. First, we increase or decrease the mean annual temperature of each year by adding or subtracting 0.5 °C steps between -1.5 °C and +2 °C. Second, we change the amplitude of the annual temperature cycle for these time series [c5]variation of each year. [c6]To do so, we modify the standard deviation of each year by 4% steps between -12 % and +16 %. We end up with five [c7]sets of climate times series (of one-year length) that differ in [c8]temperature, precipitation and radiation. Each [c9]of these five sets includes 64 time series, which differ only in temperature (see Appendix A1 , Fig. A2). 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

[c1] *Text added.*
[c2] ~~productivity (AWP)~~
[c3] *Text added.*
[c4] ~~scenarios~~
[c5] *Text added.*
[c6] ~~by modifying~~
[c7] ~~climate scenario sets~~
[c8] *Text added.*
[c9] *Text added.*

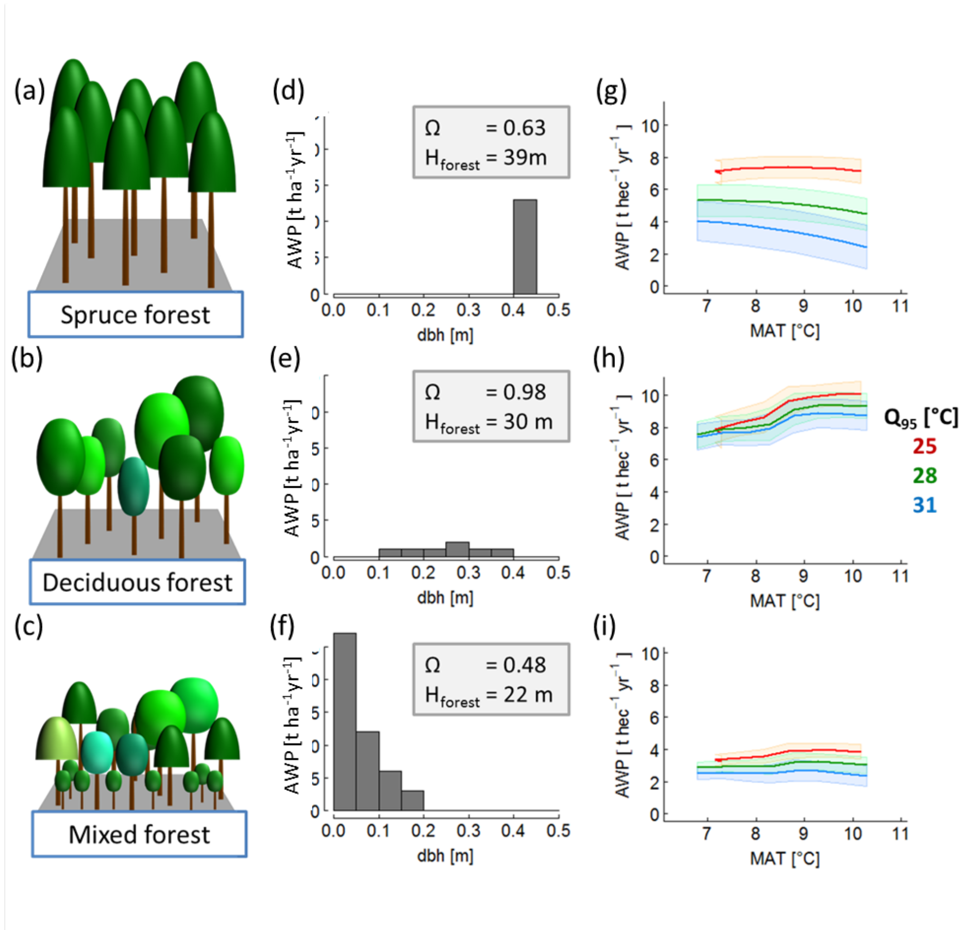


Figure 2. Overview of [c1]forest properties and resulting temperature sensitivity of above-ground wood production (AWP) of three exemplary forests: a) old even-aged spruce forest; b) mature deciduous forest; c) a quite young mixed species forest. [c2]The middle panel (subfigures d, e & f) shows the corresponding stem size distributions and inform about the forest height (the highest tree) and species distribution indexΩ_{AWP}[c3](which quantifies, how suitable a species distributed with in the forest structure regarding AWP). [c4] [c5]Each forest is treated with 320 climate time series: The last panel shows the AWP as a a function of mean annual temperature (MAT). The colours indicate different inter-annual amplitudes of the temperature (Q95) of the used time series. (The coloured bands show the standard deviation due to the variability of the five different time series, which exist for each combination of MAT and Q95).

daily temperature values of a given year. We [c10]do not model 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 [c11]wood production. Figure 2 (a-c) shows the above-ground wood production (AWP) for different annual temperatures for three different forest stands.

[c10] ~~exclude~~
[c11] ~~forest productivity~~

We analysed the sensitivity of every forest stand [c6]to temperature change by following the approach of Piao et al. (2010). For every forest stand, a general linear model is fitted relating [c7]wood production and the two temperature indices MAT and Q95, as well as the nuisance parameter year.

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

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

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

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

In our analysis we exclude all forests stands for which AWP [c1]turns negative if the temperature rises by 1 °C ([c2]This occures in 2% of all stands).

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 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).

2.4 Five forest properties to describe forest stands

We use three indices to describe the forest structure: leaf area index (LAI), [c3]maximum 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.

To describe species composition, we use Rao's Q and [c4]species distribution index (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 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

[c6] ~~against~~
[c7] ~~forest productivity~~
[c1] ~~is~~
[c2] *Text added.*
[c3] ~~maximal~~
[c4] ~~optimal species distribution~~

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).

2.5 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 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 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, 2015). This BRT-analysis was performed in the R-package gbm 2.1.1 (Ridgeway, 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 (1, 3 and 5) and the cross-validation (3-, 6- and 9-fold) assuming a Gaussian error structure [c1](the default setting). 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.

