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Forest Productivity Under Environmental Change—a Review of Stand-Scale Modeling Studies

Christopher Reyer [1]

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Abstract Climate change, including increasing atmospheric CO_2 concentrations ([CO_2]), nitrogen deposition, and recovery from past management have led to changes in forest productivity in many parts of the world. Process-based forest models have been widely used to project productivity changes under changing environmental conditions into the future. Based on a review of published simulation results from a large number of process-based models, a synthesis of impacts of environmental change on forest productivity and carbon pools is presented. This synthesis shows that most stand-scale process-based model studies have been carried out in temperate and boreal forests, focusing mostly on monospecific forests with tree species that are relevant for forestry and on analyses of the impacts of climate change and of increasing [CO_2] rather than that of other environmental drivers. Forest productivity and biomass carbon pools in these forests mainly respond positively to environmental change especially if the effects of increasing [CO_2] are included. If climate change is considered in isolation 61 % of the simulations show positive responses, but 35 % of the simulations show decreasing forest productivity and declining biomass carbon pools. Boreal forests mostly become more productive and sequester more carbon under climate change and increasing [CO_2], while temperate and especially Mediterranean forests show more mixed responses depending on the importance of individual environmental driving variables. It is recommended that future modeling studies should increasingly strive to incorporate mixed stands and tropical forests, and include other environmental drivers besides climate and [CO_2] to better capture the totality of future changes in forest productivity and carbon pools.

Keywords Carbon dioxide · Climate change · Nitrogen · Ozone · Process-based models

Introduction

In past decades, ground-based measurements and satellite data have indicated shifts in forest productivity in all major forest biomes [1–7]. These observations have been attributed not only to environmental change such as increasing nitrogen (N) deposition, increasing atmospheric carbon dioxide concentrations ([CO_2]) and climate change but also to changing management practices (e.g., [8, 9]. Recent analyses have shown that N depositions indeed have a fertilizing effect on forest productivity and increase carbon sequestration [10–12]. There is also evidence that increasing [CO_2] enhances photosynthesis and water-use efficiency, although it is unclear how strongly this ultimately affects productivity [13, 14]. In addition, climate has been identified as a major control of forest productivity throughout the world as evidenced by analysis of dendrochronological (e.g., [15]), observational [12, 16], flux [17], and satellite [4, 18] data. Increasing temperature directly affects tree productivity through its effects on growth temperatures [19] and indirectly in combination with precipitation through its effects on growing season length [20, 21] and soil water status. All these environmental factors interact with each other and with other environmental variables such as ozone (O_3) in complex and multiple ways [22, 23]. They also vary

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✉ Christopher Reyer
reyer@pik-potsdam.de

[1] Potsdam Institute for Climate Impact Research, Research Domain II: Climate Impacts and Vulnerabilities, Telegrafenberg, P.O. Box 601203, 14412 Potsdam, Germany

regionally, and more detailed reviews of the effects of environmental change on forest processes are available [23–25]. It is crucial for many forest ecosystem services such as carbon sequestration or timber production as well as for forests' adaptation to climate change to determine how forest productivity will change under projections of future environmental change.

Besides observing effects of environmental change on forest productivity, which, by definition, can only detect past changes, and carrying out experiments, which are usually limited in forests due to the large spatial and temporal scales involved in setting up experiments with trees, models can be used to analyze and project forest productivity under environmental change. An advantage of a modeling approach is that, by integrating knowledge from observations and experiments, they allow hypotheses to be generated and tested; they can include many environmental drivers and analyze influences of individual drivers over long time periods and under many different environmental change scenarios. However, this flexibility comes at the cost of simplifying the system to a degree that essential responses and feedbacks may be lost. Furthermore, model-based projections of the effects of environmental change suffer from several types of uncertainties (e.g., [26•]), which need to be accounted for when interpreting the results of model projections [27]. Summarizing the results of several models allows an evaluation of the consistency of model results across different model structures.

Therefore, the objective of this paper was to review published stand-scale process-based model projections of changes in forest productivity and carbon pools driven by environmental change. The intention of the paper was not to explain the individual models' results in terms of the underlying processes or the ways the models are constructed nor to judge the models' quality. Although it is clear that the models considered here have different structures, use different input data, and scenarios of environmental change, it was assumed that general patterns of changes in forest productivity under environmental change will transcend these methodological differences.

Model Types for Simulating Climate Change Impacts on Forests

There are many model types that have been used for simulating the impacts of changing environmental conditions on forests [28••], and much progress has been made since the early reviews of Agren et al. [29] and Shugart et al. [30] of such models. Gap-type models (see [31]) capture long-term forest dynamics but have been criticized for oversimplifying tree growth responses to climatic variables [32, 33]. Purely empirical models that rely on statistical relationships cannot be extrapolated to novel environmental conditions, which were not used for model fitting. Process-based models (PBMs) are most suitable for environmental change studies since they combine changes in environmental variables with plant responses to this change in a mechanistic way [34, 35, 36•]. Stand-scale PBMs simulate the impact of environmental drivers on forest stands and provide detailed physiological and structural output. They require detailed input data for model initialization [36•], and their mostly species-specific parameters can be derived from physiological measurements [35]. This level of detail allows the models to be used for estimating sustainable forest management indicators [37] and at the same time differentiates them from process-based dynamic global vegetation models or global biogeochemical models that simulate global or regional responses to environmental change for different plant functional types only [38].

