





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

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Abstract

1. Understanding the processes that shape forest functioning, structure, and diversity remains challenging, although data on forest systems are being collected at a rapid pace and across scales. Forest models have a long history in bridging data with ecological knowledge and can simulate forest dynamics over spatio-temporal scales unreachable by most empirical investigations.
2. We describe the development that different forest modelling communities have followed to underpin the leverage that simulation models offer for advancing our understanding of forest ecosystems.

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3. Using three widely applied but contrasting approaches – species distribution models, individual-based forest models, and dynamic global vegetation models – as examples, we show how scientific and technical advances have led models to transgress 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.
4. Synthesis. This overview shows that forest models, due to their complementarity and mutual enrichment, represent an invaluable toolkit to address a wide range of fundamental and applied ecological questions, hence fostering a deeper understanding of forest dynamics in the context of global change.

1 | UNRESOLVED QUESTIONS IN FOREST ECOLOGY: CHALLENGES AND WAYS FORWARD

Forests cover about 30% of the Earth's land surface, store almost half of the terrestrial carbon, are pivotal for the global carbon balance, supply important resources to billions of people, and host more than half of Earth's known biodiversity (Jenkins et al., 2013; Pan et al., 2011; Ramage et al., 2017; Vira et al., 2015). Yet, ongoing and future environmental changes put forests at risk. This raises 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 provide information to decision-makers (IPBES, 2016; Mori, 2017; Mouquet et al., 2015; United Nations, 2014). 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).

In the context of global biodiversity loss, for instance, understanding the link between forest biodiversity and ecosystem functioning is of high interest (Naeem et al., 2009). However, long-term effects remain underexplored and underlying mechanisms are still under debate (Loreau et al., 2001; Scherer-Lorenzen, 2014). Similarly, forest responses to perturbations can be complex and non-linear, as they involve multiple processes operating at various scales, from canopy physiology across demography to long-term adaptation and compositional changes. As a result, forest dynamics remain difficult to forecast (Felton & Smith, 2017; Ives & Carpenter, 2007), but understanding the underlying processes is critical in an epoch of global change, including changes in the intensity and frequency of climate extremes and disturbances (Field et al., 2012; Reichstein et al., 2013; Seidl et al., 2017). As another illustration, quantifying forest carbon stocks and fluxes and identifying their drivers are important tasks, in particular to inform climate change mitigation policies such as REDD (Reducing Emissions from Deforestation and Degradation; Gibbs et al., 2007). However, substantial uncertainties remain in estimated carbon and other element stocks and fluxes associated with

forests locally and worldwide (Bonan, 2008; Pan et al., 2011; Ploton, Mortier, Réjou-Méchain, et al., 2020; Réjou-Méchain et al., 2019).

Knowledge gaps may result from the lack of theoretical frameworks (Courchamp et al., 2015; Franklin et al., 2020) and/or from the limited availability of suitable data, which are often costly and time-consuming to collect. As trees are typically long-lived, experiments and field monitoring should extend over multiple decades to capture meaningful trends, which is a temporal coverage still out of reach of most empirical studies and prevents their repeatability (Schnitzer & Carson, 2016). Although an increasing amount of field and remote-sensing data have been made available at various spatial and temporal extent and resolution over the past decades, their integration into a coherent picture remains a considerable challenge (Chave, 2013; Estes et al., 2018; Levin, 1992).

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 and theories with forest modelling has been identified as a promising approach to tackle current research challenges (Franklin et al., 2020; Shugart et al., 2015; van der Sande et al., 2017; Zuidema et al., 2013). While fundamentally relying on the basic knowledge developed through theoretical considerations or empirical studies, models themselves represent an efficient tool to, under given assumptions, generate virtual data or perform virtual experiments out of reach of empirical investigations in terms of temporal and spatial scope as well as number of replicates (e.g., Fyllas et al., 2017; Morin et al., 2018; Schmitt et al., 2019). For example, using a forest dynamics model, Bohn and Huth (2017) created a database of 500,000 virtual forest plots varying in forest composition and structure, allowing to explore the drivers of the temperature sensitivity of productivity in temperate forests.

In addition, providing anticipatory predictions of possible futures, models can be used to test hypotheses about processes (explanatory or corroboratory predictions; Maris et al., 2018; Mouquet et al. 2015) by applying a range of scenarios or comparing different ways to model processes, for example, between model versions or different models, and confronting them with data

(e.g., Collalti et al., 2019; Fisher et al., 2006; Fleischer et al., 2019; Langan et al., 2017; Lovenduski & Bonan, 2017; Morin et al., 2021; Sakschewski et al., 2016). For example, using different versions of the same forest model, Collalti, Tjoelker, et al., (2020) tested two ecological theories about plant respiration. Models can thus also prove useful to pinpoint data and knowledge gaps and hence further guide the design of new experiments and empirical studies (Medlyn et al., 2016; Norby et al., 2016; Rykiel, 1996; Van Nes & Scheffer, 2005).

In the following, we evidence how the availability of various forest modelling approaches and decades of experience in assimilating observational knowledge into models offer invaluable tools to address key fundamental and applied ecological questions on forests. To do so, we first 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 and complementarity of forest modelling approaches. We then show how recent developments have allowed models to tackle similar questions, transgressing their own historical objectives and limitations, and paving the way to new synergies and opportunities for forest ecology. Finally, we 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.

