Tackling unresolved questions in forest ecology: the past and future role of simulation models

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Abstract

Understanding the processes that shape forest functioning, structure and diversity remains challenging, although an increasing amount of data documents forest systems across scales. Forest models have a long history in assimilating various data and ecological knowledge and can simulate forest dynamics over spatio-temporal scales unreachable by most empirical investigations. Here we describe the trajectories of development different forest modelling communities have followed to demonstrate the leverage that computer models offer for advancing the understanding of forest ecosystems. Using three widely applied but contrasting forest modelling approaches - species distribution models, individual-based models and dynamic global vegetation models - as examples, we show how scientific and technical advances have led models beyond their initial objectives and limitations. We provide an overview of recent model applications on current important ecological topics and pinpoint ten key questions that could, and should, be tackled with forest models in the next decade. This shows that forest models, due to their long history of assimilating empirical knowledge, their iterative and continuous development, and their complementarity, represent an invaluable toolkit to address a wide range of theoretical and applied ecological questions, hence fostering a deeper understanding of forest dynamics, particularly in the context of global change.

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Introduction

Forests cover about 30% of the Earth's land surface, store almost half of the terrestrial carbon, constitute a net carbon sink, supply important resources to billions of people, and host over half of Earth's biodiversity (Pan et al. 2011; Jenkins et al. 2013; Vira et al. 2015; Ramage et al. 2017). Yet, ongoing and future environmental changes put forests at risk. This rises the demand for a more detailed understanding of forest dynamics and for assessing the future of forest ecosystems to continuously update our knowledge base and support decision-makers (United Nations 2014; Mouquet et al. 2015; IPBES 2016; Mori 2017). Forest ecology is however confronted with the challenge of investigating complex systems that are characterized by long-term dynamics over large spatial scales, and therefore many questions remain unresolved (Sutherland et al. 2013).

During the past decades an increasing amount of field and remote sensing data has been made available, providing valuable information on forest ecological systems at various spatial and temporal scales and resolutions. However, their integration into a coherent picture remains a considerable challenge (Levin 1992; Chave 2013; Estes et al. 2018). In parallel, a variety of vegetation and forest models have been continuously developed by different scientific communities and for different purposes. Orchestrating the interplay of various data with forest modelling has been identified as a promising approach to tackle current research challenges (Zuidema et al. 2013; Shugart et al. 2015; van der Sande et al. 2017). The availability of various forest modelling approaches and decades of experience in assimilating observational knowledge offer invaluable tools to address key applied and fundamental ecological questions on forests.

Our contribution draws on the simultaneous trajectories of development that different modelling communities have followed until today to evidence the powerful capabilities models offer to understand forest ecology. In the first part, we present three widely used, but contrasting, modelling approaches to simulate forests, namely species distribution models (SDMs), individual-based forest models (IBMs) and dynamic global vegetation models (DGVMs). Our aim is to illustrate the diversity of modelling approaches to address key ecological questions for forests. In doing so, we outline the development of these different modelling approaches over the past decades. In a second part, we discuss how scientific and technical advancements have been alleviating the main constraints that initially restricted applications of forest modelling, and show how model development have progressively allowed models to tackle questions beyond their historical objectives. Finally, we will sketch out how forest models, singly and in combination, could take on an increasing role in addressing a variety of key ecological questions in the future.

1. Different approaches to model forests

Different approaches have been developed to model forest ecosystems and community dynamics, as well as forest cover and tree species distributions. They range from basic theoretical models such as neutral models (Hubbell 2001), through models of growth patterns of individual trees, to forest stand or landscape models (Shifley et al. 2017), or global vegetation models (Prentice et al. 2007). Depending on the specific objectives of the developing scientists, the model representation of biogeochemical processes, vegetation structure, or biodiversity have been more or less detailed, by means of different degrees of aggregation or abstraction or following various assumptions.

The three model types we briefly present here - SDMs, IBMs, DGVMs - have been developed by different disciplines and cover a gradient from models that initially focused on a detailed representation of individual species to models that gave initial emphasis to the representation of forest structure and tree demography, to others that focused on the representation of biogeochemical processes. We chose these model types, which have a long history and are all widely used, especially in the context of global change, to illustrate the variety of modelling approaches, but our general ideas also apply to other model types. In the following, we present these three approaches by ordering them along a gradient of decreasing resolution of biodiversity

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representation and increasing resolution of biogeochemical process representation, acknowledging other orders could have been used alternatively.

Species distribution models

Species distribution models (SDMs; Booth et al. 2014; Guisan et al. 2017) focus on the spatial distribution of species and how it varies with environmental drivers. SDMs have their origin in flora distribution maps, which laid the concepts of biogeography (Humboldt 1849; Grisebach 1872). The development and increased usage of SDMs across a wide array of taxa and environments have relied on several technical advances (Guisan & Thuiller 2005; Elith & Leathwick 2009), namely statistical approaches (e.g. MaxEnt), methods for physical environment mapping (e.g. remote sensing techniques), and increased coordinational effort to compile knowledge on species records. All these approaches have been boosted by geographic information systems (GIS).

SDMs rely on the concept of ecological niche (Hutchinson 1957; Guisan & Thuiller 2005; Soberón 2007), and can be described as a two-step process as follows. First, the ecological niche representation of a species is built in an environmental space, based on known records in places where environmental conditions have been described. Then each geographic location is assigned a probability of occurrence for the species, based on the niche model (Elith & Leathwick 2009).