Stand-scale PBMs thus represent system dynamics and processes at spatial and (to a limited extent) temporal scales similar to observational studies (e.g., eddy-covariance flux towers or intensive monitoring plots), which have been intensively used to study past and current impacts of environmental change on forest productivity (see review [9]). It is important to emphasize that they represent physiological responses to environmental drivers at the local scale and only seldom integrate processes that occur at the landscape scale such as disturbances (e.g., storms or insect outbreaks). Although PBMs, as defined here, usually work at similar spatial scales and include similar processes (e.g., photosynthesis, allocation, etc.), the level of detail in process description, temporal resolution, and way of coupling different processes can differ drastically between them. PBMs can be used either as diagnostic tools to disentangle the importance of individual environmental drivers on forest productivity in the past (e.g., [39–41]) or to generate projections of future forest productivity under environmental change (e.g., [42]). The latter can also be carried out in an experimental set-up by varying environmental drivers individually and in combinations (e.g., [43]). While such an approach enables an assessment of the relative contribution of environmental drivers to the model result, simulations combining important drivers represent the most comprehensive assessments of environmental change on forests. The change in environmental drivers can be gradual, simulating transient change (e.g., [44]), or stepwise (e.g., [45]). Thus, even within this narrowly defined model type of stand-scale PBMs, there is a broad variety of approaches towards simulating forest productivity under environmental change, which allows for an assessment of the robustness of model results over a broad range of models.

Literature Review

This review focuses on studies simulating individual forest stands with process-based models, excluding purely gap and hybrid/empirical models. This selection concurs broadly with the model types 1 and 2 (i.e., stand-scale, process-based models and biogeochemical models) as defined by Medlyn et al. [28••].

It focuses on mechanistic models applied at the stand scale without considering changing species composition. Another important criterion for the selection of studies was that model output on changes in forest productivity and carbon pools should be available for individual stands. Studies that simulated individual stands but reported only aggregated values for several stands or for an entire region were excluded. If the same set of simulations was used in several papers (e.g., under different viewpoints or response variables), only the main study was considered to avoid double-counting of the same model simulations. Different versions of the same model were accounted for by recording the names of different model versions if specified in the publications. To analyze the papers, the following information was extracted: general information (species, type of change of driving variables (stepwise or transient), model name, and biome), the driving variables (i.e., climate change (consisting of increasing temperature and/or changing precipitation), [CO_2], N, O_3, and their combinations) and the respective response variable for each simulation. In this study, only response variables that relate to forest carbon pools (e.g., volume, wood carbon) and to forest productivity (e.g., stem increment, net primary production (NPP)) were included, and no distinction was made between studies reporting carbon content or fresh biomass, etc. Although for this review, it makes sense to pool different response variables to some extent, it is important to note that different response variables describe different characteristics of a forest stand. For example, higher photosynthesis does not necessarily translate into higher tree growth [46]. However, analyzing different response variables together seems appropriate in the context of this review, since there are relationships between biomass and productivity [47, 48] and also between various variables of forest productivity (e.g., [49]). Disturbances are another important environmental driver. They can strongly affect forest biomass and carbon stocks [49, 50] and the productivity to biomass relationship. However, they had to be excluded from the analysis because they are only integrated to a very limited degree in stand-scale PBMs (e.g., [51]). Moreover, results of simulation experiments that featured different management types or intensities under changing environmental conditions were included, but these were not analyzed separately from simulations of unmanaged forests. Effects of forest management and age structure can be very important for forest productivity and carbon pools (e.g., in the USA [52, 53, 55, 56, but see [54]). However, they vary regionally and depend to a large extent on socioeconomic factors such as wood prices, agricultural policies, and demographic developments. Thus, these different management scenarios were interpreted as a variation of stand conditions that will still be influenced by changing environmental variables. The analysis thereby excludes adaptive forest management that may be implemented to cope with the changes in productivity induced by environmental change. Moreover, simulations reporting results from mixed forests at the individual species level were included if these were presented as individual simulations or at the forest level if one model simulation included several species.

To ensure comparability, relative changes of response variables were calculated for all simulations with respect to the baseline scenario of each study. Hence, changes “relative to baseline conditions” were reported throughout this paper. All figures were produced using the statistical software R [57].

Overview of Model Simulations

In total, 74 studies were reviewed. They were mostly restricted to temperate and boreal forests in the northern hemisphere, especially Europe and Northern America (Fig. 1a, Appendix Table 1). Only two studies were found for the Tropics in Asia, and none for South-America or Africa. The 74 studies represented 1209 single simulations runs carried out with 55 different models or model versions. More than 50 % of the simulations looked at the coniferous genera *Pinus* (30 %) and *Picea* (22 %). The broad-leaved genera *Betula* (12 %), *Fagus* (9 %), and *Quercus* (7 %) made up almost another third of the simulations. Most of the studies assumed a changing climate (temperature and/or precipitation) and/or increasing [CO_2], but only few considered changes in N deposition and O_3 (Appendix Table 1). Roughly 56 % of the simulations analyzed the effect of stepwise changes of environmental change drivers in their scenarios, whereas the remaining simulations featured transient responses (44 %).

The direction of change of the response to environmental change was positive for 79 %, negative for 19 %, and none for 2 % of all simulations reviewed here (Appendix Table 1). The proportion of positive and negative responses per studied site showed a distinct geographical pattern. For most studies in the boreal forests, the responses were positive, whereas the response was mixed in temperate and Mediterranean forests (Fig. 1a). There were 333 simulations that considered a changing climate (i.e., increasing temperatures and changing precipitation) without changes in [CO_2]. Thereof, 61 % showed positive, 35 % negative, and 3 % no changes (Fig. 1c). A greater number of simulations (870) had been run with a changing climate and increasing [CO_2]. Here, 87 % of the simulations were positive, 12 % negative, and 1 % not changing (Fig. 1b). Only six simulation runs did not consider climate change or increasing [CO_2] at all but the effects of N (five simulations with positive responses) and O_3 (one simulation with negative responses) individually. In the remaining simulations that included N and O_3 as driving variables, the reported responses were always confounded with climate change and/or [CO_2] scenarios.

