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Latest Trends in Modelling Forest Ecosystems: New Approaches or Just New Methods?

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Abstract

Purpose of Review Forest models are becoming essential tools in forest research, management, and policymaking but currently are under deep transformation. In this review of the most recent literature (2018–2022), we aim to provide an updated general view of the main topics currently attracting the efforts of forest modelers, the trends already in place, and some of the current and future challenges that the field will face.

Recent Findings Four major topics attracting most of on current modelling efforts: data acquisition, productivity estimation, ecological pattern predictions, and forest management related to ecosystem services. Although the topics may seem different, they all are converging towards integrated modelling approaches by the pressure of climate change as the major coalescent force, pushing current research efforts into integrated mechanistic, cross-scale simulations of forest functioning and structure.

Summary We conclude that forest modelling is experiencing an exciting but challenging time, due to the combination of new methods to easily acquire massive amounts of data, new techniques to statistically process such data, and refinements in mechanistic modelling that are incorporating higher levels of ecological complexity and breaking traditional barriers in spatial and temporal scales. However, new available data and techniques are also creating new challenges. In any case, forest modelling is increasingly acknowledged as a community and interdisciplinary effort. As such, ways to deliver simplified versions or easy entry points to models should be encouraged to integrate non-modelers stakeholders into the modelling process since its inception. This should be considered particularly as academic forest modelers may be increasing the ecological and mathematical complexity of forest models.

Keywords Forest modelling · Forests · Methods

Introduction

Forests are one of the most complex ecosystems on Earth's biosphere, as they host a large proportion of terrestrial biodiversity and exist at the interface between the atmosphere and the pedosphere. In addition, forests are defined as such because the dominant organisms are trees, which are long-lived immobile individuals that are usually large [1]. These features provide opportunity for forests to develop specific spatial and temporal structures that have direct influence on how the ecosystem functions (i.e., nutrient, water and energy cycles, gene flows, population, and successional changes).

All this natural complexity poses a true challenge for representing forest structure and functioning in scientific and technical studies, as well as for science-based management [2]. Traditionally, forest models have focused on the dominant organisms (trees) and how they grow, survive, and are distributed [3••]. This approach has been dominant since the beginning of early quantitative forestry in the eighteenth century. However, for the last few decades, it has been well known that understanding how trees function is not enough to understand how forests function, as other forest components (understory, wildlife, soil, and microbial communities) are also influencing trees. Hence, forest models have constantly evolved to incorporate some of forests' complexity into their algorithms in order to produce the estimations that model developers consider necessary to meet their objectives.

The development of the first forest growth simulator marked the beginning of a new approach to estimate

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tree growth. Since then, modelling has evolved from the data-based approach of using statistical tools to transform observed data ("empirical models") into an approach in which an understanding of causal relationships between variables was added to statistical relationships in order to predict variables of interest ("process-based models") [4]. Soon after, the advantages and disadvantages of both approaches were identified [5, 6], and with the aim of solving them, an intermediary approach was proposed [7]. Since then, forest models have evolved considerably, and in the last few years, important technical developments have revolutionized the forest modelling field [8], such as the following: the continuous increment of computing power [9]; the development of new statistical methods [10]; the great expansion in techniques for data acquisition such as LiDAR, spectral, hyperspectral, thermal, or radar sensors that can be applied at broad scales [11]; or the development of autonomous continuous measurement devices for soil, vegetation, and atmospheric variables [12]. Therefore, the aim of this review is to identify the current focuses in forest modelling that are capturing most of the research effort.

Current Main Topics in Forest Modelling

To identify the current trends in forest modelling, we first carried out a search in the Web of Science database (https://www.webofscience.com/wos/woscc/advanced-search) for the years 2018 to 2022 using the terms "forest modelling," "forest function," "forest distribution," "forest adaptation," and "modelling forest function" (with their alternative spellings) in the title and keywords of documents. We identified a total of 4933 documents. Among those, we selected 154 papers that were reviews of different modelling topics. After screening for relevance, the selected review papers used for our narrative review were reduced to 79.