SDMs thus require little information on the processes from which species distributions result. This can be an advantage, e.g. for poorly known taxa in demand of conservation actions. Also, by looking for a best model fit in species niche modelling, important environmental drivers of spatial species patterns may be revealed (e.g. Thuiller et al. 2003; Bertrand et al. 2012). SDMs have also been used to predict species distributions under future environmental conditions, such as species invasion or climate change (Thuiller 2003; Thuiller et al. 2005). However, key assumptions of SDMs, mainly that species are at equilibrium with their environment (Václavík & Meentemeyer 2019), and that the species-environment relationships are valid beyond the range of model calibration, may be violated under such applications (Svenning & Skov 2004; Araújo & Pearson 2005; Veloz et al. 2012). Classical SDMs are further limited to a species-by-species approach, and thus typically overlook the role of species interactions in shaping species distributions (Dormann et al. 2018). Additionally, the inherent spatial autocorrelation (SAC) of species distribution and environmental variables can bias the estimated performance of SDMs (Bahn & McGill 2007; Fourcade et al. 2018), calling for care when using extrapolations from SDMs (Sofaer et al. 2018). However, at the same time, accounting for SAC in SDMs by various methods (Dormann et al. 2007; Václavík et al. 2012) can improve the accuracy of SDMs because SAC is often a result of important ecological processes (e.g. dispersal limitation, colonization time lag) that drive species distributions.

The integration of processes into SDMs is likely critical to infer species distributions in novel environments or under no-present analogue conditions (Kearney & Porter 2009; Dormann et al. 2012; Urban et al. 2016). Models that combine the traditional approach of SDMs with process-based information (Morin & Lechowicz 2008; Thuiller et al. 2008), such as dispersal limitation or phenology, have been developed (Stephenson 1990; Kleidon & Mooney 2000; Chuine & Beaubien 2001; Bykova et al. 2012; Nobis & Normand 2014; Duputié et al. 2015). Progress has also been made to integrate species competition as biotic factors influencing species realized niche (Leathwick & Austin 2001; Meier et al. 2011) and further extend these ideas to full ecological communities (Ferrier & Guisan 2006).

Individual-based forest models

There is a long tradition in ecology and forestry to use individual-based forest models, to answer a broad range of scientific questions. This type of models simulates the development of each individual tree within a forest stand. A key component is the interaction between single trees (e.g. by shading) which is crucial for tree growth and influences community dynamics. The simulation of individual trees allows to capture not only forest structure but also tree species diversity. A widely known type of individual based forest models

is forest gap models (Shugart 1984; Huston et al. 1988). First developed for forest stands in North America, they have since become among the most used model types in ecology (Botkin et al. 1972; Shugart & West 1977; Shugart et al. 2018).

In the gap model approach, a forest stand is described as a mosaic of forest patches, (also named gaps). The dynamics of the forests emerges from the growth, mortality, establishment and competition of individual trees (Bugmann 2001; Porté & Bartelink 2002). Trees compete for light, water and nutrients. The vertical distribution of leaves is used to calculate the light availability for each tree, what affects growth and mortality. For competition with neighbouring trees a competition range has to be assumed (the patch size), wherein all trees compete with each other (a large tree should also fit into a patch). Due to the individual-based concept, these models are able to describe the successional dynamics of forests (mosaic dynamics, e.g. Watt 1947) and the natural heterogeneity of forest stands (Knapp et al. 2018). The coupling of biogeochemical processes is modelled in an aggregated way in forest gap models, using the concept of limiting factors (affecting tree growth rates). Gap models can simulate the impact of temperature, precipitation, CO2 and light on tree dynamics, and thus on forest productivity, biomass and species composition (Solomon 1986; Pastor & Post 1988; Overpeck et al. 1990). Some early studies also included nutrient cycles (e.g. Pastor & Post 1986). Gap models can be applied with daily time steps, but are typically used with monthly or annual time steps.

Modules for forest management (e.g. Liu & Ashton 1995; Huth & Ditzer 2001; Mina et al. 2017) and disturbances like fire (Kercher & Axelrod 1984; Fischer 2013), browsing (Seagle & Liang 2001; Didion et al. 2009) or wind through (Seidl et al. 2011, 2014a) have been included in subsequent studies. Tree mortality can thus be described as an exogenous process (e.g. by disturbances), but also as a growth-dependent and/or intrinsic process (e.g. Keane et al. 2001). Although gap models were first developed for temperate forests in the USA, they were soon applied also for European temperate forests (Kienast 1987; Bugmann 1996) and boreal forests (Leemans & Prentice 1989). Since the 90's, forest gap models for tropical forests have also been developed (Bossel & Krieger 1991; Kohler & Huth 1998; Fischer et al. 2016). To simplify the high species richness of these forests, tropical gap models typically simulate forest succession by grouping tree species that share similar ecological features into several plant functional types (PFTs). The gap model approach was also extended to grasslands (Smith & Huston 1990; Taubert et al. 2012).

From the 1990s onwards, models that keep track of the positions of each tree in a finer-grained grid (i.e. they are spatially-explicit) and thus allow for a more detailed computation of tree light availability have been developed (Pacala et al. 1996; Chave 1999; Pretzsch et al. 2002; Marechaux & Chave 2017). Other model developments have led to a more explicit representation of processes, for example by including a more detailed temperature and CO2 dependence of photosynthesis and respiration, or a more detailed water and carbon cycles or site fertility (Fischer et al. 2016; Marechaux & Chave 2017). Similarly, novel parameterizations have allowed to simulate hundreds of species within communities (Marechaux & Chave 2017; Ruger et al. 2019). Other stand-based models were designed to describe forest stand structure dynamics driven by ecophysiological processes in higher detail and finer time scales (Kramer et al. 2002; Morales et al. 2005; Medlyn et al. 2007), although often at the cost of simulation temporal or spatial coverage. Individual-based forest models have since been used to address a variety of basic and applied research questions (Bugmann & Pfister 2000; Seidl et al. 2012; Bohn et al. 2014; Fischer et al. 2016; Shugart et al. 2018). Modern extensions of these models allow also simulations of forests at large spatial scales (e.g. for whole countries or continents, Xiaodong & Shugart 2005; Sato et al. 2007; Scherstjanoi et al. 2014; Rodig et al. 2017; Thom et al. 2017).