2 | 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 scientists, the model representations of vegetation biodiversity, structure, or biogeochemical processes have various degrees of complexity due to different degrees of aggregation or abstraction resulting from the differing assumptions used to construct the respective model.

The three model types we briefly present here – SDMs, IBMs, and DGVMs – 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 widely used model types to illustrate the variety of modelling approaches that can be and have been used to address forest ecology questions in the context of global change. In the following, we present these three approaches by ordering them along a gradient of decreasing resolution of biodiversity representation and increasing resolution of biogeochemical process representation, acknowledging that other forms of presentation could alternatively have been used.

2.1 | Species distribution models

Species distribution models (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 (Grisebach, 1872; Humboldt, 1849). The development and increased usage of SDMs across a wide array of taxa and environments have relied on several technical advances (Elith & Leathwick, 2009; Guisan & Thuiller, 2005), namely, statistical approaches (e.g., *MaxEnt*), methods for physical environment mapping (e.g., remote-sensing techniques), and increasingly coordinated efforts to compile knowledge on species distributions. All these approaches have been boosted by geographic information systems (GIS).

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

Species distribution models thus require little information about the processes from which species distributions result. This can be an advantage, for example, 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 (Bertrand et al., 2012; Thuiller et al., 2003). 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, 2012), that species can always migrate to suitable environments, and that the species–environment relationships are valid beyond the range of model calibration, may be violated under such applications (Araújo & Pearson, 2005; Svenning & Skov, 2004; 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), although more recent developments aim at including species interactions (e.g., Meier et al. 2011). Additionally, the spatial autocorrelation (SAC) inherent in both species distribution and environmental variables can bias the estimated performance of SDMs (Bahn & McGill, 2007; Fourcade et al., 2018; Journé et al., 2020), 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 their accuracy because SAC is often a result of important ecological processes (e.g., dispersal limitation, colonization time lag) that drive species distributions.

The integration of eco-physiological and demographic processes into SDMs is likely critical to inferring species distributions in novel environments or under no-present analogue conditions (Dormann

et al., 2012; Kearney & Porter, 2009; 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 (Bykova et al., 2012; Chuine & Beaubien, 2001; Duputié et al., 2015; Kleidon & Mooney, 2000; Nobis & Normand, 2014; Stephenson, 1990). 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).

2.2 | Individual-based forest models

There is a long tradition in ecology and forestry to use individual-based 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 for capturing not only forest structure but also tree species diversity. A widely known type of IBMs are forest gap models (Bugmann, 2001; Huston et al., 1988; Shugart, 1984). As first developed for forest stands in North America, they have since become one of the most widely used model types in ecology (Botkin et al., 1972; Shugart et al., 2018; Shugart & West, 1977).

In the gap model approach, a forest stand is described as a mosaic of forest patches. The dynamics of the forest at the stand scale emerge from the growth, mortality, establishment, and competition of individual trees (Bugmann, 2001; Porté & Bartelink, 2002). The vertical distribution of leaves is used to calculate the light availability for each tree, which affects growth and mortality. Competition with neighboring trees usually happens within a predefined competition range, where all trees compete for resources such as light, water, and nutrients. Due to the individual-based concept, these models are able to describe different aspects of successional dynamics (mosaic dynamics, e.g., Watt, 1947) and 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 (Overpeck, Rind, & Goldberg, 1990; Pastor & Post, 1988; Solomon, 1986). Some early studies already included the carbon and nutrient cycles (Pastor & Post, 1986). Gap models are typically used with annual time steps for the demographic processes of growth, recruitment, and mortality, with finer embedded time-step to update the simulated environment.

Modules for forest management (Huth & Ditzer, 2001; Liu & Ashton, 1995; Mina et al., 2017) and disturbances like fire (Fischer, 2013; Kercher & Axelrod, 1984), browsing (Didion et al., 2009; Seagle & Liang, 2001), or windthrow (Seidl et al., 2011, 2014) 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 (Bugmann, 1996; Kienast, 1987) and boreal forests (Leemans & Prentice, 1989). Forest gap models have also been developed for tropical forests (Bossel & Krieger, 1991; Doyle, 1981; Fischer et al., 2016; Köhler & Huth, 1998). 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 plant functional types (PFTs). The gap model approach was also extended beyond forests, for example, to grassland systems (Coffin & Lauenroth, 1990; Schmid et al., 2021; Taubert et al., 2020).

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 (Chave, 1999; Maréchaux & Chave, 2017; Pacala et al., 1996; Pretzsch et al., 2002). Other 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 more detailed water and carbon cycles or site fertility (Fischer et al., 2016; Maréchaux & Chave, 2017). Similarly, by taking advantage of comprehensive trait databases or long-term inventories and the detailed information they provide on tree life histories, novel parameterizations have allowed for simulating hundreds of species within diverse forest communities (Maréchaux & Chave, 2017; Rüger et al., 2019). Other stand-based models were designed to describe forest stand structure dynamics driven by eco-physiological processes in higher detail and at finer time scales (Kramer et al., 2002; Medlyn et al., 2007; Morales et al., 2005), although often at the cost of lower temporal or spatial coverage. IBMs have since been used to address a wide variety of basic and applied research questions, concerning for example forest development under climate change, assessments of management scenarios, or the drivers of tree community composition (Bohn et al., 2014; Bugmann & Pfister, 2000; Fischer et al., 2016; Seidl et al., 2012; Shugart et al., 2018). Modern extensions of these models also allow for simulations of forests at large spatial scales (i.e., from forest landscapes to entire countries or continents; Rödig et al., 2017; Sato et al., 2007; Scherstjanoi et al., 2014; Thom et al., 2017; Xiaodong & Shugart, 2005).