Since changes in climate and [CO_2] are gradually changing and not stepwise, a subset of the full dataset was extracted, which only included those simulations in which climate change, [CO_2], and their combination changed in a transient way, and in which it was possible to calculate changes relative

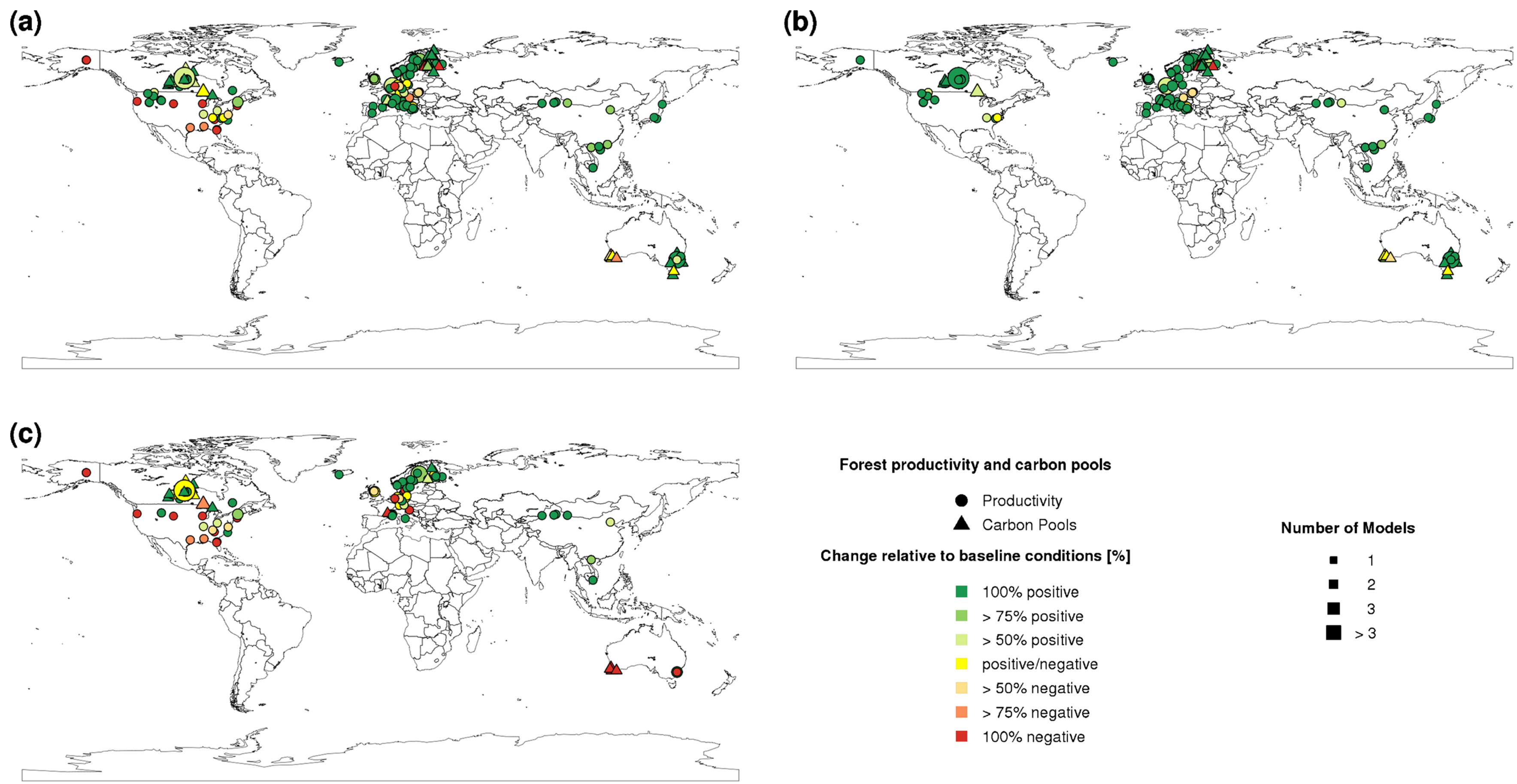

Fig. 1 Qualitative future changes in forest productivity (*circles*) and carbon pools (*triangles*) under environmental change for **a** all studies reviewed in this paper, **b** those studies considering climate change and increasing [CO_2] in conjunction, and **c** those studies considering only climate change. The *color scheme* indicates the proportion of simulations at each stand resulting in positive or negative changes of forest productivity and carbon pools under environmental change, while the size of the points indicates the number of models applied (small=1 model, medium=2 models, large=3 models, very large>3 models). Six simulations have been excluded from **b** and **c** since they do not include climate change and/or [CO_2] at all

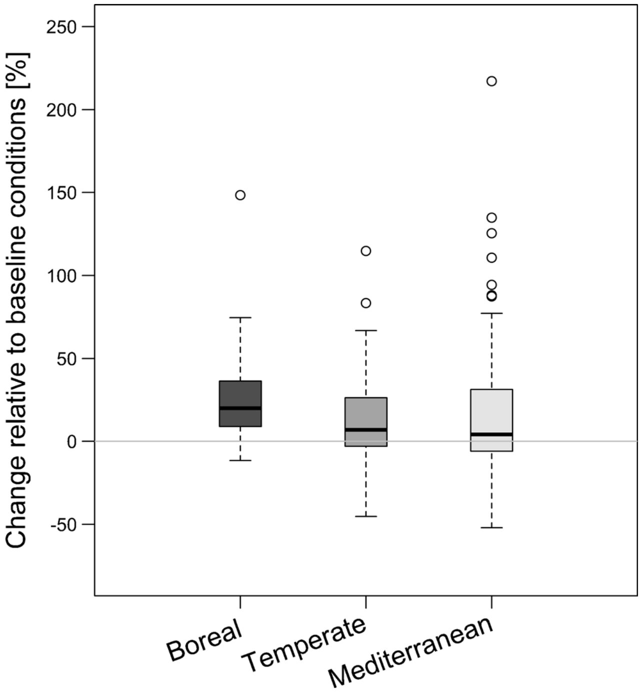

Fig. 2 Changes in forest productivity and carbon pools under different environmental change scenarios in three biomes (boreal: simulations=305, models=12, studies 26; temperate: simulations=142, models=10, studies=12; Mediterranean: simulations=78, models=4, studies=4). The *horizontal gray line* indicates no change compared to the baseline scenario. The *boxplots* show the following information: *thick line* median, *bottom and top of the box* 25th and 75th percentiles, *whiskers* maximum value or 1.5 times the interquartile range of the data depending on which is smaller. *Points* outliers larger than 1.5 times interquartile range