Dynamic global vegetation models

DGVMs have their origin in four different modelling research areas that were initially investigated separately: plant geography, biogeochemistry, vegetation dynamics, and biophysics (Prentice et al. 2007), with HYBRID, LPJ and TRIFFID as being among the first DGVMs (Cramer et al. 2001). DGVMs have been initially developed to represent the interaction between vegetation and the global carbon cycle as independent models, but also to represent vegetation dynamics in Global Circulation Models.

DGVMs simulate vegetation dynamics on daily to monthly time steps at the global scale, driven by climate, atmospheric CO2 concentration, and soil information, hence using plant physiology and biogeochemistry to explain biogeography (Sitch et al. 2003; Krinner et al. 2005). This approach results in calculating the large-scale distribution of potential natural vegetation. Main components of each DGVM are process-based representations of photosynthesis, respiration, leaf transpiration, carbon allocation, mortality and disturbance. The exchange of carbon and water fluxes is represented at the leaf level by stomatal conductance (Ball et al. 1987; Collatz et al. 1991).

Describing vegetation dynamics at the global scale inevitably entails strong model simplifications to represent vegetation. These models use PFTs to aggregate functionally similar species to represent functional properties at the biome scale. Usually global vegetation is described with 5 to 14 PFTs by differentiating life form, leaf form, phenology, or photosynthetic pathway, e.g. tropical broad-leaved raingreen tree or C3 grasses (Woodward & Cramer 1996; Prentice et al. 2007). Hence, these PFTs represent a less detailed description of species diversity within forest communities than the ones used in IMBs. Additionally, DGVMs often conduct simulations using a relatively coarse-grained grid (typically of 0.5deg lat/lon resolution) in which characteristics of each cell are assumed to be homogenous, simulating average individuals per PFT, where several of them can compete within one gridcell. Hence local competition processes are oversimplified and the influence of spatial structure within this coarse grid cell is neglected. Moreover, DGVMs typically apply the 'big-leaf' approach, whereby photosynthesis of the PFTs is simulated based on one photosynthetic surface throughout the grid cell. Most stand-alone DGVMs are not initialized with any observed vegetation distribution, nor with any values for the carbon and water pools. The global PFT and carbon-pool distribution is therefore determined by the given abiotic conditions and PFT-specific characteristics. Hence, each change in abiotic conditions (e.g. climate change) results in a non-prescribed reaction of the vegetation.

Although DGVMs were originally developed to simulate potential natural vegetation, including fire disturbance (Lenihan et al. 1998; Thonicke et al. 2001), they have been advanced by simulating land-use (Bondeau et al. 2007; Boysen et al. 2016; Langerwisch et al. 2017; Rolinski et al. 2018), water management (Jagermeyr et al. 2015), and forest management (Bellassen et al. 2010). In order to account for the role of nutrient deposition in vegetation dynamics and its interaction with the global carbon cycle, several DGVMs have further developed an explicit representation of nitrogen and phosphorus cycles (Wang et al. 2010; Smith et al. 2014; Reed et al. 2015; Goll et al. 2017; von Bloh et al. 2018). Similarly, a more explicit representation of tree hydraulics and water flows has been developed in some DGVMs to better assess the effect of climatic changes on evapotranspiration and drought-related mortality (Hickler et al. 2006; Bonan et al. 2014; Langan et al. 2017; Joetzjer et al. 2018). The need for a more realistic representation of vegetation structure and biodiversity to improve the predictive power of DGVMs has been highlighted to improve the predictive power of DGVMs (Quillet et al. 2010; McMahon et al. 2011). To achieve this, several developments have been made to include a finer representation of vegetation demographic processes (Moorcroft et al. 2001; Smith et al. 2001; Hickler et al. 2012; Fisher et al. 2018) and functional diversity (Pavlick et al. 2013; Scheiter et al. 2013; Sakschewski et al. 2015; Verheijen et al. 2015). Lately, also seed dispersal of trees and therefore the ability for tree species migration has been implemented into hybrid DGVMs (Snell & Cowling 2015; Lehsten et al. 2019).

In the following parts, we will henceforth use the terms "forest models" and "forest modelling" to describe the variety of models that have been used to simulate forest systems, among which the three above-described model types are widely-used examples, acknowledging that each model type is also used to simulate other ecological systems.

2. Forest modelling challenges and solutions

Forest model development and predictive ability have been constrained by different factors, mainly resulting from (i) data availability, (ii) technical challenges, especially the availability of computing resources, and (iii) an incomplete process understanding. While advancements were made on all these points, some challenges

are at the same time further amplified as models seek to adopt a finer-scale representation of processes, vegetation structure and diversity, while sustaining or expanding the spatio-temporal scale of simulations. Here we briefly present these main types of obstacles encountered in forest modelling and approaches that are being developed to overcome**them** .

Data availability

Forest models are data-demanding across the different steps of model development and application. A robust parameterization of the multiple processes related to plant life cycle and physiology for diverse plant types, species or individuals requires various data across scales, from plant organ to population, including environmental factors. For many processes, such data are often not available in the required quality and resolution, e.g. for tolerance of trees to resource limitations (McMahon et al. 2011; Craine et al. 2012; De Kauwe et al. 2015) or soil characteristics (Marthews et al. 2014). Additionally, a thorough initialization and validation of forest simulations over large spatial and temporal scales requires observation data encompassing both fine resolution and large coverage over long time spans, which can still be a challenge (Estes et al. 2018, Table 1).

Fortunately, data availability is increasing at a high pace. Global plant trait databases (e.g. TRY, Kattge et al. 2011; Table 1) gather data of commonly measured traits (e.g. leaf mass per area or wood density) for a wide range of species, and this effort is being expanded to other traits (e.g. stem and leaf drought tolerance, Bartlett et al. 2012, Choat et al. 2012; fine root traits, Iversen et al. 2017; litter decomposition rates, Brovkin et al. 2012). This fosters a systematic model trait-based parameterization for a range of plant species and individuals. For example, Scheiter et al. (2013) and Sakschewski et al. (2015) used reported trait coordination to constrain individual trait combinations in simulations of forest dynamics with DGVMs. In doing so, they improved model representation of functional diversity from a few discrete plant functional types to a continuum of traits, while excluding unrealistic trait combinations (Van Bodegom et al. 2012). Similarly, by taking advantage of comprehensive trait databases, but also of long term inventories and of the detailed information they provide on tree life-histories, forest IBMs have been allowed to simulate hundreds of species within diverse forest communities (Marechaux & Chave 2017; Ruger et al. 2019).