2.6 Finding the forest stands for different successional stages that benefit the most increasing temperatures

Here, we assume forest height as a proxy for the successional stage of a forest. In every height class, (H_{max}) we select those 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 ([c2]species distribution index (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

[c1] *Text added.*
[c2] ~~optimal species distribution~~

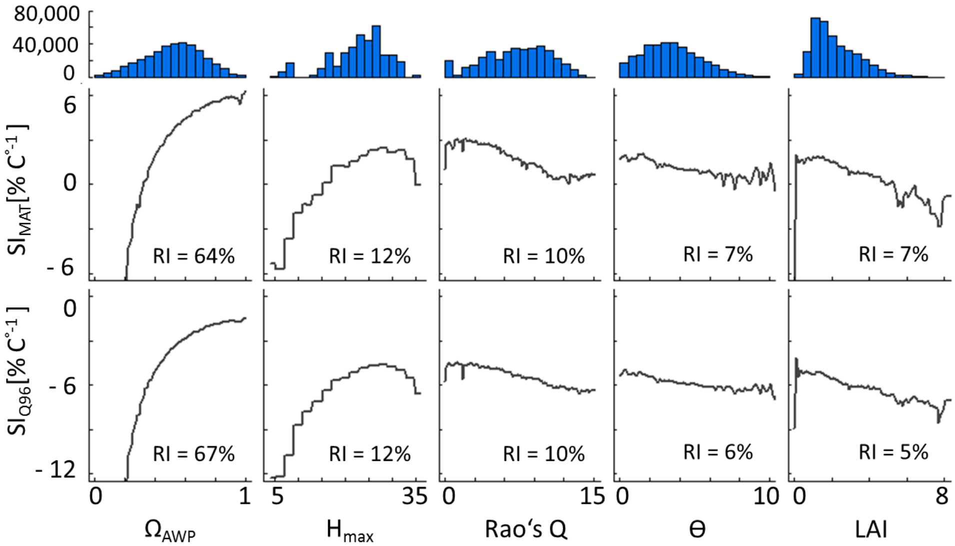


Figure 3. Partial dependency plots of the five forest properties Ω_{AWP} ([c1]species distribution index), forest height class h_{max}, Rao's Q (functional diversity), θ (tree height heterogeneity) and LAI (leaf area index) for SI_{MAT} (sensitivity against changes inthe mean annual temperature) and SI_{Q95} (sensitivity against changes in the annual temperature amplitude). [c2]Relative importance (RI) compares the influence of different input variables on the variability of a target variable. Histograms show the frequency of forest property values in the analysed data set. [c3]Note, a Ω_{AWP} is the ratio of the current AWP of a forest and the highest possible AWP optained by shuffling ony species identies without changing the forest structure.

[c3]time series. We than quantified the changes in productivity due to [c4] changes in [c5]MAT (SI_{MAT}) and [c6]Q95 (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).

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 $\pm$ 2.9 % °C $^{-1}$ (see Appendix B2 Fig. B3).The RMSE even decreases to $\pm$ 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 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 $\pm$ 1.1 % °C $^{-1}$ (see Appendix B2 Fig. B4).

[c3] ~~scenarios~~
[c4] ~~the~~
[c5] ~~mean annual temperature~~
[c6] ~~amplitude of inter-annual temperature~~

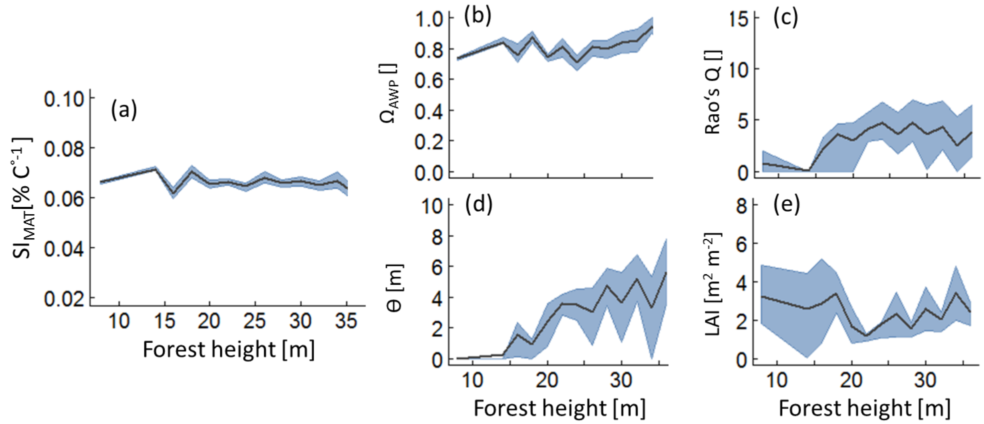


Figure 4. Analysis of those forests that show the highest 5% of the SI-values depending of forest height. Lines indicate mean values of the [c1]forest subsamples [c2]which includes the best 5% regarding SI_{MAT} [c3]of each hight class. [c4]The grey band indicates the inter quartile range. Figure a) shows temperature sensitivity of above-ground wood production [c5]over forest height, analysing only the best [c6]the forest subsample. b) to d) shows the change of the remaining forest properties within the [c7]forest subsamples (Ω_{AWP} = optimal species distribution; θ = tree height heterogeneity; LAI = leaf area index; Rao s Q quantiles functional diversity).

data set. 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 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}.

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 [c8]wood production. 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. [c9]Analysing 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

[c8] ~~forest productivity~~
[c9] ~~The analysis~~

change their character between young and intermediate forest heights. We obtain similar simulation patterns for SI_{Q95} (Appendix B3 Fig. B5).

3.1 Understanding the patterns

3.1.1 The influence of forest structure on temperature sensitivity

Forest structure affects [c1]wood production of the single trees in two ways. First, it determines the available light for each single tree and second, the size of trees influences photosynthesis and respiration rates [c2](Fig. B6). 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).