2.3 | Dynamic global vegetation models

Dynamic global vegetation models have their origin in four research areas: plant geography, biogeochemistry, vegetation dynamics, and biophysics (Prentice et al., 2007), with IBIS, HYBRID, and LPJ being among the first DGVMs (Cramer et al., 2001). DGVMs have initially been developed to represent the interaction between vegetation and the global carbon cycle as stand-alone models, but also to represent vegetation dynamics in the context of Earth System Models,

that is, along with models of the atmosphere (General Circulation Models), the oceans, and the cryosphere.

Dynamic global vegetation models simulate vegetation dynamics from half-hourly to monthly time steps at the global scale, driven by climate, atmospheric CO₂ concentration, and soil information, using plant physiology and biogeochemistry to explain biogeography (Krinner et al., 2005; Sitch et al., 2003). This approach results in the prediction of the large-scale distribution of potential natural vegetation. The main components of DGVMs are 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; Rogers et al., 2017).

Describing vegetation dynamics at the global scale inevitably entails strong model simplifications to represent vegetation. Therefore, DGVMs use PFTs to aggregate functionally similar species to represent functional properties at the biome scale. Usually global vegetation is described with between 5 and 14 PFTs by differentiating life form, leaf form, phenology, or photosynthetic pathway, for example, tropical broad-leaved raingreen tree or C₃ grasses (Prentice et al., 2007; Woodward & Cramer, 1996). Hence, these PFTs represent a less detailed description of species diversity within forest communities than the ones used in IBMs. Additionally, DGVMs often are used to conduct simulations using a relatively coarse-grained grid (typically of 0.5° lat/lon resolution) in which the characteristics within each cell are assumed to be spatially homogenous, simulating average individuals per PFT, where several of them can compete within one grid cell. Hence, local competition processes are simplified 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 measured data for carbon and water pools. The global PFT and carbon pool distribution is instead determined by the given abiotic conditions and PFT-specific characteristics, that is, in so-called "spin-up" simulations. Hence, each change in abiotic conditions (e.g., climate change) results in a 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 (Jägermeyr 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 been further developed to include an explicit representation of the nitrogen and phosphorus cycle (von Bloh et al., 2018; Goll et al., 2017; Reed et al., 2015; Smith et al., 2014; Wang et al., 2010). Similarly, a more explicit representation of tree hydraulics and water flows has been developed in some DGVMs to better assess the effect of climatic change on evapotranspiration and drought-related mortality (Bonan et al., 2014; Hickler et al., 2006; Langan et al., 2017).

The need for a more realistic representation of vegetation structure and biodiversity to improve the predictive power of DGVMs has been highlighted as an important pathway to improving their predictive power (McMahon et al., 2011; Quillet et al., 2010). To achieve this, several developments have been made to include a finer representation of vegetation demographic processes (Fisher et al., 2018; Hickler et al., 2012; Moorcroft et al., 2001; Smith et al., 2001) and functional diversity (Pavlick et al., 2013; Sakschewski et al., 2015; Scheiter et al., 2013; Verheijen et al., 2015). Lately, also seed dispersal of trees and therefore the ability for tree species migration has been implemented into hybrid DGVMs, which represent a combination of a forest gap model with a DGVM (Lehsten et al., 2019; Snell & Cowling, 2015).

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 model types described above are widely used examples, acknowledging that each model type is also used to simulate other ecological systems.

3 | FROM MODEL COMPLEMENTARITY TO SYNERGIES: OPPORTUNITIES FOR FOREST ECOLOGY

3.1 | 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 simplifications in the representation of actual vegetation (Table 1). DGVMs originally focused on bio-geochemical processes as the exchange of carbon and water between vegetation and atmosphere at the global scale, 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, and focus on the competition among them, but often at the cost of a coarser representation of some processes such as gas exchange or water flow, typically using empirical equations fitted at a coarser temporal resolution than DGVMs.

However, multiple scientific and technical advances (see Box 1, Table 2) have allowed for overcoming the constraints that modelers initially were facing. Each of these model types has thus been gaining in efficiency and capabilities as illustrated by the aforementioned recent model developments: next-generation DGVMs strive to explicitly represent tree demography and diversity within PFTs, and account for forest structure, IBMs refine their representation of biogeochemical cycles, while SDMs endeavor to include process-based information. In doing so, their trajectories of development have been progressively converging. As a result, each model type

TABLE 1 Advantages, limitations, and challenges of three different approaches to model forests: species distribution models (SDMs), individual-based models (IBMs), and dynamic global vegetation models (DGVMs)