On a second phase, to objectively identify the most popular topics in the most recent literature, we used the visualization tool VOSviewer [13] with the database of 4933 documents to map the relationships between their keywords. However, as the statistical term "random forests" was distorting the database (data not shown), we removed the documents with this term. As a result, we retained 2040 documents for keyword mapping with VOSviewer v1.6.18 (Centre for Science and Technology Studies, Leiden University, the Netherlands, http://www.vosviewer.com). We limited the minimum number of occurrences for each keyword displayed in the map to 30 (Fig. 1). As a result, 20 different keywords were selected. This search was not intended to be a formal or in-depth quantitative review but merely a way to gain an unbiased and up-to-date insight on current popular modelling trends.

As main result of the keyword mapping, we found the term "climate change" as the most cited. Climate change also stood out in a central position among all other terms. In addition, four different clusters of terms were identified, with climate change being the main connector among them. The first cluster (in red in Fig. 1) could be considered as

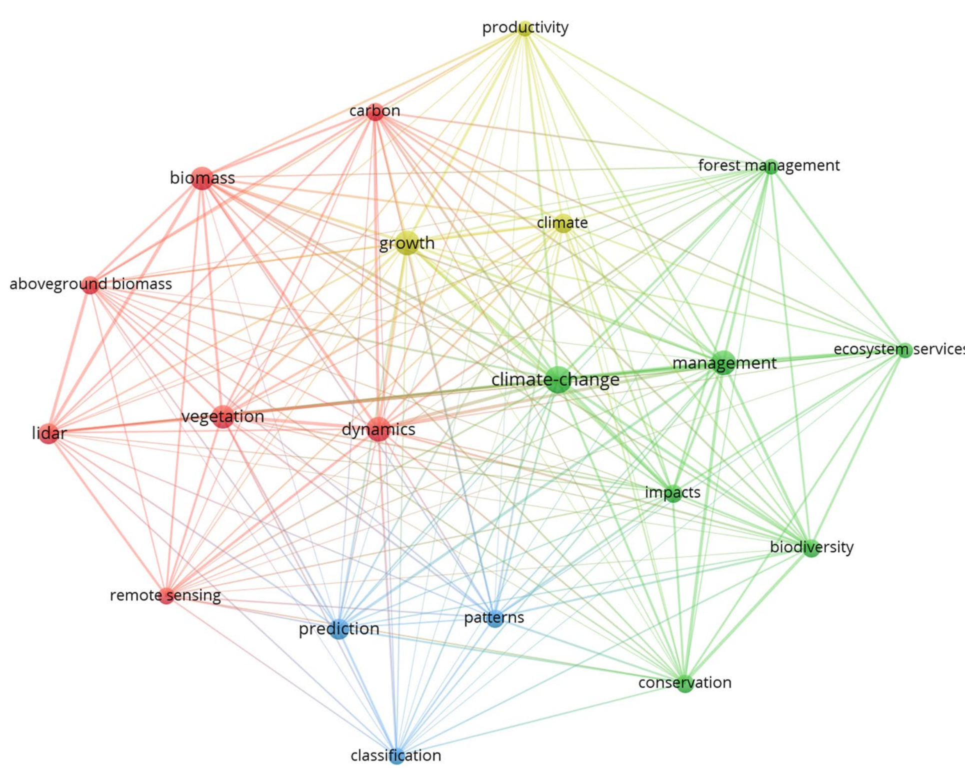

Fig. 1 Keyword map showing relationships between the 20 most common keywords in documents related to forest modelling published in the Web of Science in the 2018–2022 period. Different line and dot colors indicate different clusters of terms. Dot size is proportional to the frequency of each keyword, and line thickness is proportional to the frequency of co-occurrence of connected keywords

built around quantitative assessments of vegetation biomass (or carbon) using remote-sensing techniques (either aerial or terrestrial). The second cluster (in yellow in Fig. 1) was composed of the relationships between growth, productivity, and climate. The third cluster (in blue in Fig. 1) was limited to more technical terms related to model building. Finally, the fourth cluster (in green in Fig. 1) was related to ecosystem services and management, in combination with climate change. Below, we discuss the main trends in each of these clusters in the following sections, based on the 79 review papers identified as relevant.