[c3]In [c4]even-aged forest[c5]s [c6], all trees have the same height and receive full light (e.g., [c7] Fig. 5[c8], forest C). Such forests show a bell-shaped relationship between forest height and temperature sensitivity (Fig. 5 SI values for 100% available light depending on tree height). [c9]

[c13]In case of a forest consisting of trees with different heights [c14]smaller trees receive less light due to shading. Note that, even if trees reveive less light, the bell-shaped relationship between tree height and productivity persists (Fig. 5). Two cases will be discussed [c15](assuming identical LAI as forest C, Fig. 5 [c16]). [c17]In the first case all trees have not yet reached their maximal SI-values (Fig. 5, forest A,); and [c18]in the second case all trees [c19]already passed their maximal SI-values (Fig. 5, forest B). 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 (Fig. 5,[c20] tree 1). Hence, if maximal SI-Values are not reached, increasing height heterogeneity decreases SI-values of a forest.

[c1] ~~productivity~~
[c2] *Text added.*
[c3] ~~For instance, i~~
[c4] *Text added.*
[c5] *Text added.*
[c6] ~~of even-aged trees~~
[c7] ~~forest C in~~
[c8] *Text added.*
[c9] ~~Even if trees receive less light, the bell-shaped curve persists (see also Fig. 3)~~
[c13] ~~In a forest that consists~~
[c14] ~~(but similar LAI as an even-aged forest), smaller trees receive less light due to shading.~~
[c15] *Text added.*
[c16] *Text added.*
[c17] ~~first, a case in which~~
[c18] ~~second, a case in which~~
[c19] ~~are larger than~~
[c20] *Text added.*

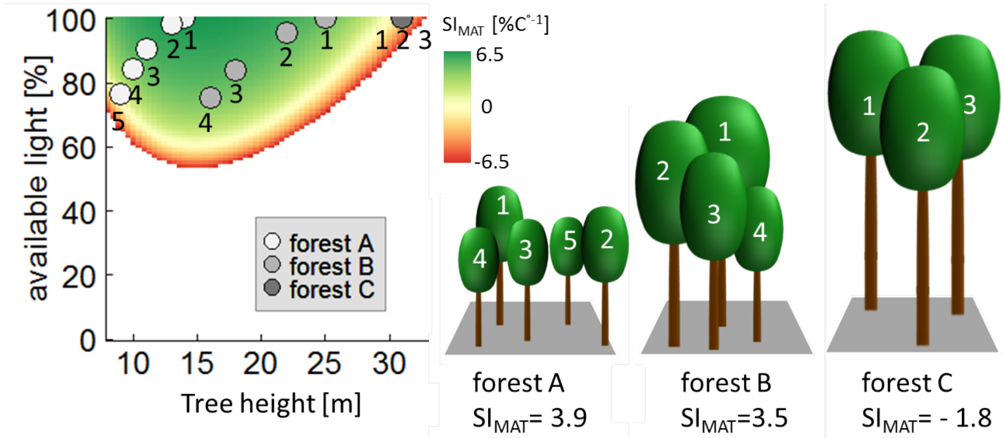


Figure 5. Analysis of SI_{MAT} values of single trees within three different forests. The diagram shows the calculated SI_{MAT} value of individual trees for every combination of tree height and available light [c10](for pinus sylvestris between SI_{MAT} [c11]-levels of 6.5 and - 6.5; other species show similar patterns). The dots indicate the different trees of the three forest examples [c12]The white dots belong to trees with the corresponding number of forest A, gray dots belong to the trees of forest B and dark gray dots belong to forest C. 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.

In forest B [c21](Fig. 5), SI-values of the shaded trees can be similar (or even higher) than the SI-value of the largest trees in the forest [c22](SI-values of tree 1 show similar levels as tree 2, 3 and 4 in forest B, Fig. 5). [c23]Hence, if maximal SI-values are passed, increasing tree height heterogeneity results in similar [c24] (or even [c25]more positive) temperature sensitivity levels compared to an even-aged forest [c26] trees [c27](an even-aged forest consisting only of trees similar to tree 1 of forest B in Fig. 5).

These general considerations explain the change from low levels of height heterogeneity in young forests to a more heterogeneous structure [c1]in the analysis of those forests, which will benefit from increasing temperature (see Fig. 4 d).

3.1.2 The effect of species composition on temperature sensitivity

In this study, we use the new index Ω_{AWP} called [c2]species distribution index (Bohn and Huth, 2017). Ω_{AWP} [c3] is the ratio between current AWP and the highest possible AWP of the forest which can be reached due to shuffling of species identities. Its huge importance on forest temperature sensitivity might be illustrated by the following considerations: If species are

[c21] *Text added.*
[c22] *Text added.*
[c23] ~~SI-values of tree 1 show similar values to trees 2, 3 and 4. This~~
[c24] ~~to~~
[c25] ~~higher than~~
[c26] ~~which only consists of the largest~~
[c27] *Text added.*
[c1] ~~for the optimal forests analysis~~
[c2] ~~optimal species distribution~~
[c3] ~~describes the ratio of the realized to the maximal possible productivity, which can be reached by shuffling species identities in the given forest stand~~