	SDMs	IBMs	DGVMs
Advantages	<p>allow a quick assessment of potential climate-change vulnerability</p> <p>can serve as a coarse filter for more detailed/process-based approaches</p> <p>are easily applicable to many taxa due to low data and computational demands, as well as available R-packages and methods</p>	<p>simulate the growth and demography of every tree in a forest from decades to centuries</p> <p>can easily integrate field data since forest monitoring is mainly done at the tree level</p> <p>are able to simulate dynamics of forest structure and project changes in species composition by including important ecological processes (e.g., competition between species)</p> <p>can integrate disturbances, climate change and forest management</p> <p>are mostly process-based and therefore useful for extrapolations to new conditions</p>	<p>simulate vegetation on large spatial (up to global) and temporal scales (decades to centuries)</p> <p>simulate climate impacts on vegetation dynamics and associated biogeochemical and water cycles due to the process-based simulation of stocks and fluxes</p> <p>are able to consider physiological and plant-competition processes and increasingly plant-trait diversity</p> <p>can incorporate managed grasslands and crop growth under land-use change.</p>
Limitations	<p>represent potential rather than realized species niches</p> <p>are static models, as equilibrium with environment is assumed, which can lead to misinterpretations by stakeholders</p> <p>their accuracy depends strongly on the spatial resolution, as there can be strong effects of spatial autocorrelation.</p>	<p>are data demanding for parameterization and initialization</p> <p>can be computationally demanding to apply at large spatial scales (countries, continents) since millions of trees have to be simulated in these cases</p> <p>can raise problem of overfitting and erroneous extrapolations when calibrated using local field data</p>	<p>often represent species diversity using plant functional types (PFTs), and species-specific parameterization is limited by a lack of information for important parameters (e.g., on ecophysiology).</p> <p>have high computational demand at large scales</p> <p>have often a poor representation of forest structure and certain ecological processes (e.g., seed dispersal, forest regrowth, tree mortality)</p> <p>show – by design – no or only rudimentary simulation of forest management</p>
Challenges and future developments	<p>deal with missing absence data</p> <p>include more ecological processes and species interactions</p> <p>include genetic variability</p> <p>include demographic processes and dispersal limitations</p> <p>better account for the impact of extreme climatic events</p>	<p>speed up the parameterization step</p> <p>upscale while keeping essential behavior</p> <p>improve the coupling of remote-sensing data with model outputs</p> <p>include intra-specific variation and plasticity</p> <p>more realistically represent below-ground processes</p>	<p>increase the number of PFTs to an optimal number, to represent major competing functional groups</p> <p>simulate actual vegetation consisting of managed forests and remaining natural vegetation as monitored by forest inventories or remote sensing</p> <p>improve the implementation of vegetation structure to allow its integration at the global scale</p> <p>improve the representation of ecological processes (e.g., vegetation re-growth and seed dispersal)</p>

has broadened its field of applications beyond its initial scope, creating synergies among models, including model coupling, to address key ecological research questions in a mutually informative way.

Box 1: New levers to foster model development for forest ecology

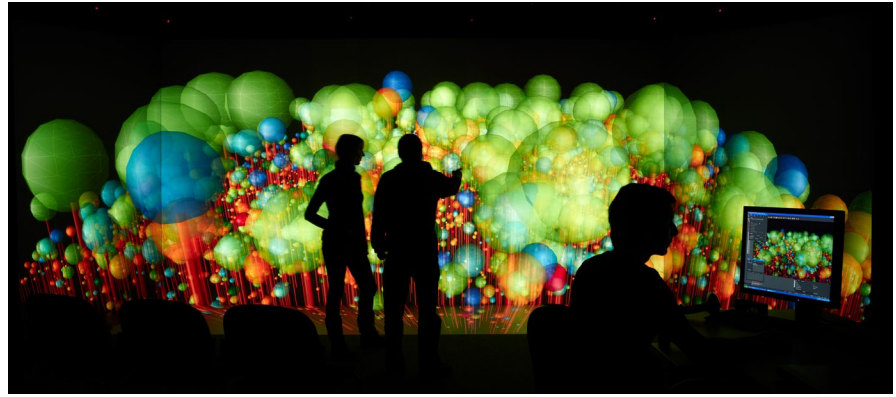
Forest model development and predictive ability have been constrained by different factors. Forest models are data-demanding across the different steps of model development and application, from a robust parameterization of the multiple processes related to plant life cycle and physiology for diverse plant types, species or individuals, to the initialization and validation of forest simulations

over large spatial and temporal scales. Fortunately, data availability is increasing at a high pace (Table 2). Global plant trait databases (e.g., TRY, Kattge et al., 2011) 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. If data coverage remains incomplete however (Kattge et al., 2020), the combination of organization principles such as natural selection-based