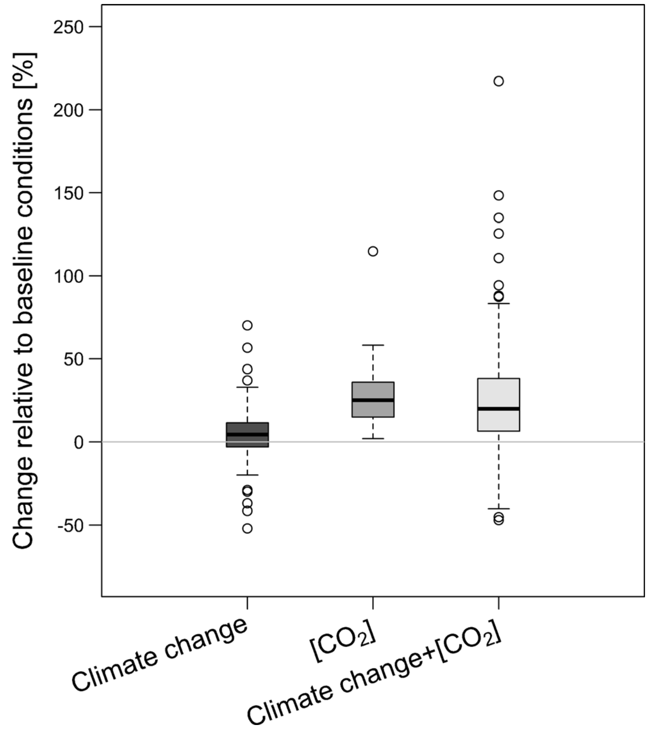

Fig. 3 Changes in forest productivity and carbon pools under different drivers of global change. *Climate change* changing temperature and precipitation, *[CO_2]* increasing atmospheric CO_2, *Climate change+[CO_2]* combination of climate change and [CO_2] (climate change: simulations=137, models=15, studies=19; [CO_2]: simulations=48, models=11, studies=12; climate change+[CO_2]: simulations=340, models=17, studies=31). The *gray line* and *boxplots* are as in Fig. 2

to baseline conditions. This selection resulted in 525 simulations from 23 models and 40 different studies. These simulations showed distinct changes in forest productivity and carbon pools under environmental change in different biomes (Fig. 2). Whereas the response in boreal forests was mostly positive, it was less clear in temperate and especially Mediterranean forests, although the median response was positive even in those regions. While for boreal forests, the change in forest productivity and carbon pools relative to baseline conditions varied from −11 to 75 % (up to 148 %), the change varied from −45 to 67 % (up to 115 %) and from −52 to 77 % (up to 217 %) in temperate and Mediterranean forests, respectively (Fig. 2).

To synthesize the effects of climate change, [CO_2], and their combination on the changes in biomass and productivity relative to baseline conditions, the transient simulations in terms of driving environmental change variables were pooled (Fig. 3). The effects of a changing climate investigated separately from increasing [CO_2] led to both positive and negative changes in forest productivity and carbon pools relative to baseline conditions ranging from −20 to 33 % including several negative and positive outliers. In contrast, the simulations including only the effects of increasing [CO_2] always resulted in positive changes (from 2 to 58 % with one larger outlier). When climate change effects and increasing [CO_2] were simulated in combination, most of the simulations showed positive changes in forest productivity and carbon pools relative to baseline conditions (with several outliers showing very strong positive changes).

It is important to note that the data shown on Figs. 2 and 3 might only appear skewed towards positive changes because they are expressed on a linear scale (i.e., percentage changes can reach very high positive values while negative changes cannot exceed −100 %). When data were displayed on a proportional scale using log transformation, it showed, however, that the skew towards positive productivity changes still remained although the general picture with positive and negative outliers became more balanced (results not shown).

Discussion of Model Simulations

The analysis presented here reveals several important foci of current efforts to model the effects of environmental change on forest productivity and carbon pools at the stand scale. Firstly, there is a clear regional focus on temperate and boreal forests in North America and Europe. The literature review did not reveal any study in South America and Africa matching the selection criteria, although there is strong—and partly conflicting—evidence that forest productivity is changing in these regions as well (e.g., [58, 59] but [5, 60]), and detailed model simulations are urgently needed.

Secondly, the forest types described by detailed stand-scale process-based models are mostly restricted to mono-specific forests and tree species that are relevant for forestry. Forests types and species that are more important for other ecosystem functions and services such as mixed forests with high biodiversity value are only rarely addressed. This imbalance in plot and forest type selection can be partly explained by the large amount of physiological and environmental data that is necessary to initialize and drive PBMs and which is mostly available from long-term and intensive monitoring plots, which usually have been installed in typical, representative forests of a region. Such forests are often then also managed for timber production or at least heavily influenced by past management decisions such as species choice and silvicultural regime.

Thirdly, the assessment of the different environmental drivers being covered reveals a focus on climate change and increasing [CO_2]. Few studies looked at other drivers such as N or O_3 (especially not in isolation) although these have been identified as important drivers of forest change [61, 62]. This selection bias may be less important since, for example, the effect of N is considered to be comparably low in the future [63]. Nonetheless, it would still be important to assess and test this finding with forest models.