Simultaneously, networks of forest plot inventories are being complemented by remote-sensing data (Table 1), offering novel opportunities to initialize and/or validate model simulation over large spatial scales (Shugart et al. 2015) or complement predictors of SDMs (Fedrigo et al. 2019). Recent advances in remote sensing tools, such as the possibility to derive tree-level information within dense canopies (Ferraz et al. 2016) or fuse spectrometer data with co-registered LiDAR data (Jucker et al. 2018), provide new ways to parameterize models (e.g. allometries, Jucker et al. 2017; Fischer et al. 2019). Citizen science programs have also been developed to create new opportunities of forest data sampling over large areas (Delbart et al. 2015; Giraud et al. 2016; Affouard et al. 2017; Waldchen et al. 2018).

The development of machine learning techniques offers new possibilities to use the resulting huge datasets for model development and evaluation (Botella et al. 2018; Forkel et al. 2019; Reichstein et al. 2019). Rammer & Seidl (2019), for instance, have used deep neural networks to estimate vegetation transitions across large spatial scales. Additionally, bayesian and/or inverse modelling approaches can be used to take advantage of diverse sources of data to estimate process parameters and calibrate entire models (van Oijen et al. 2005; Hartig et al. 2011, 2014; LeBauer et al. 2013; Dietze et al. 2014; Lehmann & Huth 2015; Fischer et al. 2019). For example, van Oijen et al. (2013) found a strong reduction of uncertainty in most forest models after a Bayesian calibration.

Table 1

Technical challenges

Several technical obstacles constrain model developments and runtime. First, computing power – in terms of speed and memory – imposes a trade-off between simulation resolution and coverage, still today limiting large-scale applications or the fitting of fine-grained models. For example, the finer-grained representation of forest biodiversity and structure recently implemented in a DGVM model (LPJmL-FIT, Sakschewski et al. 2015) was restricted to one biome (Tropics of South America) as opposed to the global scale typically reached by classic DGVM simulations. However, computing power will probably continue to increase in the next years (Kurzweil 2005), which, together with parallel processing, model upscaling and improved algorithms, allows continuous reduction of computing time (von Bloh et al. 2010; Snell 2014). As an illustration, using Fast Fourier Transformations for seed dispersal instead of modelling dispersal from each cell to each other increased the computing speed by a factor of 100 (Lehsten et al. 2019). Additionally, remote-sensing observations allow the up-scaling of individual-based forest models at lower costs (Shugart et al. 2015). For example, by using remote-sensing-derived measurements of forest height across a gridded map over the Amazonian basin and a locally optimized gap model, it was possible to estimate the forest successional stages of every cell in this area and derive maps of aboveground biomass and productivity of the whole basin (Rodig et al. 2017, 2018). However, a fundamental change of an algorithm in complex models can invoke unplanned side-effects, sometimes forcing modelers to invest substantial time and effort to stabilize the new model versions.

Second, expanding model development and applications relies on code and data sharing within and among larger communities of model developers and users, which is also accompanied by technical challenges. Several modeller teams make the model code (partly) freely available. Additionally, version control systems allow to track changes and collaborate on model code in an efficient way (e.g. Git, Ram 2013; e.g. Collalti et al. 2016). Besides code sharing, simulation data are increasingly available following data open access requirements, allowing subsequent analyses or model comparisons (Box 1). In many modelling studies, the preparation of data (e.g. for input/initialization, calibration or validation) and the analyses of model outputs are very work- and time-intensive. Sharing scripts for analysing forest simulations, e.g. through dedicated platforms (e.g. LeBauer et al. 2013) or R (R Core Team 2018) package (e.g. Duursma et al. 2012), is also of great help. Furthermore, the development of visualisation tools to illustrate simulation results in virtual forest scenes (e.g. Dufour-Kowalski et al. 2012; Fig. 1) represents a valuable lever to communicate on model structure, functioning and outputs, to inspire for new model developments and applications, but also to detect model errors.

Figure 1

Box 1

Process understanding

Another challenge in forest modelling results from the imperfect knowledge of processes that shape forest dynamics, e.g. regeneration (Vacchiano et al. 2018), mortality (Hartmann et al. 2018b), carbon allocation (De Kauwe et al. 2014; Hartmann et al. 2018a), photosynthesis, autotrophic respiration as well as leaf conductance (Rogers et al. 2017; Collalti & Prentice 2019). Due to the lack of consensus on the mechanisms underlying these basic processes, their representations differ substantially across models (e.g. response to increased temperature, Galbraith et al. 2010; response to water stress, Powell et al. 2013, Restrepo-Coupe et al. 2017; tree mortality, Johnson et al. 2016, Hulsmann et al. 2018). As an illustration, one of the first fully coupled simulations between a Global Circulation Model and a DGVM (Box 2) predicted a critical transition of the Amazonian rainforest towards a much drier savannah-type ecosystem under continuing deforestation and increased atmospheric CO_2 concentration (Cox et al. 2004). An updated model version projected much smaller changes of the Amazonian forest extent for the 21st century (Good et al. 2013). These differences partly resulted from our improved understanding of respiration acclimation to high temperatures (Smith & Dukes 2013; Huntingford et al. 2017). Similarly, a better inclusion of nitrogen limitation in a DGVM

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reduced the simulated CO2 fertilization effect in agreement with observations (Smith et al. 2014). Therefore the lack of one or some critical processes in a model can potentially lead to diverging projections.