TABLE 2 Types of available forest data

Short description	Extent (space; time)	Resolution (space; time)	Examples (references and links)
Data type: experimental data Monitoring of plant responses to a set of controlled or manipulated biotic (e.g., competition) or abiotic (e.g., nutrients, climate) conditions	Very local-to-stand-scale; variable	Small-scale; variable	Bussotti et al., (2018); FACE experiment (Free-Air CO ₂ enrichments), Norby et al., (2016); rainfall manipulation, Grossiord et al., (2018); Meir et al., (2015)
Data type: tree performance data Direct or indirect measurements of components of tree performance or functioning, such as tree growth (e.g., tree-ring analysis, automatic dendrometers), resource use, (e.g., sapflow), or reproduction (e.g., seed traps)	Local; from snapshots to tree life span.	individual to forest stand; Intra-annual to annual	tree-ring databases, Treydte et al., (2007), https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring ; tree sapflow database, Poyatos et al., (2016); seed production database, Ascoli et al., (2017); Muller-Landau et al., (2008)
Data type: trait data Measurement of plant individual features (morphological, physiological or phenological) which impacts components of individual performance	Local; snapshots or repeated over e.g., season, ontogeny	Individual to species; punctual or repeated over e.g., season, ontogeny.	TRY, Kattge et al., (2011); sPlot, Bruehlheide et al., (2019)
Data type: species presence records Report of presence or absence of species in localities	Across species range, from local to global; snapshots or repeated over longer term	Variable; punctual	Global Biodiversity Information Facilities, GBIF, https://www.gbif.org/
Data type: inventory data Systematic identification and size measurements of all trees above a given size threshold within a forest stand	Local stands or stand network; snapshots or repeated over longer term	Individual; punctual or typically from seasonal to every few years.	German national inventory, https://bwi.info/start.aspx?lang=eng ; CTFs-ForestGeo, https://forestgeo.si.edu/
Data type: eddy-flux data Measurement of vertical turbulent fluxes of water and CO ₂ between the atmosphere and the vegetation layer	Stand (tower footprint of typically few hectares); continuous measurements over years	Stand; Half-hourly	FLUXNET, Baldocchi et al., (2001); Pastorello et al., (2020)
Data type: remote-sensing observations Record of vegetation characteristics and abiotic conditions from above, based on propagated signal such as electromagnetic waves, either active (e.g., LIDAR, RADAR) or passive (visible light).	Regional, global; covering several years Stand to regional scale; snapshot or repeated over e.g., seasons or years. Local to stand scale; snapshots or repeated over e.g., weeks or seasons Local to stand scale; snapshots or repeated over e.g., seasons or years	Spaceborne: down to meter-scale; several measurements per year. Airborne: down to cm-scale; Punctual or repeated flights Drone-based: down to cm-scale; punctual or repeated flights Terrestrial: down to mm-scale; mostly punctual	e.g., MODIS: https://modis.ornl.gov/cgi-bin/MODIS/global/subset.pl ; Justice et al., (2002); Running et al., (2004) https://gihl.gsfc.nasa.gov/ ; Goetz and Dubayah, (2011); Zolkos et al., (2013) Brede et al., (2017); Park et al., (2019); Roşca et al., (2018) Disney, (2018); Takoudjou et al., (2018)

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



optimality or entropy maximization to constraint plant and ecosystem behavior can alleviate the data demand for parameterization while improving model predictive ability (Franklin et al., 2020). Simultaneously, networks of forest plot inventories are being complemented by remote-sensing data, 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, Fischer et al., 2019; Jucker et al., 2017).

New tools of data processing have been developed to leverage these new sources of data. 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; Rammer & Seidl, 2019; Reichstein et al., 2019). Additionally, Bayesian and/or inverse modelling approaches can be used to take advantage of diverse sources of data to estimate process parameters, calibrate entire models, and thus reduce model uncertainty (Dietze et al., 2014; Fischer et al., 2019; Hartig et al., 2014; Hartig et al., 2011; LeBauer, Wang, Richter, Davidson, & Dietze, 2013; Lehmann & Huth, 2015; van Oijen et al., 2013; van Oijen et al., 2005). See also Appendix A for more studies that benefit from increasing data availability.

Besides data availability, 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 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 IBMs at lower costs (Rödig et al., 2017, 2018; Shugart et al., 2015). 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. Furthermore, the development of visualization tools to illustrate simulation results in virtual forest scenes (e.g., Dufour-Kowalski et al., 2012; Figure 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. See also Appendix B for more examples and details about technical challenges.

3.2 | Strength in unity: Insights from model inter-comparison and coupling

Two main types of synergies among models have been increasingly leveraged to better inform forest ecology, namely, model inter-comparisons and model coupling efforts.

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. First, they allow for understanding differences between models by relating the simulated pattern of each model to its underlying processes. This can identify model structural uncertainties, which have been highlighted as a major source of model uncertainties (Famiglietti et al., 2020; Lovenduski & Bonan, 2017; Raiho et al., 2020), and thus foster new model developments as well as novel empirical investigations. Although the increasing complexity of models makes the interpretation of model inter-comparison results challenging (Fisher & Koven, 2020; Appendix B), model benchmarking is facilitated by new tools of code and data sharing (e.g., Ram, 2013) as well as the availability of detailed standardized databases (Collier et al., 2018; Reyer et al., 2020). Additionally, simulation experiments where different versions of a model are compared allow for insights into the effects of specific process representation in addition to comparisons among models. For example, using 15 different models, including DGVMs and forest gap models, each with alternative mortality sub-models, Bugmann et al. (2019) explored the influence of different simulated

mortality processes on forest dynamics, providing insights into the effects of process uncertainties. The second objective of model inter-comparison is to provide ensemble simulations that allow for a quantitative assessment of the uncertainties underlying the predictions of the different models.

Model comparisons have a long history within each model community (e.g., among forest gap models – Bugmann et al., 1996 –, forest landscape models – Petter et al., 2020 –, stand-based eco-physiological models – Kramer et al., 2002; Morales et al., 2005 –, DGVMs – Cramer et al., 2001; Sitch et al., 2008 –, or SDMs – Araújo & New, 2007). More recently, the increasing ability of different model types to use inputs and provide outputs of similar nature and structure has allowed to compare models across model types (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).