Having this in mind, this paper shows that most of the responses of forest productivity and carbon pools to the different environmental change drivers and their combinations were always positive when only increasing [CO_2] was considered and mostly positive when climate change and increasing [CO_2] were combined. If only climate change was considered, 61 % of the simulations still showed positive responses, but 35 % also showed negative responses. This highlights the importance of the effects of increasing [CO_2] on plant productivity in the models by enhancing photosynthesis and water use ([13, 14; see also discussion of the inclusion of [CO_2] effects in models by Reyer et al. [64]). There is increasing observational and experimental evidence that the strength and persistence of the [CO_2] effect may be limited or overridden by a lack of N, physiological acclimation to higher [CO_2], or droughts [65, 66] and whether studied at the leaf, canopy, or landscape scale [67]. These effects are often not fully accounted for in models (see also [36•, 64, 68]), and thus, model simulations may overestimate the productivity responses to increasing [CO_2]. At the same time, a recent analysis argues that mesophyll diffusion is not properly captured in the most common photosynthesis models, and therefore, the [CO_2] effect may actually be underestimated [69].

The positive response in model simulations for boreal forests is consistent with ground-based and satellite measurements [1, 8, 9, 18, 24, 60] and with the current understanding that temperature is a strongly limiting factor of forest productivity. Increasing temperatures and a concomitant lengthening of the growing season as well as increasing nutrient availability (through decomposition and mineralization) exert a positive effect on forest productivity [19, 70, 71]. If, under climate change, water becomes a more limiting factor, photosynthesis and subsequent stem volume production may be reduced [72].

These mechanisms are also relevant in temperate forests, but there is evidence that a broader variety of environmental conditions controls productivity in these systems (e.g., [73–75]). This variability and increased vulnerability to drier and warmer conditions seem to be reflected by the larger amount of negative changes in forest productivity and carbon pools relative to baseline conditions in the dataset presented here. In Mediterranean conditions, drier and warmer conditions in recent decades have strongly influenced forest conditions and growth [76–78]. While this sensitivity is supported by some of the simulations yielding negative changes in forest productivity and carbon pools in the dataset presented here, a majority of the simulations actually show positive changes even in the Mediterranean region, which contradicts the common expectation of growth decline under climate change.

This finding is strongly related to the importance of [CO_2] in the models and the climate change scenarios used in the simulations. Under water shortages, the most important effect of elevated [CO_2] is decreased stomatal conductance, which leads to enhanced water use efficiency [22, 79]. However, recent carbon isotope tree ring studies have shown that this effect has not been translated into increased tree growth but may have been overridden by drought, warming, N limitation, or physiological adjustments, which may not be sufficiently covered in the models [60, 66, 80]. Interestingly, those simulations in the Mediterranean in the dataset presented here that were run without including the effects of elevated [CO_2] (i.e., [81, 82] project exclusively negative changes in forest productivity and carbon pools relative to baseline conditions.

One other important issue is that the summary of responses reviewed here does not differentiate between soil and biomass carbon. Actually, there are only four studies that explicitly consider soil variables (Appendix Table 1); hence, most of the results presented here are valid for the responses of vegetation only. In reality, increasing productivity from higher temperatures or [CO_2] can lead to higher N demand, which may lead to reduced soil N availability and reduced productivity unless soil N mineralization itself will be strongly stimulated by higher temperatures [24]. Results from model applications confirm that soil and vegetation responses to climate change can be opposite, i.e., increasing productivity but decreasing soil carbon (e.g., [83]).

In summary, the review of available stand-scale forest simulations with process-based models shows a mostly positive response of boreal forests to climate change and increasing [CO_2], which is mostly consistent with expectations from observations, experiments, larger-scale modeling efforts, and theory, while temperate and Mediterranean forests show more mixed responses. These findings are consistent over different models with different model structures. They highlight the regional differentiation of climate change effects on forest productivity and carbon pools (increasing if temperature-limited and decreasing if water-limited) in contrast to a general positive effect of increasing [CO_2]. This regional differentiation is consistent with findings from recent stand-scale carbon isotope studies [60]. In general, the results presented here are also consistent with model applications at more regional or even global scale [42, 84, 85].

Limitations of Model Simulations

The studies presented here do not consider the impacts of altered disturbances regimes and extreme events such as fire, insects, or storms on forest productivity and carbon pools, which may limit or reverse positive effects of climate change already at lower degrees of warming (e.g., [50, 86]). It is also unclear to which degree PBMs include higher-order interactions such as higher growth rates that lead to decreased longevity [87, 88] and non-linear responses to change or extreme events [64, 68]. The latter are probably more important predictors of forest productivity and carbon pools (e.g., [18]) than mean climate [16].

Moreover, this review did not evaluate the models regarding their quality or ability to precisely describe relevant processes but assumed that the models are equally good and independent. This is a common but not unchallenged assumption in model comparison studies [28••, 89]. In reality, the models are not fully independent since they share submodels for specific processes such as the description of photosynthesis. Additionally, some models are more widely used than others, have more published applications, or more simulations per application so that they may be overrepresented in the dataset presented here. Moreover, weighting the model simulations by their ability to simulate observed data could help to quantify uncertainties but would require more synchronized model comparisons (e.g., [90•,] which was beyond the scope of this synthesis. The formulation of different processes in the models was not analyzed, which would explain the results of each individual model because this has been done in an exemplary way elsewhere [28••].

Conclusions

This paper shows that stand-scale process-based models are able to capture the broad regional variety of responses of forest productivity and carbon pools in response to climate change and elevated [CO_2]. The models agree on mostly positive responses in boreal forests but show more mixed responses in temperate and Mediterranean forests depending on the importance of individual environmental variables in the model simulations. These broad, overall responses transcend the variability of data sets, time frames, assumptions, etc. that are made in the different models. However, uncertainties remain regarding these responses as a result of different model structures, site conditions, magnitudes of environmental change considered, and the long-term persistence of [CO_2] effects. It is important to note that the studies reviewed here cover the physiological response to environmental change, but that there is a possibility that at larger spatial scales, the effects of disturbances and management regimes shape the state of forest ecosystems. This paper provides a synthesis of published model-based changes in forest productivity and carbon pools with which the results of future studies can be compared. Furthermore, this paper serves to inform regional studies that strive to integrate changes in forest productivity and carbon pools with disturbances or socioeconomic drivers to, for example, develop adaptive management strategies. The results of this review can be refined by more structured model inter-comparisons with improved stand-scale process-based models.