Knowledge gaps often result from a limited availability of suitable data that are costly and/or time-consuming to collect. As trees are typically long-lived, experiments and field monitoring should extend over multiple decades to capture long-term trends, which is a temporal coverage still out of reach of most empirical studies and prevents their repeatability (Schnitzer & Carson 2016). While fundamentally relying on the basic knowledge developed through empirical studies, models themselves represent key tools to investigate unresolved questions through the generation of virtual data. For example, using a gap model, Bohn & Huth (2017) created a database of 500,000 virtual forest plots varying in forest composition and structure, allowing to explore the drivers of temperature sensitivity of productivity in temperate forests.

Additionally, models can be used to test hypotheses about processes (Maris et al. 2018) by applying a range of scenarios or comparing different ways to model processes, e.g. between model versions or different models (e.g. Fisher et al. 2006; Sakschewski et al. 2016; Langan et al. 2017; Lovenduski & Bonan 2017; Collalti et al. 2019a; Box 1). For example, using 15 models, including DGVMs and forest gap models, Bugmann et al. (2019) explored the influence of different simulated mortality processes on forest dynamics, providing insights into the effects of process uncertainties. Similarly, but within the same model, Collalti et al. (2019b) tested two ecological theories about plant respiration. Models can thus prove useful to pinpoint data and knowledge gaps and hence further guide the empirical development of knowledge (Rykiel Jr. 1996; Van Nes & Scheffer 2005; Medlyn et al. 2016; Norby et al. 2016).

Converging trajectories of model developments

As illustrated above, the different forest modelling approaches were initially motivated by different specific objectives, leading to different choices and compromises in the representation of actual vegetation. DGVMs originally focused on biogeochemical processes as the exchange of carbon and water between vegetation and atmosphere at the global scale, but this was at the cost of a realistic representation of forest diversity, competition, and structure. Conversely, SDMs adopted a species-level representation of vegetation diversity, but have long relied on a correlative-only approach, bypassing the mechanistic processes underlying species distribution. Similarly, IBMs typically used a finer-grained representation of vegetation structure than DGVMs, as they simulate many individuals, focusing on the competition among species, but often at the cost of an aggregated representation of some processes such as leaf gas exchanges or water flow.

The multiple scientific and technical advances described above have allowed to overcome the constraints that modellers initially faced. As a result, each of these model types has been gaining in efficiency and capabilities. Next-generation DGVMs strive to explicitly represent tree demography and diversity within PFTs, and forest structure, IBMs refine their representation of biogeochemical cycles, while SDMs endeavour to include process-based information. In doing so, their trajectories of development have been progressively converging. As a result, each model type has broadened its field of applications beyond its initial scope, encouraging the synergies among models, including their coupling (Box 2), to address key ecological research questions in a mutually-informative way..

Box 2

3. Forest modelling as tools to address key ecological questions

Forest models from different communities have been following converging trajectories of development, leading to a generation of models capable of addressing similar topics and taking on an increasing role to address novel ecological questions beyond their traditional focus. We detected different ecological fields for which we expect forest modelling to make important contributions in the next decade, by increasing our understanding

of forest ecosystems and helping generalize ecological findings. To illustrate this, we now provide examples of recent model applications to these topics, and suggest 10 important questions for future studies (Table 2).

Carbon stocks and fluxes

Quantifying forest carbon stocks and fluxes is an important task, in particular to inform climate change mitigation policies such as REDD (Gibbs et al. 2007). However, substantial uncertainties remain in estimated carbon and other element stocks and fluxes associated with forest locally and worldwide (Bonan 2008; Pan et al. 2011; Rejou-Mechain et al. 2019). Their quantification has motivated large efforts of data collection (Table 1), including labor-intensive forest inventories (Brienen et al. 2015), flux measurements (Falge et al. 2002), or remote-sensing (Running et al. 2004; Saatchi et al. 2011). Forest models provide a framework to connect empirical data of various nature, and this connection is even more powerful as models adopt resolutions that match with a broader range of empirical data, such as individual-based modelling approaches, including individual-based DGVMs (Smith et al. 2001; Sakschewski et al. 2015; Rodig et al. 2017; Fisher et al. 2018).

Models have thus been used to upscale and infer dynamic estimates of forest productivity and biomass (e.g. Fischer et al. 2015) using allometries derived from field measurements (Chave et al. 2005, 2014). Recently, assimilation of remote-sensing data within forest models has allowed to account for the heterogeneity in forest structure and land-use history in those estimates at stand to continental scales (Joetzjer et al. 2017; Rodig et al. 2017, 2018). Beyond estimations of carbon stocks and fluxes, forest models can be used to understand the drivers of their spatial variation. For example, through simulation experiments using an IBM, Fyllas et al. (2017) showed that solar radiation and trait variation driven by spatial species turnover explain the decline of forest productivity along a tropical elevation gradient. Similarly, using a forest demographic model, Berzaghi et al. (2019) showed that elephant disturbances enhance carbon stocks in central African forests through their effects on forest structure and composition. Models can also prove useful to create benchmarks against which methods to estimate carbon stocks and fluxes from measurements can be evaluated and improved (e.g. LiDAR, Knapp et al. 2018; eddy-flux tower, Jung et al. 2009).

Tree mortality and carbon allocation are key drivers of forest productivity and biomass (Bugmann & Bigler 2011; Johnson et al. 2016) but remain poorly understood processes (Holzwarth et al. 2013; Malhi et al. 2015; Hartmann et al. 2018b; Merganičová et al. 2019), and future modelling studies should seek to foster our understanding of these critical processes through model-data fusion approaches (Q9, Q10, Table 2).