Since each model has its own aim, history and therefore specific advantages and limitations (Table 1), the coupling of a model with other types of models can be a valuable approach to expand the initial scope of model applications, or reduce uncertainties in model projections. 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, 2009b; Wang et al., 2018). Similarly, a forest demographic model has been coupled to models of soil microbe-mediated bio-geochemistry 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). SDMs have been coupled to models of habitat colonization in order to take into account dispersal limitation in species distribution projections (Iverson et al., 2004; Nobis & Normand, 2014; see also Franklin, 2010). Fire disturbance models have been implemented in several DGVMs (Lasslop et al., 2014; Schaphoff et al., 2018; Yue et al., 2014, 2015); but also in forest IBMs for a long time (Knapp et al., 2018; Pausas, 1999; Shugart & Noble, 1981), helping to explore different modelling approaches on the interaction between vegetation dynamics and fire (Forkel et al., 2019; Hantson et al., 2016) 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), allowing the investigation of forest resilience by means of different modeling approaches (Albrich et al., 2020). 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 (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 (Table 1) 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., Sakschewski et al., 2015; Smith et al., 2001). Similarly, approaches to include seed dispersal (Lischke et al., 2006), which originate from IBMs (Groeneveld et al., 2009; Urban et al., 1991), can be integrated into large-scale forest models (Lehsten et al., 2019) to account for dispersal limitation in predictions of species distribution changes under climate change. SDMs have also been coupled to gap models to account for the effects of changes in species distribution at the regional scale on forest composition and functioning at the local scale (García-Valdés et al., 2020). Model coupling can thus help to improve model realism. In all cases, uncertainties resulting from error propagation across models need to be carefully assessed (e.g., Dunford et al., 2015) to master the resulting increasing complexity while maintaining model reliability and robustness (Famiglietti et al., 2020; Fisher & Koven, 2020; Franklin et al., 2020; Prentice et al., 2015; Saltelli, 2019).

4 | FOREST MODELLING TO ADDRESS KEY ECOLOGICAL QUESTIONS

Forest models from the different communities have been following converging trajectories of development, leading to a generation of models capable of addressing similar topics and taking on an important role to address novel ecological questions that go far beyond their traditional focus. We identified a number of 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 provide examples of recent model applications to these topics, from the most fundamental to applied ones, and collate ten important questions for future studies (Table 3).

4.1 | Community assembly

Understanding the drivers of community assembly, that is, 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 for separating the effect of different drivers through the use of null models and sequential simulation set-ups. For instance, forest IBMs have recently been used to investigate the role of trait-mediated trade-offs and their size dependency in shaping forest community (Chauvet et al., 2017; Falster et al., 2017; Kunstler et al., 2009). In doing so, they used a more realistic modelling framework than most theoretical investigations that are 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 are increasingly becoming available (Box

TABLE 3 Ten unresolved key questions of forest ecology

We here provide examples of key questions in high need of research effort in forest ecology, for which modelling approaches represent promising tools, as illustrated in the text (see section “Forest modelling to address key ecological questions”). For a more complete list of unanswered ecological questions regarding forest systems, we refer the reader for example, Ammer et al. (2018) or Sutherland et al. (2013).

Q1 How are forest functional and structural characteristics related to climate and soil, and how does this influence forest system functions across space and time?

Q2 Which coexistence mechanisms shape forest communities across environmental gradients?

Q3 How important are rare species for the functioning of forest ecosystems?

Q4 Which forest systems and which of their properties are most sensitive to changes in community composition across scales and why?

Q5 Which factors control the resilience of forest ecosystems to various disturbances?

Q6 What makes forests susceptible to rapid system shifts and how can we project tipping points?

Q7 How do disturbance regimes and global change affect sustainable forest management strategies?

Q8 How do native and invasive tree species move with global change?

Q9 What are the main drivers of carbon allocation within plants and forest ecosystems?

Q10 Why and when do trees die?

1). Modelling also helps to disentangle the contribution of stochastic versus deterministic processes through the assessment of variability among repeated runs (Savage et al., 2000).

Although many mechanisms have been identified empirically 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 intra-specific variability on species coexistence (Hart et al., 2016; Lischke & Löffler, 2006; Q2, Q4, Table 3). 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), and functional trade-offs (Sakschewski et al., 2015) in a heterogeneous environment.

4.2 | Biodiversity and ecosystem functioning

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 observed patterns (Maréchaux & Chave, 2017; Morin et al., 2011, 2020), 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 and Huth (2017) showed that this positive effect is stronger if species are well distributed vertically across the forest canopy. 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 the dominance of the complementarity effect in recently disturbed systems to the dominance of the selection effect in old forests, suggesting a way to reconcile contrasting results obtained with snapshots of ecosystem state in empirical studies.

A more detailed model-based 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 3). 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 (Sakschewski et al., 2015; Scheiter et al., 2013), could further investigate how functional diversity supports forest productivity and carbon storage under climate change, from the local to the biome scale.

4.3 | Resilience and stability

Forest models can help to disentangle the different mechanisms shaping forest responses to perturbations through virtual experiments that are beyond the reach of empirical approaches (Albrich et al. 2020). Simulations using an individual-based and trait-based DGVM showed that 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) and 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 multi-model 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 that involves multiple processes at various spatial and temporal scales (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 3).

4.4 | Carbon stocks and fluxes

The quantification of carbon stocks and fluxes has motivated large efforts of data collection (Table 2), including labor-intensive forest inventories (Brienen et al., 2015; Ploton, Mortier, Barbier, et al., 2020), flux measurements (Falge et al., 2002; Pastorello et al., 2020), 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 feature resolutions that match with a broader range of empirical data, such as individual-based modelling approaches, including individual-based DGVMs (Fisher et al., 2018; Rödig et al., 2017; Sakschewski et al., 2015; Smith et al., 2001).