This synthesis also found that past modeling efforts have largely focused on species that are important for forestry, particular biomes, and prominent environmental variables. This is partly due to constraints in data availability to parameterize complex process-based models. Nevertheless, further studies may exploit newly available datasets as well as data integration and uncertainty quantification techniques to cover a larger array of forest stands, species, biomes, and environmental drivers and thus different ecosystem services and functions and corresponding challenges for sustainable management. Moreover, further studies could make better use of the strengths that differentiate modeling approaches from observational and experimental studies: to simulate the effects of a multitude of single environmental drivers and their combinations in full factorial designs in a transient way. In general, however, it is encouraging to see that many valuable and complex models exist, which allow us to explore the distant futures of forests in times of rapidly changing environmental and societal conditions.

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Compliance with Ethics Guidelines

Conflict of Interest Dr. Reyer reports grants from EU 7th Framework Program, grants from German Federal Ministry of Education and Research, during the conduct of the study.

Human and Animal Rights and Informed Consent This article contains no studies with human or animal subjects performed by the author.

Appendix

Table 1 Summary of changes in forest productivity and carbon pools as simulated by stand-scale process-based models reviewed in this paper

Response variable	Response	Number of simulations				Time scale	Model	Biome	Country/region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
Productivity											
NPP (aboveground)	Minus	10	0	0	10	na[a]	PnET	Boreal, temperate	USA	P+T	[91]
NPP	Plus	0	3	0	3	10 years[a]	SDGVM	Boreal	Norway	$[CO_2]$, T, $[CO_2]$+T	[92]
NPP	Plus/minus	2	28	0	30	3 years[a]	BIOMASS	Boreal	Europe	$[CO_2]$, T, $[CO_2]$+T	[93]
NPP	Plus	0	6	0	6	100 years[a]	SIMFORG-SICA	Boreal, Mediterranean, temperate	Europe	$[CO_2]$+T	[94]
GPP	Plus	0	12	0	12	na[a]	SICA	Boreal, Mediterranean, temperate	Europe	$[CO_2]$+T, $[CO_2]$+P+T	[95]
NPP	Plus/minus	1	17	0	18	1950–2089[b]	BIOME-BGC	Temperate	USA	$[CO_2]$+N+P+T	[96]
Volume increment	Plus/minus	2	49	0	51	10 years[a]	CenW	Tropics (plantation)	Vietnam	$[CO_2]$, P+T, $[CO_2]$+P+T	[97]
NPP	Plus	0	4	0	4	2000–2100[b]	PnET-BGC	Temperate	USA	P+T	[98]
NPP	Plus/null	0	5	1	6	1990–2050[b]	Hybrid	Temperate	UK	$[CO_2]$, N, T, $[CO_2]$+N, $[CO_2]$+T, $[CO_2]$+N+T	[99]
NPP	Plus	0	6	0	6	1990–2050[b]	ITE-EFM	Temperate	UK	$[CO_2]$, N, T, $[CO_2]$+N, $[CO_2]$+T, $[CO_2]$+N+T	[99]
Yield	Plus	0	1	0	1	150 years[a]	SECRETS	Temperate	Belgium	$[CO_2]$+P+T	[100]
NPP (stem)	Plus	0	4	0	4	2040–2060[b]	StandLEAP-v0v6	Boreal	Canada	P+T	[101]
NPP	Plus	0	1	0	1	70 years[b]	Ecosys	Boreal	Canada	$[CO_2]$+P+T	[102]
NPP	Plus	0	1	0	1	150 years[b]	Ecosys	Boreal	Canada	$[CO_2]$+P+T	[103]
NEP[c]	Plus/minus	2	10	0	12	3 years[a]	Ecosys	Boreal	Canada	T	[104]
NEE[c]	Plus/minus/null	5	3	1	9	11 years[a]	INTRASTAND	Temperate	USA	$[CO_2]$, O_3, P, T, $[CO_2]$+P+O_3+T	[105]
Increment (stem)	Plus/minus	16	5	0	21	1961–2100[b]	BIOME-BGC	Temperate	Slovakia	$[CO_2]$+N+P+T	[106]
NPP	Plus	0	3	0	3	2008–2050[b]	VISIT	Boreal, temperate	Japan	$[CO_2]$+T	[107]
NPP	Plus	0	8	0	8	100 years[b]	CoupModel	Boreal	Sweden	P+T	[108]
GPP	Plus/minus	11	3	0	14	1 year[a]	PERUN_3	Temperate	Slovenia	$[CO_2]$, T, $[CO_2]$+T	[109]
Production (stemwood)	Plus/null	0	8	2	10	76–100 years[b]	FINNFOR	Boreal	Finland	$[CO_2]$, P, T, P+T, $[CO_2]$+P+T	[110]
CAI (stemwood)	Plus	0	4	0	4	1950–2030[b]	CenW-1.0.5	Temperate	Australia	$[CO_2]$+T, $[CO_2]$+N+T, $[CO_2]$+P+T, $[CO_2]$+N+P+T	[111]
CAI (stemwood)	Plus	0	4	0	4	50 years[b]	CenW-1.0.5	Temperate	Australia	$[CO_2]$, $[CO_2]$+N, $[CO_2]$+P, $[CO_2]$+N+P	[111]
CAI (stemwood)	Plus	0	11	0	11	20 years[a]	CenW-1.0.5	Temperate	Australia	$[CO_2]$, N, P, T, $[CO_2]$+N, $[CO_2]$+P, N+P, P+T, $[CO_2]$+N+P, N+P+T	[111]