Climate Change: the Main Driver for Forest Modeling

It is not surprising that climate change is at the center of current forest modelling efforts, a pattern already noticed in other recent reviews [14]. This result could just reflect the generalized wish by forest researchers to link their work to the current widespread scientific polices focused on addressing climate change, but it could also genuinely indicate the need for understanding how complex systems such as forests will behave under unknown climate conditions. Climate change is being observed as a major force behind many changes in current and future forest environmental changes [15–18]. Such changes will affect in different ways the key factors driving tree physiology, and therefore, new modelling approaches need to disaggregate climate influences on those drivers. Hence, understanding detailed effects of climate change, alone or in combination with other major drivers for change such as land-use change or biodiversity loss, is obviously the ultimate goal of much of the current modelling effort.

The realization of the first signs of climate change and the need for early action in forest management well in advance of other economic sectors (due to the long-lived nature of trees) has meant that for at least two decades, the need to provide forest models with capabilities to simulate climate change has been recognized [19, 20]. Such need has meant that the use of simple correlational models using traditional data from permanent plots or inventories has long been seen as inadequate among the scientific community for climate change-related studies, although such an approach can be very suitable for other research and management applications [21]. In addition, other models that had implicit representation of climate influences have moved into explicit representations to keep up with the knowledge demands on climate change effects on forest systems from different stakeholders [22–25].

Nevertheless, for the successful implementation of climate change simulation capabilities into forest models, modelers need to move beyond direct effects on temperature and precipitation. For example, a scarce availability of models able to link climate change with ecological disturbances has been identified [26]. Similarly, most regeneration algorithms used in forest models do not capture the effect of climate change [27]. In any case, climate change needs to be directly linked to modelling physiological responses (e.g., phenology, photosynthesis, respiration) and to frequency and severity of disturbances (fire, drought, insects' outbreaks, etc.). In turn, changes in these processes will also affect other ecosystem processes (allocation, allometry, growth at tree level, biodiversity, and competition at ecosystem level), and therefore, simulating climate change effects will indirectly be needed to improve how such processes are modelled.

Remote Sensing and Biomass Accounting

Biomass (in the form of timber, firewood, cork, fruit, resin, charcoal, etc.) has traditionally been the most important commodity obtained from forests. Therefore, it is not surprising that the different ways to estimate forest biomass and other closely related variables (i.e., timber volume, carbon) are still among the most important topics in current forest modelling efforts (Fig. 1). Among them, modelling strategies to sequester C stands out as one of the most important topics [28]. The large size and immobile nature of trees allow individual features such as diameter and height to be measured at different times over extended periods. Such an inventory-based approach can provide a wealth of data, but it quickly becomes a cumbersome task when large and diverse forest areas need to be assessed. However, the explosive development of remote-sensing techniques, the lowering prices of unmanned aerial vehicles, and the continuous growth in computing capabilities are generating the ability to finally obtain detailed assessment of not only the basic population features but also the structure and spatial distribution of individual trees over large areas [29••].

A model convergence towards the tree scale for meaningful C-cycle modelling, both from upscaling more physiologically oriented models and downscaling stand-level C accounting models, has been noted [30•]. However, not until very recently have researchers looked for ways to incorporate structural diversity into process-based models. A detailed review on the potential and limitations of using terrestrial laser scanning to calibrate functional-structural plant models is available [31•]. One of the main advantages of linking both modelling approaches is the potential to include physiological models into a realistic structure of plant communities. This could move structural modelling from individual to community level. In fact, there are suggestions that the merging of allometry, empirical observation, remote sensing, and individual-based modelling will contribute to a more unified vision of forest ecology [32]. However, to reach such a level of integration, proper processing of terrestrial laser scanning data is needed. In addition, researchers should avoid the temptation of upscaling functional-structural plant models to the landscape level, as it will be challenging due to the potential to misrepresent other ecological processes more relevant at such a spatial scale [33, 34].

Another important challenge to incorporate more remote sensing into forest models is the need for increased measures of standardization and uncertainty in observations [35]. However, these authors also highlight the high potential of remote-sensing data to automatize carbon models, which currently need manual and time-consuming calibration. In this respect, several issues have been identified when increasing the importance of remote data acquisition of canopy structure, such as the need for standardization of modeling approaches, the need for open datasets, the need to improve allometric models, and the need for stronger validation protocols [29••].

Allometric models are as important as remote sensing to estimate timber volume, biomass, or carbon stocks. Such models have been extensively used in the past but usually using data from pure and coetaneous stands [14, 35]. This situation introduces an important bias when estimating carbon or biomass stocks in natural forests, which are usually multispecies and multiaged, as species allometry changes in the presence of competitors [36]. Hence, using allometric equations from pure stands could be a source of uncertainty when modelling mixed stands, as there are significant differences in allometry for a given species when growing in a single- vs. multiple-species stand [37]. In addition, many of these allometric models do not include climatic or stand-level features [14], although recent research has been undertaken to address these shortcomings [25, 36].