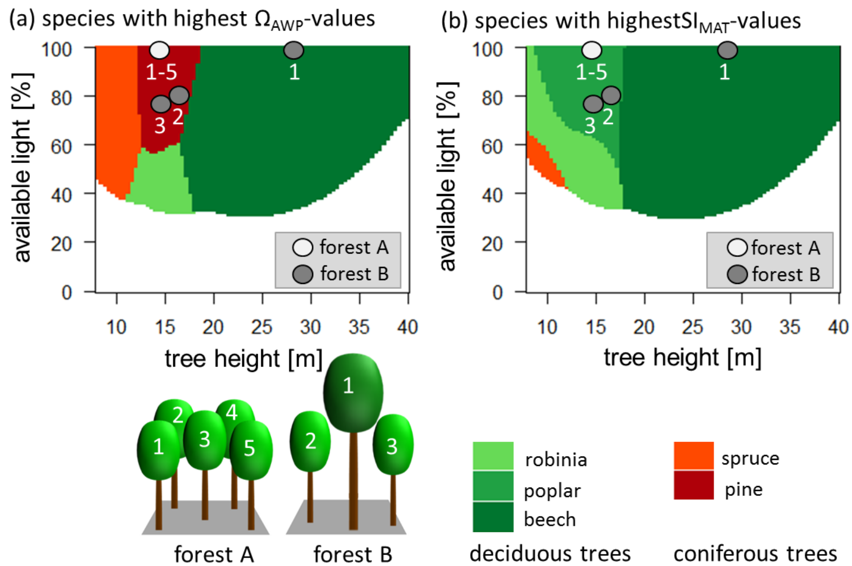


Figure 6. Graphic (a) shows which species [c1]have the highest productivity (Ω_{AWP} [c2] value of 1) under the current climate for different heights and different light conditions. Graphic (b) shows which species shows the highest [c3]increase of productivity due to rising temperatures for different 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[c4](A and B). The white dots belong to trees with the corresponding number of forest A. Note, that all trees have the same height and the same light, so all five dots are at the same place in the diagram. Gray dots belong to the corresponding trees with the same number of forest B.

unfavourably distributed within the forest (low Ω_{AWP}), the AWP of the forest is low [c4]. If AWP is low the forest will suffer from increasing temperatures, which results in negative slopes (ΔAWP / ΔT). These values are than divided by low AWP values (Equation 4), which results in large negative values of SI_{MAT} and SI_{Q95}. (See Appendix B5).

Increasing functional diversity (Rao's Q) [c5]stabilizes the forests' sensitivity to temperature. This corresponds to results of Morin et al. (2014) and the theoretical consideration of Yachi and Loreau (1999). The analysis of the 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 needle-leaf species. The highest functional diversity (Rao's Q) instead occurs in mixtures of deciduous and needle-leaf trees (Appendix B5 Fig. B7). As only two needle-leaf 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 consequence, mixtures with high Rao's Q values which mostly include both functional types react more poorly (Fig. 3; Appendix B5 Fig. B7).

[c4] ~~and in consequence, the SI values are low as well (see Appendix)~~

[c5] ~~has a stabilizing effect (in the case of mean temperature sensitivity)~~

We developed two diagrams that show the species with the highest temperature sensitivity and with the highest productivity for different conditions (available 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 to increasing temperatures obtain forests with high but not maximal Ω_{AWP} (Fig. 4). Additionally, deciduous trees benefit more than coniferous trees from rising temperatures (Fig. 6, Appendix B5, Fig. B7). 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).

4 Discussion

In this study, we analyse how temperature changes affect [c1]above-ground wood production (AWP) and quantify the effect of five different forest properties on this relationship. The change of [c2] AWP was investigated for 370,170 forest stands under 320 different climate [c3]time series. Our analysis shows a high influence of Ω_{AWP} and H_{max} on the temperature sensitivity of AWP. Further, for all successional stages of forests, we detect some forests with a specific [c4]set 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 [c5]climate sensitivity analysis ([c6]regarding temperature) on [c7] 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.[c8]Our approach includes only forest stands in which every tree in a forest has a positive productivity and enough space for its crown. Hence it is impossible for instance, that light demanding species grow below a closed canopy or forests are overcrowded. However, the data set include also a few very unusual stands structures or species combinations, which can not emerge in a natural system, but may result from disturbances or managment. 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 [c9]AWP with the FORMIND-model in temperate forests has been successfully compared to Eddy flux sites Rödig et al. (2017b), the national German forest inventory (Bohn and Huth, 2017), and European yield tables Bohn et al. (2014).

[c1] ~~forest productivity~~
[c2] ~~forest productivity~~
[c3] ~~scenarios~~
[c4] ~~value combination~~
[c5] ~~approach to investigate the effects of climate change~~
[c6] ~~here~~
[c7] ~~forest productivity~~
[c8] *Text added.*
[c9] ~~forest productivity~~

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 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.). [c10] 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 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 [c11]sets of time series. This guarantees no relationships between the target 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.[c1]6 climate scenarios IPCC (2013), this study focuses on temperature change. [c2]This RCP scenario predicts only small changes of annual precipitation levels for temperate regions. Hence, our approach focuses only impacts of change in temperature. However, this might be critical for analysis of strong temperature changes (e.g. RCP 8.5), which will result in an increase of droughts and changes in the annual temperature cycles and a strong change in CO_2. Such more complex scenarios should be analyzed in future studies. Further, we neglect the effect of time lags (e.g. bud building in the previous year). However, it is possible to extent the used time series to analyze the behaviour of the forest over longer time periods and study not only productivity, but also effects on regeneration or mortality.

[c3]To characterize the annual cycles of temperature we used two variables: mean annual temperature (MAT) and inter annual temperature amplitude (Q95). Both variables can be varied independently. In case of higher MAT we observe an elongation of the vegetation period. This leads to higher forest productivity (if other resources are not limiting (Luo, 2007) [c4]and explains why SI_{MAT} is often positive. However, warmer summer temperatures can also lead to a decline in wood production due to an increase in respiration. In case of increasing Q95, more days with extreme temperatures will occur in a year. Thus, an increase

[c10] ~~However, it would be possible to reconstruct a forest succession based on three forest factory by selecting forest stands in an appropriate order.~~

[c11] ~~scenarios~~

[c1] ~~5~~

[c2] ~~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.~~

[c3] ~~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 citep Luo et al. 2007. On the other hand, high temperatures increase respiration citep Piao et al. 2010 , resulting in higher respiration rates, especially in years with high intra-annual temperature amplitude (whereby MAT could stay constant).~~

[c4] *Text added.*

of 1 $°C^{-1}$ of Q95 will increase respiration more strongly compared to an increase of 1 $°C^{-1}$ of MAT. Hence, the increase of Q95 has normally negative effects on the productivity (negative SI values).