Table 1 (continued)

Response variable	Response	Number of simulations				Time scale	Model	Biome	Country/region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
NPP	Plus/minus	6	5	1	12	100 years[a]	FORGRO	Temperate	The Netherlands	$[CO_2]$+P+T	[112]
NPP	Plus/null	0	11	1	12	100 years[b]	FORGRO	Temperate	The Netherlands	$[CO_2]$+P+T	[112]
Gross photosynthesis	Plus/minus	6	18	0	24	14 years[a]	FORGRO	Temperate	The Netherlands	$[CO_2]$, $[CO_2]$+T	[45]
Gross photosynthesis	Plus	0	24	0	24	14 years[a]	FORGRO-PGEN	Temperate	The Netherlands	$[CO_2]$, $[CO_2]$+T	[45]
Gross photosynthesis	Plus/minus	5	17	2	24	14 years[a]	ITE-FORGRO	Temperate	The Netherlands	$[CO_2]$, $[CO_2]$+T	[45]
NPP	Plus/minus	31	65	0	96	50 years[a]	FORGRO	Temperate	The Netherlands	$[CO_2]$, $[CO_2]$+T	[113]
Net photosynthesis	Plus/minus/null	5	42	1	48	1 year[a]	MAESTRO	Temperate	Scotland	$[CO_2]$, T, $[CO_2]$+physiological adjustments, T+physiological adjustments, $[CO_2]$+T+ physiological adjustments	[114]
MAI	Plus/minus/ null	22	25	1	48	2041–2070[b]	4C	Temperate	Germany	P+T	[115]
Net photosynthesis	Plus/minus/ null	1	4	1	6	90 years[a]	OAKWBAL	Temperate	USA	T	[116]
NPP	Plus	0	2	0	2	2000–2050/2100[b]	FORGRO-phen	Boreal	Scandinavia	T	[117]
NPP	Plus	0	1	0	1	24 years[a]	FORDYN	Temperate	USA	$[CO_2]$	[118]
NPP	Plus	0	8	0	8	10 years[a]	FORDYN	Temperate	USA	$[CO_2]$	[118]
Carbon sequestration	Minus	2	0	0	2	1987–2085[a]	TGS	Temperate	USA	$[CO_2]$	[119]
Carbon Sequestration	Plus	0	2	0	2	1987–2085[b]	TGS	Temperate	USA	$[CO_2]$	[119]
NPP	Plus/null	0	46	2	48	na[a]	BIOME-BGC	Tropical	China	$[CO_2]$, $[CO_2]$+T	[120]
GPP	Plus	0	6	0	6	1 year[a]	SPA	Temperate	Australia	$[CO_2]$+physiological adjustments	[121]
NEE[c]	Plus/minus	2	13	1	16	Range 1990–2095[b]	HYDRALL	Mediterranean	Italy	$[CO_2]$+P+T	[122]
NPP	Plus	0	4	0	4	300 years[a]	G'DAY	Temperate	Australia	$[CO_2]$	[123]
Canopy carbon gain	Plus/minus	1	2	0	3	1 year[a]	BIOMASS	Temperate	Australia	$[CO_2]$, T, $[CO_2]$+T	[124]
Canopy carbon gain	Plus/minus	1	1	0	2	8 years[a]	BIOMASS	Temperate	Australia	$[CO_2]$, T	[124]
NPP	Plus	0	1	0	1	100 years[b]	G'DAY	Boreal	Sweden	T	[125]
NPP	Plus	0	4	0	4	100 years[a]	G'DAY	Boreal	Sweden	N, T	[125]
NPP	Plus/minus	19	5	0	24	40 years[a]	PnET-IIS	Temperate	USA	P, T, P+T	[126]
NPP	Plus	0	11	0	11	100 years[a]	G'DAY	Boreal, Temperate	Australia	$[CO_2]$, T, $[CO_2]$+T	[127]
NPP	Plus/minus	1	26	0	27	100 years[b]	Century-4.0	Boreal	Canada	$[CO_2]$, P+T, $[CO_2]$+P+T	[128]
NPP	Plus/minus	1	26	0	27	100 years[b]	Century-4.0	Boreal	Canada	$[CO_2]$, P+T, $[CO_2]$+P+T	[129]
NPP	Plus	0	5	0	5	1996–2100[b]	G'DAY	Boreal	Sweden	$[CO_2]$, T, $[CO_2]$+N, $[CO_2]$+T, $[CO_2]$+N+T	[130]
NPP	Plus/minus	1	4	0	5	1996–2100[b]	DAYCENT	Boreal	Sweden	$[CO_2]$, T, $[CO_2]$+N, $[CO_2]$+T, $[CO_2]$+N+T	[130]

Table 1 (continued)