Biodiversity and ecosystem functioning

Understanding the link between biodiversity and ecosystem functioning is of high interest in the context of global biodiversity loss (Naeem et al. 2009). Long-term effects remain underexplored, and underlying mechanisms are still under debate (Loreau et al. 2001; Scherer-Lorenzen 2014). By virtually manipulating the composition of simulated forest communities, forest IBMs have proven useful in exploring the effect of species richness and functional composition on ecosystem properties (e.g. Fischer et al. 2018). Simulations reproduced positive relationships between (species or functional) diversity and productivity or biomass, in agreement with the few observed patterns (Morin et al. 2011; Maréchaux & Chave 2017), further motivating a finer-grained representation of diversity in DGVMs. These studies demonstrated how competition for light can induce this positive effect in heterogeneous forests. Going beyond the effect of bulk species richness, Bohn & Huth (2017) showed that this positive effect is stronger if species are well distributed across the forest canopy vertical gradient. García-Valdés et al. (2018) showed that climate change-driven extinctions of tree species may affect forest productivity or biomass more severely than random extinctions. Schmitt et al. (2019) found that the mechanisms through which biodiversity influences forest functioning depend on the ecosystem state, shifting from a dominant complementary effect in recently disturbed systems to a selection effect in anciently disturbed systems, suggesting a way to reconcile contrasting results obtained with snapshots of ecosystem state in empirical studies.

A more detailed modelling investigation of the effect of tree species diversity and species loss on other forest ecosystem functions (e.g. water and nutrient cycles) should follow in the near future (Q1, Q3, Table 2). Another potential field of model exploration considers the influence of species diversity on crown- and surface-fire intensity as recently investigated empirically for the boreal zone (Rogers et al. 2015). Forest models, including flexible-trait DGVMs (Scheiter et al. 2013; Sakschewski et al. 2015), can further investigate how functional diversity supports forest productivity and carbon storage under climate change, from local- to biome-scale.

Resilience and stability

Forest responses to perturbations can be complex and non-linear (Ives & Carpenter 2007; Felton & Smith 2017), but their understanding is critical in an epoch of global change, including changes in intensity and frequency of climate extremes (Field et al. 2012; Reichstein et al. 2013) and disturbances (Seidl et al. 2017). Forest models can help to disentangle the different mechanisms shaping forest responses to perturbations through virtual experiments unreachable by empirical approaches. Simulations using a individual-based and trait-based DGVM showed that a higher trait diversity increases the resilience of the Amazon rainforest under future climate (Sakschewski et al. 2016). This positive effect was attributable to ecological sorting, in agreement with results from forest IBMs in temperate (Morin et al. 2018) or tropical (Schmitt et al. 2019) forests. Higher temporal stability of productivity for forests with higher diversity was also attributed to the asynchrony of species responses to small disturbances (Morin et al. 2014). Using a multimodel analysis, Radchuk et al. (2019) showed that the multiple properties of stability, such as resistance, recovery or persistence (Donohue et al. 2013) can vary independently depending on the disturbance type.

However, we still have an insufficient understanding of forest ecosystem stability (Donohue et al. 2016), and future modelling studies should help disentangling the multiple drivers of forest resilience while paying attention to the elements leading to feedbacks (e.g. the adult – regeneration feedback). This will foster our predictive ability of potential critical transitions (Q5, Q6, Q10, Table 2).

Community assembly

Understanding the drivers of community assembly, i.e. the processes that shape the number, identity and abundance of co-occurring species, has been an important question in ecology since its inception (Clements 1916; Gleason 1926; MacArthur & Levins 1967; McGill et al. 2006). Forest models allow to separate the effect of different drivers through the use of null models and sequential simulation set-ups. For instance, forest IBMs have been recently used to investigate the role of trait-mediated trade-offs and their size dependency in shaping forest community (Kunstler et al. 2009; Chauvet et al. 2017; Falster et al. 2017). In doing so, they used a more realistic modelling framework than most theoretical investigations generally developed to address these questions and typically restricted to systems with few species. This approach may be further developed and applied to various forest communities as trait data is being increasingly available. Modelling also helps to disentangle the contribution of stochastic vs. deterministic processes through the assessment of variability among repeated runs (Savage et al. 2000).

Although many mechanisms have been empirically detected to contribute to species coexistence in forest communities (Nakashizuka 2001; Wright 2002), their relative strengths in observed communities across environmental gradients remain poorly known. Forest modelling could help quantifying their relative contributions through a combination of simple theoretical models and data-driven simulation experiments, and exploring the debated role of intraspecific variability on species coexistence (Lischke & Löffler 2006; Hart et al. 2016; Q2, Q4, Table 2). To do so, models need to include key aspects of community assembly or known coexistence mechanisms, such as regeneration processes (Vacchiano et al. 2018), negative density-dependence (Lischke & Löffler 2006; Maréchaux & Chave 2017), or functional trade-offs (Sakschewski et al. 2015) in a heterogeneous environment.

Biodiversity conservation

Conservation efforts have so far not been successful to alleviate biodiversity loss across the globe (Butchart et al. 2010), calling for renewed effort and biodiversity forecasts (Urban et al. 2016). As SDMs could be calibrated for almost all species for which reliable distribution data are available, these models have long been identified as tools for conservation (Davis & Zabinski 1992; Guisan et al. 2013; Araújo et al. 2019). Predictions of SDMs under climate change scenarios could be used to help refine conservation areas (Ferrier 2002), or predict invasion ranges of introduced species (Thuiller et al. 2005; Broennimann et al. 2007). Although this claim is still put forward very often (Fernandes et al. 2018), case-studies reporting applications remain sparse (Mouquet et al. 2015), likely because of the uncertainty of SDMs predictions (Barry & Elith 2006; Dawson et al. 2011; Journé et al. 2019).

Mixed predictions carried out jointly with different model types (process-based or hybrid distribution models, Morin & Thuiller 2009; Evans et al. 2015; Box 2) could make more robust projections available to conservation managers (e.g. Thom et al. 2017). Such an approach appears especially feasible for tree species, as individual- and process-based models are typically more available for forests than for other ecosystems. Therefore, DGVMs and gap models should be encouraged to address the challenges of biodiversity conservation planning (e.g. Fischer et al. 2016), in complement of species-level process-based models already available (e.g. Chuine & Beaubien 2001; Keenan et al. 2011; Serra-Diaz et al. 2013; Q1, Q4, Q8, Table 2).