The combination of different remote-sensing techniques such as LiDAR and radar can help to accurately model forest structure [29••]. An additional feature of models based on remote sensing is the potential to simulate and estimate radiation levels through the canopy and on the understory based on 3D data from LiDAR measurements. For example, the division of the canopy into volumetric pixels (or "voxels") allows for simulating the interaction between trees, understory, and radiation at individual-tree levels or even smaller scales. In fact, 3D canopy simulation can be a more reliable way to estimate energy and C fluxes than traditional inventory-based approaches [38]. In addition, such models could help in improving connections between forest and atmosphere models [39].

Additional issues when simulating C fluxes, particularly C allocation, have been identified [40•]. These authors have highlighted that the common use of fixed ratios for allocating C to plant organs is a severe oversimplification under climate change, as it removes from the model the sensitivity to environmental conditions and disturbances. In addition, the usual time steps in forest models (seasonal or annual) are too large to capture C allocation dynamics and resource acquisition. In summary, the generalized use of allometry and inventory-based approaches is just not adequate to capture short-term C dynamics [40•].

Patterns vs. Processes

A second main topic in current forest modelling research is the development of new and refined methodological approaches, mostly through the use of advanced mathematical or statistical tools or by borrowing them from other fields. New progress is made almost daily in deep learning methods than are revolutionizing modern ecology [41]. These methods have great potential to improve computationally costly tasks such as classification of information from remote sensing or simulation of interactions between individuals in large forest areas. The use of these advanced statistical techniques is greatly expanding modelling capabilities to link research done at multiple scales, to simulate larger regions, and to incorporate dynamic changes at shorter temporal scales (crucial for accurate C flux modelling).

The need for such increasingly powerful approaches is clear by the two keywords highlighted in our review for this cluster ("prediction" and "pattern," Fig. 1). There is a dire need for tools that can provide usable predictions for managers, as the forestry sector needs to adapt to climate change even earlier than other sectors, given the long-term consequences of current management decisions [42]. Hence, using techniques to simplify model use will undoubtedly facilitate the generation of tools easy to interpret and to share with non-modelers, and that can be easily compared with expert knowledge [43]. This idea of simplification while retaining the behavior of complex process-based models is behind the developments of "model emulators" [44].

Model emulators are built to mimic the same outputs from complex (usually process-based) models, with the main objectives of reducing computing requirements. This simplification allows for integration of the emulator in other modelling platforms (and therefore connectivity with other models or submodules different from the original process-based model), to expand temporal and spatial scales not reachable with the original process-based models or to simplify interaction with model users. Such expansion of the basic model could be crucial to understand ecological patterns that emerge at higher scales and that otherwise would not have been directly inferred by the underlying process-based model [45]. Hence, emulators could be valuable tools in the future to understand ecological patterns at large scales, particularly under novel ecological conditions created by the combination of climate, biodiversity, and land-use changes.

However, the development of emulators also brings an important challenge to the field of ecological modelling. The substitution of process-based algorithms by machine-learning based decision rules offers clear advantages. Nonetheless, it could also be considered as a process to create "black box" models in which scientific understanding of ecological process is impeded, as the mechanisms behind such processes are simplified to just algorithms that have the same outcomes. A detailed review on model simplification is available [46].

Obviously, this situation highlights the need for a dual direction in scientific advancement: while emulators are clearly useful tools to study ecological patterns, ecological processes can be better studied with mechanistic process-based models (although such a division is not so clear [44]). Advancement along both lines will also support the development of "digital twins": computer-based copies of real forests constructed to mimic the most intricate patterns and processes, with visualization of virtual stands as one of their main strengths. These digital tools are already being proposed to train managers and researchers in understanding how climate change and new management techniques could facilitate the transition of the forest sector towards novel conditions [47]. Obviously, digital twins depend not only on the simulation and visualization techniques used but also on particularly the availability of quality data to calibrate them. Here again, remote sensing, forest inventories, and traditional fieldwork data will be crucial, as the old-fashioned rule in ecological modelling is still valid: in the absence of adequate data, all different modelling options are equally valid [43].