The temperature sensitivity values obtained here are in the same range as that found for temperate ecosystems in heating experiments (Lu et al., 2013, 4.4 ± 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 Zealand, 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 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 Implications for forest management

[c1] Our findings might be relevant for future management strategies of temperate forests. Specifically, our new understanding of which species benefit most from rising temperatures (Fig 6), suggests possible strategies, e.g. replacing spruce monocultures with mixtures of deciduous trees. Further, based on the analysis of which forest structure benefits most from rising temperatures (Fig. 4, Fig 5, Fig 6), early stage even-aged forests should include mainly pioneer species. In the mature stage, we predict a positive effect of temperatures on wood production for a mixture of climax species including different tree sizes. These climax species could be planted below the canopy of the pioneer species in young forests. In our approach, we do not simulate the establishment of very young trees. However, during the conversion between these two forest types one big challenge might be the removal of the pioneer trees without damaging the young trees, which will build the mature forest.

4.3 Implications for global vegetation modelling

[c2] Most global vegetation models (DGVM) represent vegetation as fractional cover of different plant functional types within a grid cell (e.g. LPJ Sitch et al., 2003). [c3] Only a few global vegetation models include a more detailed representation of vegetation structure and functional diversity (Sato et al., 2007; Scheiter et al., 2013; Sakschewski et al., 2016). [c4] It would be interesting to perform the here presented analysis also with global vegetation models which include structure, to better understand the mechanisms driving the sensitivity of forest systems against climate change. Beside the global vegetation models, forest gap models, which have been restricted to local stands in the past are now able to simulate forest dynamics in regions or even entire continents (Seidl and Lexer, 2013; Rödig et al., 2017a). [c5] Studies using DGVMs or large scale forest gap models sim-

[c1] *Text added.*
[c2] *Text added.*
[c3] *Text added.*
[c4] *Text added.*
[c5] *Text added.*

ulate natural succession. Our analysis indicates that natural and managed (or disturbed) forest systems, which differ in forest structure, might react differently on climate change. Hence, we suggest considering forest structure in future analysis of global vegetation. Such information on forest structure might be derived from remote sensing.

5 Conclusions

[c1]The temperature sensitivity of wood production in temperate forests is influenced by forest structure and species diversity as our study showed. The species distribution index (Ω_{AWP}) and forest height seems to be the most important forest properties influencing temperature sensitivity.

Temperate forests that benefit most from temperature rise are those which consist of even-aged deciduous pioneer species in the case of young forests. Mature forests benefit most if tree height heterogeneity is large and the forest includes different deciduous climax species.

This study tries also to explain why certain forests types will decrease their productivityand others not. Our findings highlight the importance of forest structure for future studies investigating wood production under climate change.

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".

[c1] ~~The temperature sensitivity of above-ground wood production 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.~~

Appendix A: Additional information regarding methods and validation

A1 Climate data

The development of the 320 climate [c1]time series, is 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).

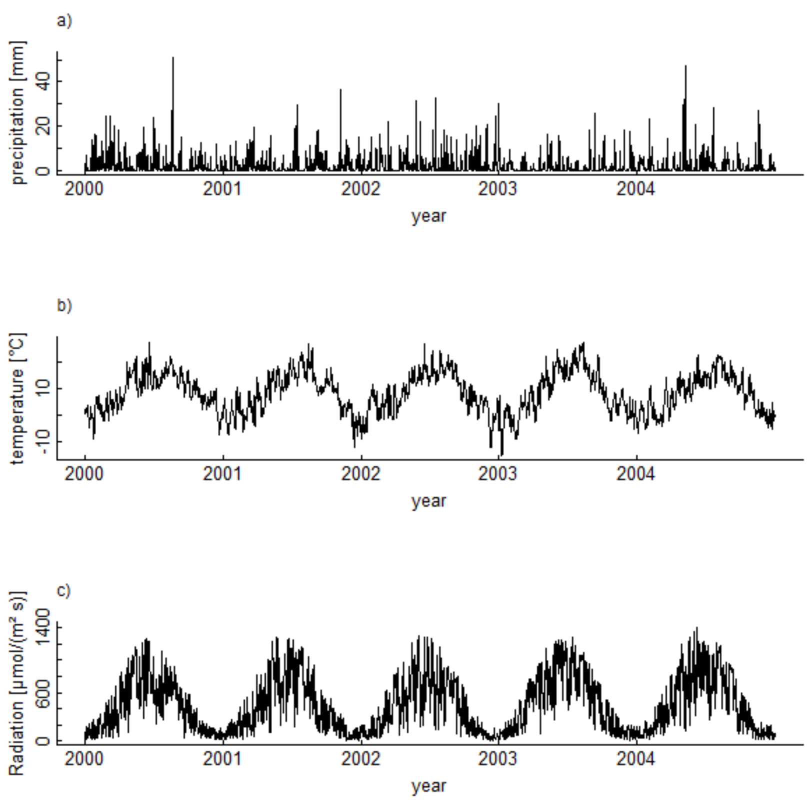


Figure A1. The climate time series measured at FLUXNET-station Hainich from 2000 to 2004 which are used to generate the 320 climate [c2]time series: (a) daily precipitation [mm], (b) daily air temperature [% °C $^{-1}$], (c) daily incoming radiation [photoactive photon flux density $\mu molm^{-1}s^{-1}$].

[c1] ~~scenarios~~

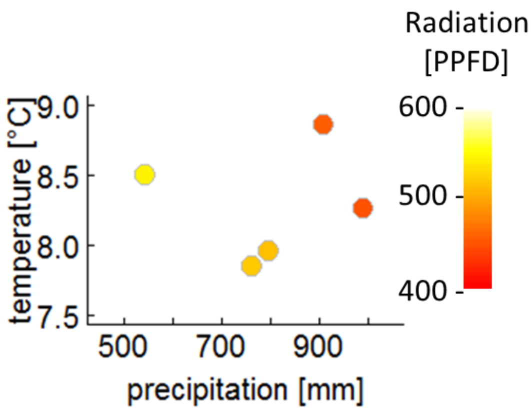


Figure A2. Mean annual temperature, [c3] annual precipitation [c4]sum and mean annual radiation of the five climate [c5]time series measured at Hainich station from 2000 to 2004.