Models have been used to upscale and infer dynamic estimates of forest productivity and biomass (Fischer et al., 2015) using allometries from field measurements (Chave et al., 2005, 2014). Recently, assimilation of remote-sensing data within forest models has allowed accounting for the heterogeneity in forest structure and land-use history in those estimates at stand to continental scales (Joetzier et al., 2017). 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 (Rödig 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 other methods to estimate carbon stocks and fluxes can be evaluated and improved (e.g., LiDAR, Knapp et al., 2018; eddy-flux tower, Jung et al., 2009).

Plant respiration, tree mortality, and carbon allocation are key drivers of forest productivity and biomass (Bugmann & Bigler, 2011; Johnson et al., 2016) but remain poorly understood (Hartmann et al., 2018; Holzwarth, Kahl, Bauhus, & Wirth, 2013; Malhi et al., 2015; Merganičová et al., 2019; Collalti & Prentice, 2019; Collalti, Ibrom, et al., 2020), and future modelling studies should seek to foster our understanding of these critical processes for example, through model-data fusion approaches (Q9, Q10, Table 3).

4.5 | Forest responses to global change

Models represent a key tool to assess forest responses to the interacting factors of future climate change (Bugmann, 2014; García-Valdés et al., 2020; Medlyn et al., 2011; Sabaté et al., 2002).

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 (Alo & Wang, 2008; Cramer et al., 2001; Friend et al., 2014; Jarvis, 1998; Keenan et al., 2008; Mohren et al., 1997). However, stand-scale models, such as individual-based gap models, have also been used to explore forest dynamics under climate-change scenarios (Bugmann & Fischlin, 1996; Collalti et al., 2018; Fischer et al., 2014; Pastor & Post, 1986; Reyer, 2015; 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 (Bohn et al., 2018; Fyllas et al., 2017). Additionally, SDMs have been used to project species distributions under future climate change (Noce et al., 2017; Thuiller, 2004), although, as mentioned above, their correlative nature has raised criticisms regarding their use for forecasting under no-present analogues (Table 1). Overall, a variety of models are utilized to simulate forest responses to climate change, allowing comparisons of different approaches and the assessment of model uncertainties (Cheaib et al., 2012), 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 (Pérez-Méndez et al., 2016; Pütz et al., 2014), such as the impacts of defaunation or fragmentation on forest dynamics (Dantas de Paula et al., 2015, 2018; Pütz et al., 2011). 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 (di Porcia e Brugnera et al., 2019; Pachzelt, Rammig, Higgins, & Hickler, 2013). Another challenge is the representation of tree species dispersal and migration of tree species at large scales (Lehsten et al., 2019; Neilson et al., 2005; Snell et al., 2014; Q8, Table 1), 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 (Duputié et al., 2015; Richter et al., 2012) remains a challenge, as knowledge about these processes remains incomplete. However, optimality principles may provide a promising approach to predict trait variation with environmental conditions (Franklin et al., 2020). To seek additional insights in estimating future forest responses, a number of studies have used forest models to estimate past forest dynamics (Heiri, Bugmann, Tinner, Heiri, & Lischke, 2006; Lischke, 2005; Lischke et al., 2013; Schwörer et al., 2014). Overall, while differences among model predictions remain large (Prentice et al., 2015), these developments, together with model benchmarking and inter-comparisons, should help to better understand the long-term effects of multiple interacting factors of global changes on forests (Seidl et al., 2017; Q4, Q5, Q10, Table 3).

4.6 | Biodiversity conservation

So far, conservation efforts have not been successful to alleviate biodiversity loss across the globe (Butchart et al., 2010), calling for renewed efforts and biodiversity forecasts (Urban et al., 2016). As SDMs can be calibrated for almost all species for which reliable distribution data are available, these models have long been identified as tools for conservation (Araújo et al., 2019; Davis & Zabiniski, 1992; Guisan et al., 2013). Predictions of SDMs under climate-change scenarios could be used to help refine conservation areas (Ferrier, 2002), or predict invasion ranges of introduced species (Broennimann et al., 2007; Thuiller et al., 2005). Although this claim is put forward frequently (Fernandes et al., 2018), case studies reporting applications remain sparse (Mouquet et al., 2015), likely because of the uncertainty in SDM predictions (Barry & Elith, 2006; Dawson et al., 2011; Journé, Barnagaud, Bernard, Crochet, & Morin, 2020).

Mixed predictions carried out jointly with different model types (process-based or hybrid distribution models, Evans et al., 2015; Morin & Thuiller, 2009) could provide more robust projections for conservation managers (Thom et al., 2017). Such an approach appears especially feasible for tree species, as individual- and process-based models are typically more abundant for forests than for other ecosystems. Therefore, DGVMs and gap models should be increasingly used to address the challenges of biodiversity conservation planning (e.g., Fischer et al., 2016), in complement to the 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 3).