Productivity Still a Concern

A third popular topic in current forest modelling is related to forest productivity and growth (Fig. 1). This indicates that, even if for more than two decades efforts have been made to add non-timber forest products to forest models (i.e., [48]), estimating forest productivity is still a major issue in the field. This research cluster is clearly focused on how tree growth is influenced by climate. One of the key features of the research on this topic are the continuous calls for development of new growth models for species and regions outside North America, Europe, and to a lesser extent Asia [49, 50••]. An example of successful model application around the world is the spread in the use of 3-PG, which was originally developed for Australian eucalyptus plantations but has been embraced and modified for its application in multiple regions and stand types [51]. The widespread application of 3-PG by scientists and managers was recognized in 2020 by the Marcus Wallenberg Prize which was awarded to their developers (https://mwp.org/link-to-mwp-digital-ceremony-and-symposium/).

Productivity estimations will remain crucial in the near and medium future, as commercial forestry will likely become more focused on high-yield intensively managed plantations to sequester and substitute carbon-intensive materials. Conservation forestry will increasingly expand into forest reserves around the world to increase stored carbon and protect biodiversity. In this context, the development of basic (but management-friendly) correlational models such as allometric and inventory-based models is needed [35, 52, 53]. However, the need to include climate in all these new models is certainly a challenge for new regions and species, as they would need either long-term data series or an extensive network of inventory plots to account for climatic influences on tree growth rates or allometry. Hence, new developments in automatic and climate-sensitive tree monitoring devices may be helpful [12].

Modelling Forests Beyond Trees

While tree growth and productivity are still an important topic, the largest cluster of research topics identified was related to modelling forest components other than trees. Most of this research is based on the clear understanding that for models to be able to handle climate change effects, it is essential to include more ecosystem components that historically have received less attention [21].

Some key issues are the improved assessment of carbon and water cycles. For example, it has been stated that those models using drought indexes that include an evaporative component work better, but also that there is just a small number of studies actually evaluating drought indexes against physiological indicators of water stress [54]. In this respect, a recent review of the way in which the representation of evapotranspiration processes has evolved in forest models has noticed a trend towards the simplification from the initial attempts, achieved by the availability of more empirical data and model evaluation tests that have allowed the refinement of simulation algorithms [55]. These authors have pointed that such simplification allows for further connections to water flow models and the scalability of such research. This is an important advance, as the common oversimplification of eco-hydrological processes in models makes linkages with socio-economic values more difficult to evaluate [56•]. These authors also pointed to a lack of empirical work on effects of water availability in forest productivity. Further developments that mechanistically link hydraulic conductance with physiology, growth and mortality are taking place [57–59].

How biodiversity is integrated into forest models is another of the issues in this keyword cluster. Traditionally, there is a biodiversity bias towards trees in forest models [60]. This is not surprising, as biodiversity interactions (both animal and vegetal) in forests are a complex and broad field that have not been incorporated into models until relatively recently, and that still remains largely ignored in operational models used in forest management. In this regard, a lack of integration of modelling approaches at different spatiotemporal scales has been identified as a barrier to implement biodiversity into forest modelling [61]. Similarly, calls for more attention to the role of understory in key ecological processes have been raised [62], even if early examples of the importance of tree-understory interactions when simulating commercial forestry are available [e.g., 63]. It is currently advocated that the most efficient approach is to use plant functional traits that can accommodate the inherent complexity of understory communities. To do so, models must have detailed time and spatial scale to allow for the different ecophysiological behaviors (many times resource opportunistic) that understory species usually display, particularly following disturbances [64].