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).

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} = [c1]species distribution index

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			

A3 Validation with the German forest inventory

We analyse the influence of forest structure on temperature sensitivity within the German forest inventory. We analyzed forest stands of beech monocultures and spruce monocultures. 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). 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 m). 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).

[c1]The comparison between the SI_{MAT}[c2]-estimation based on the German forest inventory with SI_{MAT}[c3] values of corresponding forests from the forest factory show a quite good agreement. However, the simulated SI_{MAT}[c4]-values of the forest factory slightly overestimate the sensitivity compared to the inventory-based values. The reason might be the difference in the methods as in case of the inventory we use basal area instead of LAI and altitude instead of temperature. Another reason could be, that in our approach the climate time series show relative high and regular precipitation. In the German forest inventory instead, warmer sites might exposed more often to water stress, which than reduces the SI-Values.

[c1] *Text added.*
[c2] *Text added.*
[c3] *Text added.*
[c4] *Text added.*

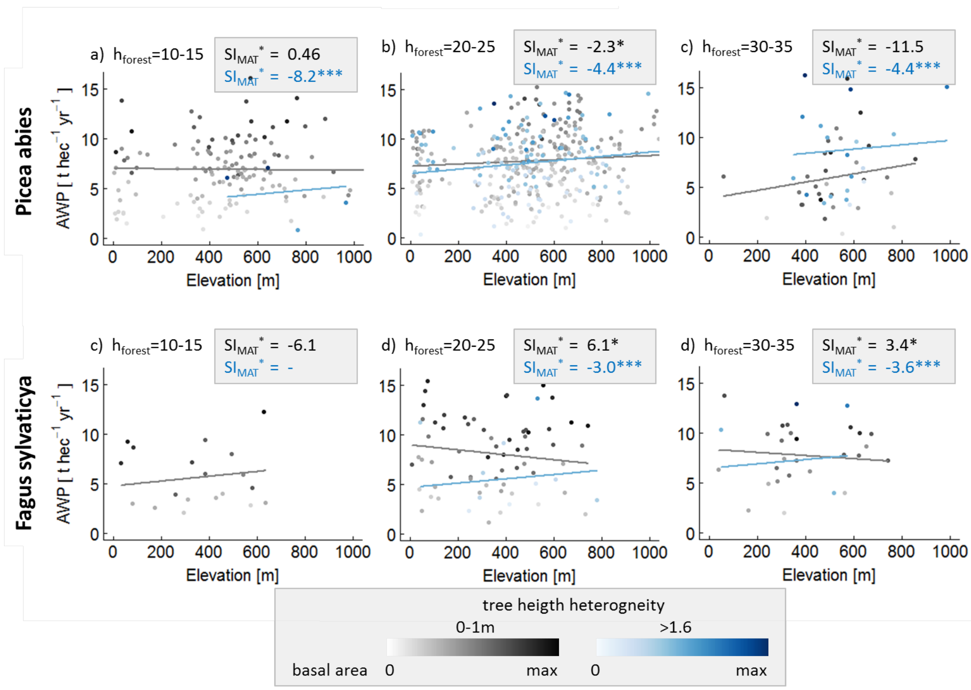


Figure A3. Analysis of the influence of forest structure on the relationship between elevation and above-ground wood production. Figure (a) - (c) are based on spruce monocultures and d)-e) are based on beech monocultures. For each species, forest stands are classified into three forest height classes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

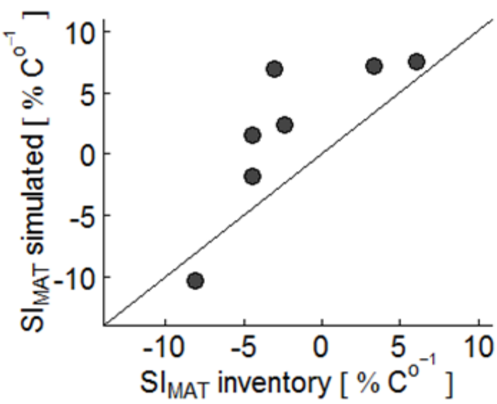


Figure A4. SI_{MAT}*-values derived from the BWI-analysis vs. SI_{MAT}-values derived from corresponding forest types of the forest factory. Only field data with p-values smaller 0.05 are analysed.

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} in case of SI_{MAT} (Fig. ref4Bf1a). [c1]This means that one forest increases it productivity by 8.5% due to an increase of the mean annual temperature by one $^{\circ}C$. [c2]In case of the annual temperature amplitude, the best forest reduces its productivity by -0.5 $\% \, ^{\circ}C^{-1}$ (Fig. ref4Bf1b). The mean SI_{MAT} is 1.5 % °C^{-1} and the interquartile range (iqr) ranges from 1.6 % °C^{-1} 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}.

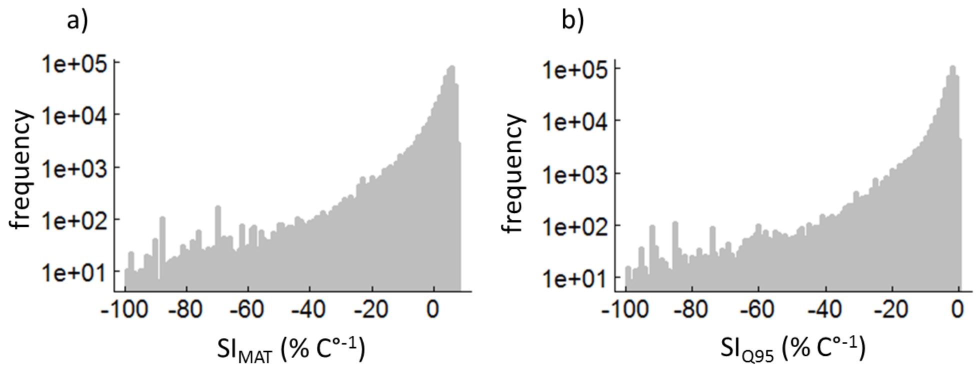


Figure B1. Frequency distribution of SI_{MAT}-values (a) and SI_{Q95}-values (b) of all forest stands.