Response variable	Response	Number of simulations				Time scale	Model	Biome	Country/region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
NPP	Plus/minus	2	2	0	4	1 year[a]	BEPS	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus/minus/null	1	1	2	4	1 year[a]	BGC	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus/minus/null	1	1	1	3	1 year[a]	NASA-CASA	Boreal	Canada	P, T	[131]
NPP	Plus/minus	1	3	0	4	1 year[a]	CLASS	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus	0	4	0	4	1 year[a]	Ecosys	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus/Minus	3	1	0	4	1 year[a]	FORFLUX	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus/minus/null	2	1	1	4	1 year[a]	Lotec	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP	Plus/minus	2	1	0	3	1 year[a]	SPAM	Boreal	Canada	P, T	[131]
NPP	Plus	0	4	0	4	1 year[a]	TEM	Boreal	Canada	$[CO_2]$, P, T	[131]
NPP (aboveground)	Plus	0	45	0	45	30/31 years[a]	BIOME3C	Mediterranean	France	$[CO_2]$, P+T, [CO2]+P+T	[132]
NPP	Plus	0	4	0	4	2000–2044[b]	4C	Temperate	Germany	$[CO_2]$+P+T	[133]
NPP	Plus	0	18	0	18	1960–2049/2099[b]	GOTILWA+	Mediterranean	Italy, Spain	$[CO_2]$+P+T	[134]
Forest carbon production	Plus	0	6	0	6	1994–2100[b]	Century-4.5	Temperate	USA	P+T	[135]
NPP	Plus/minus	1	7	0	8	8 years[a]	BIOME-BGC	Temperate	China	P, T, $[CO_2]$+P, P+T, $[CO_2]$+P+T	[136]
NPP	Plus/minus	1	27	0	28	40 years[a]	BIOME-BGC	Boreal	China	P, T, $[CO_2]$+P, P+T, $[CO_2]$+P+T	[43]
NPP (wood+leaf+root)	Plus	0	1	0	1	10 years[a]	PnET-II	Temperate	USA	P+T	[137]
NPP	Plus/minus	1	7	0	8	60/120 years[b]	ITE-EFM	Temperate	UK	T, $[CO_2]$+N, $[CO_2]$+N+T	[138]
NPP	Plus	0	7	0	7	2005–2062[b]	BIOME-BGC	Boreal	USA	$[CO_2]$, T, $[CO_2]$+T, P+T, $[CO_2]$+P+T	[139]
Net photosynthesis	Plus	0	1	0	1	1 year[a]	Vitale et al. 2003	Mediterranean	Italy	T	[140]
NPP	Plus	0	3	0	3	3 years[a]	BIOMASS	Boreal	Norway	$[CO_2]$, T, $[CO_2]$+T	[141]
Total productivity		168	718	18	904						
Pools											
Total yield (timber)	Plus	0	96	0	96	100 years[b]	FINNFOR	Boreal	Finland	$[CO_2]$+P+T	[142]
Total carbon (above+belowground)	Plus/null	0	35	1	36	2000–2100[b]	FINNFOR	Boreal	Finland	$[CO_2]$+P+T	[143]
Volume (stem)	Minus	3	0	0	3	2000–2099[b]	FINNFOR	Boreal	Finland	$[CO_2]$+P+T	[72]
Stem wood	Plus/minus	4	8	0	12	2000–2099[b]	FINNFOR	Boreal	Finland	$[CO_2]$+P+T	[144]
Carbon (wood)	Plus	0	2	0	2	150 years[b]	Ecosys	Boreal	Canada	$[CO_2]$+P+T, $[CO_2]$+N+P+T	[145]
Carbon (wood)	Plus	0	2	0	2	100 years[b]	Ecosys	Boreal	Canada	$[CO_2]$+P+T	[51]
Carbon (wood)	Plus	0	2	0	2	126 years[b]	Ecosys	Boreal	Canada	$[CO_2]$+N+P+T	[146]
Total production (stem)	Plus	0	6	0	6	100 years[b]	FINNFOR	Boreal	Finland	$[CO_2]$, P+T, $[CO_2]$+P+T	[44]

Table 1 (continued)

Response variable	Response	Number of simulations				Time scale	Model	Biome	Country/region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
Total (wood)	Plus	0	6	0	6	200 years[a]	CenW-3.0	Temperate	Australia	[CO_2]	[147]
Biomass (stem)	Plus/minus	3	7	0	10	50 years[b]	FORGRO-phen	Boreal, Mediterranean	Finland, France	[CO_2], T, [CO_2]+T, [CO_2]+P+T	[81]
Carbon (stem+foliage)	Plus/minus	5	2	0	7	100 years[a]	Century-4.0	Boreal	Canada	[CO_2], P, T, [CO_2]+P, P+T, [CO_2]+P+T	[148]
Carbon (stem+foliage)	Plus/minus	2	5	0	7	100 years[a]	Forest-BGC	Boreal	Canada	[CO_2], P, T, [CO_2]+P, P+T, [CO_2]+P+T	[148]
Total yield	Plus	0	6	0	6	100 years[b]	FINNFOR	Boreal	Finland	[CO_2]+T	[149]
Total yield	Plus	0	18	0	18	100 years[b]	FINNFOR	Boreal	Finland	[CO_2]+T	[150]
Biomass (wood)	Plus	0	4	0	4	1990–2100[b]	RipFor	Boreal	Estonia	[CO_2]+P+T	[151]
Biomass (wood)	Plus	0	3	0	3	100 years[b]	ForSVA	Temperate	Canada	P+T	[152]
Volume	Plus/minus/Null	6	17	1	24	10 years[a]	CABALA	Temperate	Australia	[CO_2]+P+T	[153]
Biomass (above+belowground)	Plus	0	9	0	9	100 years[b]	Century 4.0	Boreal	Canada	P+T	[154]
Biomass (above+belowground)	Minus	6	0	0	6	6 years[a]	BALANCE	Temperate	Germany	P, P+T	[155]
Harvested wood	Plus	0	4	0	4	145 years[b]	EFIMOD-2	Boreal	Canada	P+T	[156]
Accumulated NEP[c]	Plus/minus	28	12	0	40	2036–2066[b]	CenW 3.1	Mediterranean	Australia	[CO_2], P, T, [CO_2]+N+P+T	[82]
Total mass (stem)	Plus	0	2	0	2	100 years[b]	FINNFOR	Boreal	Finland	T, [CO_2]+T	[157]
Total pools		57	246	2	305						
Total productivity and pools		225	964	20	1209						

The studies are differentiated whether their response variables relate to forest productivity or to carbon pools

NEP net ecosystem production, *NPP* net primary productivity, *GPP* gross primary productivity, *NEE* net ecosystem exchange, *CAI* current annual increment, *MAI* mean annual increment, *[CO2]* atmospheric CO_2-concentration, *T* temperature, *P* precipitation, *N* nitrogen, *O_3* ozone, *na* information could not be derived from the paper

[a] Stepwise

[b] Transient without specifying future period

[c] Including soil variables

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