An important effort currently taking place in vegetation science is determining how functional traits can be applied to models to understand how species with different traits interact. An important and ongoing development is to expand the functional trait approach being developed for vegetation studies [65]. This is particularly important in highly diverse ecosystems such as tropical forests in which it is unrealistic to simulate forest dynamics with only a few dominant species.The functional trait approach is now being expanded to model species interactions including animals, particularly herbivores. However, mechanistic models of forest pests are usually based on correlations between environmental variables (e.g., degree days) and growth rates (usually at individual or population scales), and limited to some of the pest's life cycle stages. Hence, there is a need for models able to integrate current algorithms that simulate specific pest and pathogens at different development stages to obtain meaningful estimates of their interactions with the rest of forest components [43]. More intriguingly, concerns have been raised around the usually forgotten role of megafauna in forest models [3••]. Although it has been traditionally assumed that the effects of megafauna are realized at the forest level through seed dispersal, arguments exist to also consider their impacts on nutrient cycling and plant demography, such as the role of megafauna on predation of plant reproductive organs, mortality caused by herbivory or trampling, and nutrient redistribution related to animal residues [3••]. A serious effort to better understand the role of megafauna in forests is needed, given the current situation of defaunation in many areas of the world, which in some areas is trying to be reversed by rewilding actions. The use of "herbivore functional traits" (equivalent to the already accepted concept of plant functional traits) and different ways to incorporate linkages between plant and herbivores into process-based models have been suggested [3••]. This issue is not limited to tropical or natural forests, as the influence of large herbivores on tree and shrub density in boreal [66] and temperate forests [67] has been reported, with or without management.

Other approaches to account for biodiversity include the use of habitat and species distribution models. They link the smallest (habitat) to the largest (distribution) spatial scales and provide a better understanding of the potential impacts of novel ecological conditions over the mid to long term. The dramatic increase of available data on climate, soils, and species distributions allows for finely gridded modelling at both temporal and spatial scales. This advance allows statistically based species distribution models to be linked to process-based models [16, 68], although better understanding of absence data and improved inclusion of abiotic interactions will become crucial to estimate effects of climate change [69, 70].

Finally, an always-important topic in forest models is the integration of management into modelling. Such integration has two clear foci: simulation of management practices and involvement of forest managers into the modelling process [71]. As forest management is inherently an ecological disturbance, including management simulation in forest modelling should not be limited to anthropogenic actions but should include natural disturbances as well. However, the main limitation that needs to be solved is the lack of information on the specific mechanisms that link climate change with disturbances [26]. This is especially important when several disturbances can be connected through cascading effects on the ecosystem [42, 72].

Important conceptual advances in disaggregating disturbances into their constituent components and embedding disturbances into system dynamics have been recently completed [50••]. These authors have identified as important challenges the need for simulating nondeterministic competitive interactions between tree species and their responses to disturbances and suggest using life history traits to overcome this issue. However, although these linkages among disturbances have been long recognized in forestry, little research has actually incorporated them into forest models, particularly as multi-disturbance models [50••]. In addition, most models that incorporate disturbances predict probabilities for such disturbances to happen depending on different stand features, but not the disturbances effects [26]. Among disturbances, wildfire modelling is an important field by itself. As in the case of other disturbances, abiotic factors such as slope, elevation, distance to roads, or weather patterns are important for incorporating complexity at small spatial and temporal scales [73]. However, getting good quality for such small-scale variables could be a challenge in areas with dense forest cover and sparse road networks, as is the case in most tropical or boreal forests [74].

Another important step in making forest models more meaningful for stakeholders include modifying the way models are created. The focus on participatory processes in which model users and forest stakeholders interact with forest modelers during the inception of the modelling studies is being increasingly recognized as fundamental for the model to make actual impact in the forest sector [44]. This approach aims to bring nonacademic forest stakeholders into the process at the beginning, so they develop a sense of ownership of the research outcome and therefore are much more likely to implement the model outcomes. Three models for science-policy interaction have identified [74]: the "linear phase" when science informed policy-making in a unidirectional manner, the "interactive phase" when both sides found themselves in a continuous interaction, and the "embedded phase." Our own experience is that the linear phase is still dominant in many regions, with scientists developing models and scenarios of their interest and then approaching nonacademic stakeholders with their results. Only in some scarce cases the interaction has progressed and moved into the second stage of science-policy interaction (i.e., [44]). It is then time to push towards a multi-actor approach (the second "interactive" phase of bringing science into practice). However, to achieve this goal, models need to be accessible, relevant, and user-friendly for non-modelers and address current forest management concerns to actually bring change into forestry practices [76]. A comparison on how different European decision support systems are facing these challenges has identified the need to incorporate forest owner behavior and accurate spatial analysis to better estimate landscape-level provisioning of ecosystem services [77].