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 relationship of input and target variables (Friedman, 2001). [c3]. [c4]The comparisons between SI values of the forest factory and predicted SI values (based on the five properties as input), show a very high agreement (Fig. B2 & B3[c5]). The optained vertical patterns for SI_{Mat} [c6]= 0 and SI_{Q95} [c7]= -6 are probably artefacts of the boosted regression tree algorithm.

[c1] *Text added.*
[c2] ~~and up to~~
[c3] ~~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)~~
[c4] *Text added.*
[c5] *Text added.*
[c6] *Text added.*
[c7] *Text added.*

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.

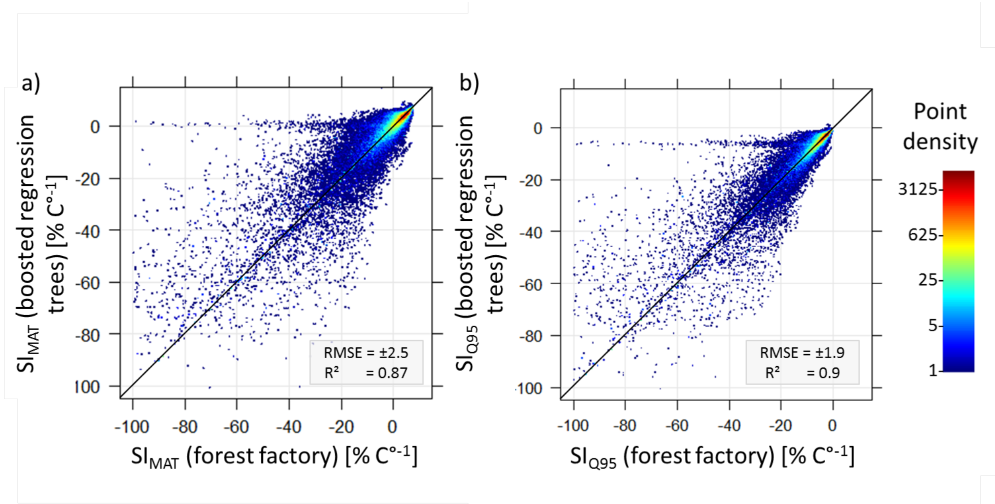


Figure B2. Comparisons of temperature sensitivity (SI_{MAT} and SI_{Q95}) based on Forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line.

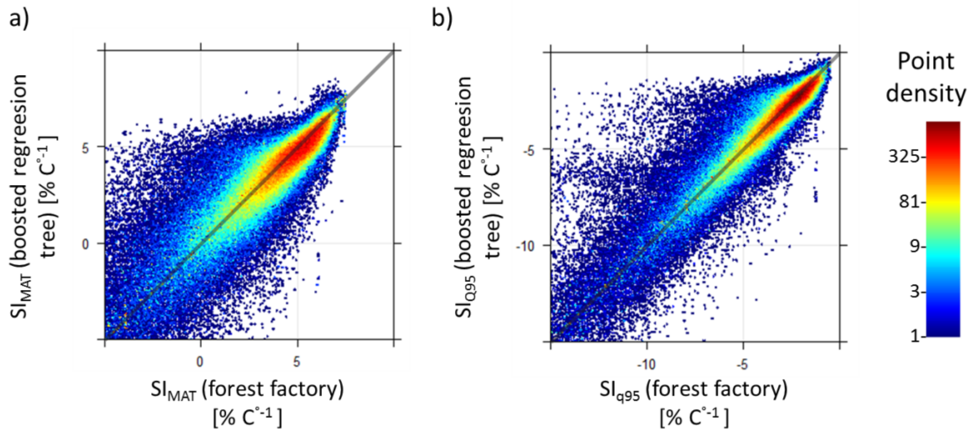


Figure B3. Comparison of temperature sensitivity calculations (SI_{MAT} and SI_{Q95}) based on the forest factory and boosted regression tree model. Colours indicate point density. Diagonal is the 1:1 line. a) Contains 90% of the forest factory data set and b) contains 93% of the forest factory data set.

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

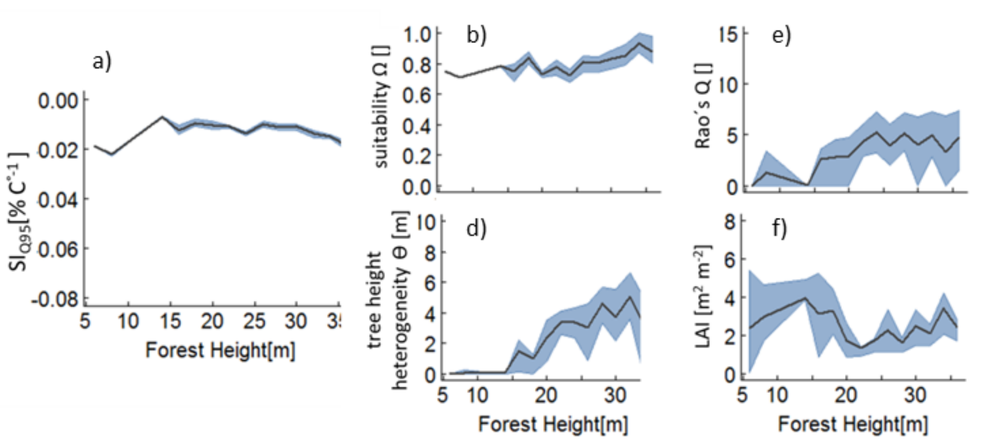
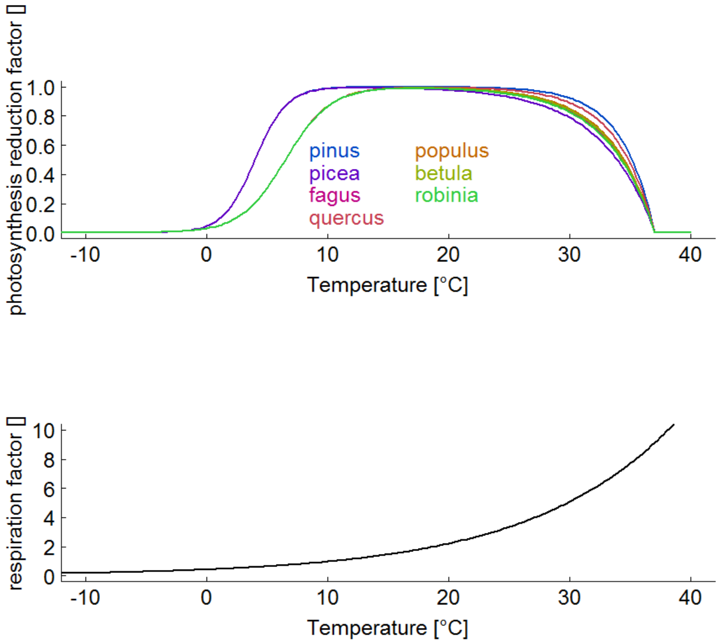