Forest responses to global change

Ongoing climate change has already altered forest functioning globally (Nemani et al. 2003; Allen et al. 2010). Models represent a key tool to assess forest responses to the interacting factors of future climate change (Sabate et al. 2002; Medlyn et al. 2011; Bugmann 2014). Simulating the dynamics of vegetation, including forests, under climate change is the main objective of DGVMs, and has been the focus of a sustained effort from this modelling community (Mohren et al. 1997; Jarvis 1998; Cramer et al. 2001; Alo & Wang 2008; Keenan et al. 2008; Friend et al. 2014). However, stand-scale models, such as individual-based gap models, have also been used to explore forest dynamics under climate change scenarios (Pastor & Post 1986; Bugmann & Fischlin 1996; Fischer et al. 2014; Reyer 2015; Collalti et al. 2018; Shugart et al. 2018). Such finer-scale models can further inform the role of forest composition and structure in shaping forest responses to environmental drivers (Fyllas et al. 2017; Bohn et al. 2018). Additionally, SDMs have been used to project species distributions under future climate change (Thuiller 2004; Noce et al. 2017), although, as mentioned above, their correlative nature has raised some criticisms regarding their application to forecasting under no-present analogues. Overall, a variety of models are utilized to simulate forest responses to climate change, allowing comparisons of different approaches and assessment of model uncertainties (Cheaib et al. 2012; Box 1), and usually showing that process-based forest models are more conservative than correlative SDMs (Morin & Thuiller 2009).

Some recent model developments further aim at accounting for other components of global change (Putz et al. 2014; Perez-Mendez et al. 2016), such as the impacts of defaunation or fragmentation on forest dynamics (Putz et al. 2011; Dantas de Paula et al. 2015, 2018; Box 2). Calls for a better integration of plant-animal (Berzaghi et al. 2018) and plant-plant interactions, such as the effect of the increasing liana abundance on tree growth and survival (Verbeeck & Kearsley 2016), should further foster such developments (Pachzelt et al. 2013; di Porcia e Brugnera et al. 2019). Another challenge is the representation of tree species dispersal and migration of tree species at large scales (Neilson et al. 2005; Snell et al. 2014; Lehsten et al. 2019; see Box 2, Q8, Table 2), in combination with evolutionary processes to account for species adaptive evolution and trait displacement under environmental changes and fragmentation (DeAngelis & Mooij 2005; McMahon et al. 2011; Scheiter et al. 2013). Moreover, accounting for the adaptive capacity of tree individuals within their lifetime via acclimation and phenotypic plasticity (Richter et al. 2012; Duputie et al. 2015) remains a challenge, as knowledge about these processes remains incomplete. To seek additional insights in estimating future forest responses, a number of studies have used forest models to estimate past forest dynamics (e.g.

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Heiri et al. 2006; Schworer et al. 2014). Overall, these developments should further help to understand the long-term effects of multiple interacting factors of global changes on forests (Q4, Q5, Q10, Seidl et al. 2017).

Forest management

Forests provide important ecosystem services, such as timber production, carbon sequestration, recreation and protection against natural hazards, whose persistence or improvement is of high societal relevance (De Groot et al. 2002, MEA 2005). This is the focus of forest management (e.g. Nabuurs et al. 2017; Yousefpour et al. 2018). Forest IBMs have a long history in helping management planning (e.g. Makela et al. 2000; Courbaud et al. 2001; Huth & Ditzer 2001; Porte & Bartelink 2002; Huth et al. 2005; Keenan et al. 2008; Pretzsch et al. 2008; Hiltner et al. 2018). As global change challenges current and future management strategies (Seidl et al. 2014b), forest model developments have aimed to help design adaptive forest management practices and mitigation strategies under multiple disturbances (Fontes et al. 2010; Rasche et al. 2011; Elkin et al. 2013; Kunstler et al. 2013; Lafond et al. 2014; Maroschek et al. 2015; Reyer et al. 2015; Mina et al. 2017; Seidl et al. 2018). DGVMs have long disregarded the effect of forest management, as their aggregated representation of vegetation structure typically prevents a realistic representation of tree size distribution and density relevant to simulate silvicultural practices. However, some DGVMs used a simplified representation of wood extraction to simulate its effect on forest carbon stocks (Zaehle et al. 2006), and recent efforts have led to the development of more explicit forest management modules, inspired by finer-scale forest gap models, forest growth and yield models (Bellassen et al. 2010; Collalti et al. 2018).

The integration of societal and economic dynamics generate new challenges (Q7 Table 2, Box 2), while future applications and communications with forest stakeholders will benefit from developments regarding visualisation of results from forest models (Fig. 1, section 2).

Table 2

Conclusion

Forests play multiple important roles for the Earth system. Sound, quantitative knowledge of forest functioning, structure and diversity is therefore essential, especially in times of global change. However, many scientific questions regarding forest properties and dynamics remain partly unresolved, ranging from understanding tree community assembly and projecting forest responses to environmental changes, to assessing the management of forest ecosystems. We illustrated how different forest modelling approaches, due to their continuous development, their complementarity and mutual enrichment, represent an invaluable toolkit to address multiple ecological questions that require a renewed research effort.