Next Challenges for Forest Model Convergence

Understanding how complex ecosystems such as forests are structured and function as a system has been, still is, and will be challenging. The challenge lies in understanding how climate change affects forests, while our understanding on how to model forests under "normal" conditions is still far from complete. In addition to the most popular topics currently being explored in forest modelling discussed earlier, we have identified through our review several topics that deserve mention due to their relevance, even if they did not explicitly appear in the keyword map in Fig. 1. Such topics include the following:

- *Small forests*: Landscapes around the globe are becoming increasingly fractioned, making small forests of a few hectares or smaller increasingly common. Managers of such forests usually have limited resources to access and use models, and models usually lack representations of external factors (such as the vicinity of agriculture lands) that can be relevant for the functioning and structure of small forests [76].
- *Urban forests*: As urban landscapes expand, urban forests are becoming very important in delivering a multitude of ecosystem services. However, urban forest models have been developed only for few regions around the world (i.e., USA, Europe, and China) and are mostly correlational in nature. To better assess the effects of climate change on ecosystem services, better linkages with ecophysiological mechanisms must be incorporated into urban forest models [49]. Among the potential ecosystem services that could be modelled in urban forests are not only carbon sequestration [78] but also aesthetic values [79].
- *The Global South*: A recurrent finding in all recent forest modelling reviews is the strong bias towards North America and Europe [38, 50••, 52], followed by East Asia to a lesser extent (mostly China and Japan). Some isolated modelling hotspots in the southern hemisphere are Australia (which has generated one of the most successful forest models, [51]) and Brazil (mostly focused on modelling plantation forests but also generated some work on Amazonian forests). More effort must be made to better understand the applicability of models from other regions to these areas that are underrepresented in the scientific modelling literature. This is an important research area given regional variations in terms of tree, understory and wildlife species composition, and other environmental constraints such as climate, edaphic factors, or human management models.
- *Overlooked physio-ecological processes*: Two important mechanisms have attracted little attention in forest models until now. One is regeneration (including masting), which is now recognized as a process that can significantly affect biomass allocation and hence carbon and energy flows. Even if detailed conceptual models on forest regeneration have been available for some time (i.e., [80]), regeneration has usually been oversimplified in forest models [81]. However, recent important advances in understanding the masting process allow for the implementation of mechanistic models [82]. Giving the inherent complexity and current incomplete understanding of the process, modelling regeneration patterns could be a more practical approach than modelling processes in order to avoid error propagation, especially if models are to be scaled up to regional or larger areas [83••]. Another overlooked topic is root growth and function. Traditionally, the simulation of fine roots has been underdeveloped compared to leaves, and hence, a common approach has used allometric relationships of fine roots to other biomass fractions

[84]. However, the latest research indicates that this is not always appropriate, but also that enough data for mechanistic root models are starting to be available [85]. Given the important role of roots in carbon, nutrient and water cycles, and the influence of such cycles on tree mortality [86], a more mechanistic modelling approach would be desirable.
- *Uncertainty assessment*: Traditionally, the study of climate change effects on forest has relied on modelling different climate scenarios, management options, and their interactions. However, such an approach does not provide a clear picture of the uncertainty around model predictions. Hence, moving from scenario assessment towards uncertainty analysis has been proposed [56•, 63]. To do so, using predictions from different models would be useful, particularly if the models use different approaches [16]. The viability of assessing uncertainty through using envelopes of models has been demonstrated and refined [19, 87].

Conclusions

Our review of current trends in forest modelling has shown that climate change is the main driving force that is stimulating researchers to develop new approaches and methods to model forest ecosystems and forest managers to use such models. It has also shown that we are at an exciting moment, in which the development of new statistical and measurement techniques is finally creating opportunities for developing true inter-scale models, from individuals to regions and beyond. In addition, the present need to incorporate users into the modelling process is stronger than ever, and options exist to simplify science-based models into operational models without losing accurate representation of ecological patterns. However, the need to better understand ecological process is also more important than ever as climate, biodiversity, and land-use changes move forest ecology of the Earth to novel conditions. Hence, improving the mechanistic representation of ecological process in an integrative manner that moves beyond trees will be crucial for meaningful predictions of forest ecosystem development under novel conditions. In conclusion, we have shown that the traditional division between process-based and statistical models lacks actual meaning, as the major trend is towards cross-scale integration of different modelling approaches.

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Declarations

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

Conflict of Interest Juan A. Blanco and Yueh-Hsin Lo declare that they have no conflict of interest.

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•• Of major importance

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