Figure B4. Analysis of those forests which lie above the 95% percentile of SI_{MAT}, depending on forest height. Lines indicate mean values of the subsamples and the gray bands indicate the inter quartile range. Figure a) shows the temperature sensitivity of productivity against forest height, analysing only Values above the 95% percentile b) to d) shows the change of the remaining forest properties within the subsamples.



h[!h!b]

Figure B5. 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.

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. B5 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. B5 a). In case of deciduous trees the length of the vegetation period [c1](leaf onset to fall) affects additionally the annual photoproduction (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[c2]; for instance, low ratio of maintenance respiration to photosynthesis (RMP) under full light in Fig. B6 b), the positive effect of temperature on photosynthesis causes an increase of AWP in [c3]some simulated years. If both rates show the same magnitude [c4](RMP under full light is closed to 1 in Fig. B6 b), higher temperatures increase respiration stronger than photoproduction (in most years)[c5], which result in a decrease of AWP.

[c1] *Text added.*
[c2] *Text added.*
[c3] ~~most~~
[c4] *Text added.*
[c5] *Text added.*

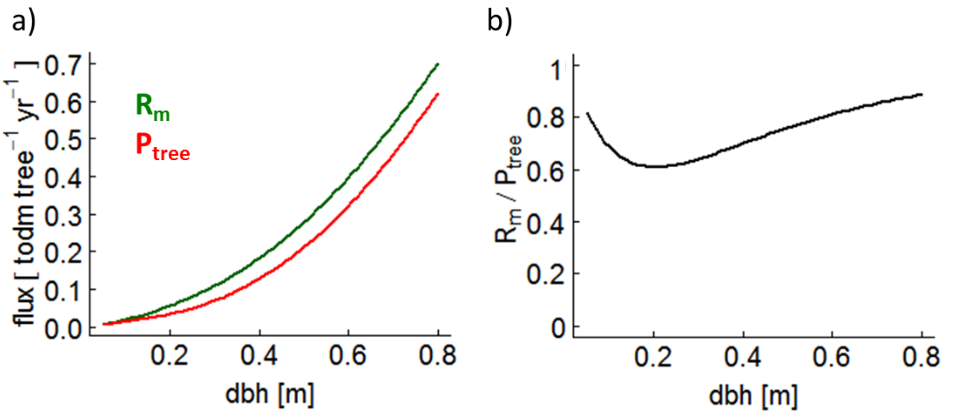


Figure B6. a) Photosynthesis (green) and maintenance respiration (red) rates of a single beech tree over stem diameter (dbh) under full light. b) The ratio between maintenance respiration and photosynthesis of the same beech tree.

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 [c1]calculate 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^{-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 (Fig. B7). Mixed forests with deciduous and needle leaf trees show lower values than the deciduous forests, but higher Rao's Q-values.

[c1] ~~build~~

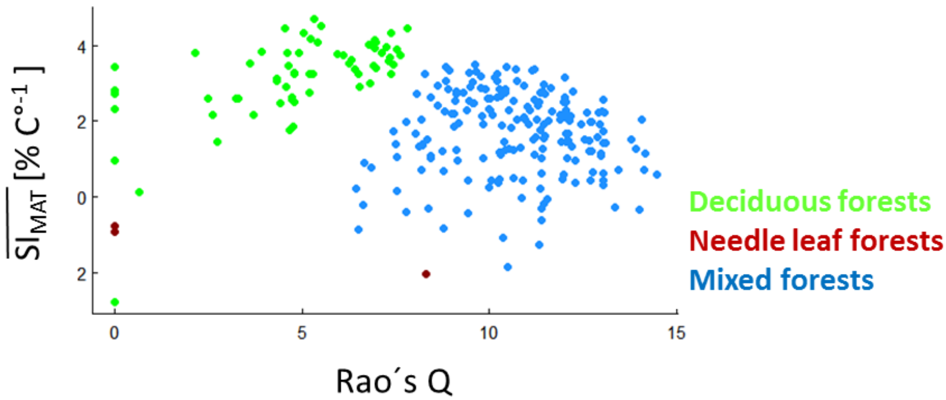


Figure B7. Rao's Q (with equal abundances) against $barSI_{MAT}$-values of all possible species mixtures (from the forest factory). The $barSI_{MAT}$-values are the average over all $SI_{h,l}$ values for all light-height combinations and with values larger than -7.5 % °C^{-1}. For mixtures, we assume 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.

Author contributions. F.J.B. F.M. and A.H. conceived of the study. F.J.B. implemented and analysed the simulation model and wrote the first draft of the manuscript. A.H. and F.M contributed to the text. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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