The development of forest models crucially benefits from the interactions among scientists from various fields, within and across modelling communities, but also with field ecologists, physiologists, data scientists, computer engineers, remote-sensing researchers, and a variety of stakeholders. Owing to their long and successful history in integrating data and knowledge from these various sources, the models used to simulate forests have progressively reached maturity to tackle a broader array of ecological problems. For instance, forest models prove essential to understand the multiple drivers of forest productivity and biomass by combining field and remote-sensing data across space and time, and, as a result, provide informed quantification of carbon stocks and fluxes. Forest models also provide tractable platforms to perform virtual experiments still out of reach of empirical approaches on forest systems that are characterized by slow dynamics and large spatial extents. This notably allows to shed light on the complex links between forest biodiversity, functioning and resilience in the long term. Furthermore, forest models can disentangle the drivers of community assembly in forest communities, thus complementing theoretical approaches that typically remain limited to simplified systems. Last but not least, ongoing global change and the resulting biodiversity crisis, changing climate and disturbance regimes crucially increase the demand of informed projections on forest socio-ecosystems,

for which forest models have a proven long history, while new developments allow for the integration of an increasing number of interacting factors.

We further demonstrated that the converging trajectories of the different modelling approaches used to simulate forests have provided new opportunities for comparisons among their outputs. This allows for the quantification of simulation uncertainties and the identification of their sources, and hence informs and fosters new model developments as well as empirical investigations. Overall, iterative model-data fusion approaches and the resulting cycles of simulation-assessment-improvement are continuously increasing the scope of model applications. Forest models will thus keep on contributing to a deeper understanding of forest structure and functioning, and they offer promising routes to fill remaining knowledge gaps and to take on future challenges of forest ecology.

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Figure 1. An example of visualisation of outputs of a forest model. Visualisation of species diversity (crown colours) of a tropical forest simulated by the FORMIND model (Fischer *et al.*2016) in the 3D visualisation center of UFZ – Helmholtz-Centre for Environmental Research, Leipzig, Germany.

Box 1. Model inter-comparison

Comparing the outputs from different models that are run under comparable or even identical conditions of driving variables offers valuable insights beyond single model simulations. Model comparisons in environmental sciences typically have two main objectives. The first is to understand differences between models by relating the simulated pattern of each model to its underlying processes and hence to understand how different model processes influence model behaviour and to pinpoint model structural uncertainties. The second objective is to provide ensemble simulations that allow for a quantitative assessment of uncertainties related to the actual predictions of the different models.

Model comparisons have a long history in ecology and environmental sciences. Prominent examples are comparisons of different forest gap models (Bugmann et al. 1996, 2019), forest landscape models, stand-based ecophysiological models (Kramer et al. 2002; Morales et al. 2005), dynamic global vegetation models (Cramer et al. 2001; Sitch et al. 2008) and species distribution models (Araújo & New 2007). More recently, the focus of model comparisons has expanded to also compare models across different model types (e.g. including both DGVMs and SDMs, Cheaib et al. 2012) and even across a wide range of sectors such as vegetation, water, agriculture or biodiversity to study the interaction of these under climate change (Frieler et al. 2017).

Beside the development of the study design, another challenge of model comparisons is the development of the simulation framework and the standardisation of both model inputs and outputs. Moreover, when complex process-based models are involved, whose uncertainties can not simply be attributed to individual processes, a major challenge is to interpret the ensemble runs and to understand which model processes actually explain the differences between models. To address all these issues, transparent model documentations and intensive exchange between modellers is needed accompanied by systematic tests of models and their components.

Box 2. Coupling of models

Each model has its own aim, history and therefore specific advantages and limitations. The coupling of a vegetation model with other types of models can be a valuable approach to take advantage of model complementarity or expand the initial scope of model applications.

For instance, several stand-scale forest models, including IBMs, have been coupled to models of emissions of biogenic volatile organic compounds, revealing that tree species composition and species-specific emission potentials were important drivers of the feedbacks between climate change and air quality (Keenan et al. 2009a, b; Wang et al. 2018). Similarly, a forest demographic model has been coupled to models of soil microbe-mediated biogeochemistry and competition for nutrients, revealing that spatial variation in soil properties can drive a large variation of forest biomass and composition (Medvigy et al. 2019; see also Sato et al. 2007 for another example of coupling between a forest model and more detailed soil modules). SDMs have been coupled to models of habitat colonization in order to take into account dispersal limitation in species distribution projections (e.g. Iverson et al. 2004; Nobis & Normand 2014; see also Franklin 2010). Fire disturbance models have also been implemented in several DGVMs (Yue et al. 2014, 2015; Lasslop et al. 2014; Schaphoff et al. 2018), but also in forest IBMs for a long time (Shugart & Noble 1981; Pausas 1999; Knapp et al. 2018), helping to explore different modelling approaches on the interaction between vegetation dynamics and fire (Hantson et al. 2016; Forkel et al. 2019) to explain the declining trend in global burnt area (Andela et al. 2017). More generally, forest models have been coupled to models of disturbances, such as wind storms (Seidl et al. 2011; Thom et al. 2017). Other examples include the coupling of a DGVM to a global economy model to dynamically include technical and societal changes in simulating future vegetation dynamics (e.g. Dietrich et al. 2019), allowing to investigate the possible trade-offs between bio-energy production and several sustainable development goals (Humpenöder et al. 2018).

Model development can also take advantage of the complementarity of different vegetation model types by coupling their different approaches into one model (McMahon et al. 2011). As an illustration, the gap model approach was implemented into a DGVM framework to better account for demographic processes and diversity in regional- to continental-scale studies (e.g. Smith et al. 2001; Sakschewski et al. 2015). Similarly, the seed dispersal (Lischke et al. 2006), which originates from individual-based forest models (Urban et al. 1991; Groeneveld et al. 2009), can be integrated into large scale forest models (Scherstjanoi et al. 2014; Lehsten et al. 2019) to account for dispersal limitation in predictions of species distribution changes under climate change.

Model coupling is usually challenging, since, in most models, some processes are hidden in parameters or strongly simplified functions and the model is usually balanced by fitting these parameters. If the simplified process or the parameter is replaced by a more complex submodel for the process, often the balance can be

lost. Additionally, error propagation among models can also prove difficult (Dunford et al. 2015). Several model systems and software frameworks have been developed to facilitate multi-model coupling in a systematic way, and they even allow for switching between different models during a simulation (Haas et al. 2013).

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