4.7 | 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). Sustaining these ecosystem services is the focus of forest management (Nabuurs et al., 2017; Yousefpour et al., 2018). Forest IBMs have a long history in helping management planning (Courbaud et al., 2001; Hiltner et al., 2018; Huth & Ditzer, 2001; Huth et al., 2005; Keenan et al., 2008; Mäkelä et al., 2000; Porté & Bartelink, 2002; Pretzsch et al., 2008). As global change is challenging current and future management strategies (Seidl et al., 2014), forest model development has aimed to help design adaptive forest management practices and mitigation strategies under multiple disturbances (Elkin et al., 2013; Fontes et al., 2010; Kunstler et al., 2013; Lafond et al., 2014; Maroschek et al., 2015; Mina et al., 2017; Rasche et al., 2011; Reyer et al., 2015; 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 (Table 1). 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 as well as forest growth and yield models (Bellassen et al., 2010; Collalti et al., 2018).

The integration of societal and economic dynamics generates new challenges (Q7, Table 3), while future applications and communications with forest stakeholders will benefit from developments regarding visualization of results from forest models (Figure 1).

5 | CONCLUSION

Forests have multiple important roles for the Earth system and human livelihoods. Sound, quantitative knowledge of forest functioning, structure, and diversity are therefore essential, especially in times of global change. However, many scientific questions regarding forest properties and dynamics remain 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 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 and can tackle a broader array of ecological problems. For instance, forest models can disentangle the drivers of community assembly in forest communities, thus complementing theoretical approaches that typically remain limited to simplified systems. Forest models also provide tractable platforms to perform virtual experiments still out of reach of empirical approaches in forest systems that are characterized by slow dynamics and large spatial extents. This notably allows shedding light on the complex links between forest biodiversity, functioning and resilience in the long term. Furthermore, forest models prove essential to understanding 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 quantifications of carbon stocks and fluxes. Last but not least, ongoing global change and the resulting biodiversity crisis as well as changing climate and disturbance regimes crucially increase the demand of informed projections on forest socio-ecosystems, for which forest models have a long and successful history, while new developments allow for the integration of an increasing number of interacting factors.

We demonstrated that the converging trajectories of the different modelling approaches used to simulate forests provide new

opportunities for comparisons among their outputs. This allows for the quantification of simulation uncertainties and the identification of their sources, and hence 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 while controlling for simulation uncertainties. Forest models will thus keep 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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CONFLICT OF INTEREST

The authors state that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

Maréchaux I., Langerwisch F., and Bohn F. J. equally performed conceptualization, data curation, formal analysis, investigation, writing-original draft, and writing-review and editing. **Huth A.**, supported for conceptualization, project administration (Lead), and writing-review and editing. **Bugmann H., Morin X., and Seidl R.** supported for conceptualization and writing-review and editing. **Reyer C.P.O.** supported for conceptualization, funding acquisition (Lead), and writing-review and editing. **Collalti A., Dantas de Paula, M., Fischer R., Gutsch M., Lexer M.J., Lischke H., Rammig A., Rödiger E., Sakschewski B., Taubert F., Thonicke K., and Vacchiano G.** supported for writing-review and editing.

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REFERENCES

- Albrich, K., Rammer, W., Turner, M. G., Ratajczak, Z., Braziunas, K. H., Hansen, W. D., & Seidl, R. (2020). Simulating forest resilience: A review. *Global Ecology and Biogeography*, 29(12), 2082–2096. <https://doi.org/10.1111/geb.13197>
- Alo, C. A., & Wang, G. (2008). Potential future changes of the terrestrial ecosystem based on climate projections by eight general circulation models. *Journal of Geophysical Research: Biogeosciences*, 113(G1), <https://doi.org/10.1029/2007JG000528>
- Ammer, C., Fichtner, A., Fischer, A., Gossner, M. M., Meyer, P., Seidl, R., Thomas, F. M., Annighöfer, P., Kreyling, J., Ohse, B., Berger, U., Feldmann, E., Häberle, K.-H., Heer, K., Heinrichs, S., Huth, F., Krämer-Klement, K., Mölder, A., Müller, J., ... Wagner, S. (2018). Key ecological research questions for Central European forests. *Basic and Applied Ecology*, 32, 3–25. <https://doi.org/10.1016/j.bae.2018.07.006>
- Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., DeFries, R. S., Collatz, G. J., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F., Mangeon, S., Melton, J. R., Yue, C., & Randerson, J. T. (2017). A human-driven decline in global burned area. *Science*, 356, 1356–1362. <https://doi.org/10.1126/science.aal4108>
- Araújo, M. B., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, 5(1), eaat4858. <https://doi.org/10.1126/sciadv.aat4858>
- Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- Araújo, M. B., & Pearson, R. G. (2005). Equilibrium of species' distributions with climate. *Ecography*, 28(5), 693–695. <https://doi.org/10.1111/j.2005.0906-7590.04253.x>
- Ascoli, D., Maringer, J., Hackett-Pain, A., Conedera, M., Drobyshev, I., Motta, R., Cirolli, M., Kantorowicz, W., Zang, C., Schueler, S., Croisé, L., Piusi, P., Berretti, R., Palaghianu, C., Westergren, M., Lageard, J. G. A., Burkart, A., Gehrig Bichsel, R., Thomas, P. A., ... Vacchiano, G. (2017). Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*, 98(5), 1473. <https://doi.org/10.1002/ecy.1785>
- Bahn, V., & McGill, B. J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, 16(6), 733–742. <https://doi.org/10.1111/j.1466-8238.2007.00331.x>
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., & Wofsy, S. (2001). FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, 82(11), 2415–2434. [https://doi.org/10.1175/1520-0477\(2001\)082<2415:FANTTS>2.3.CO;2](https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2)
- Ball, J. T., Woodrow, I. E., & Berry, J. A. (1987). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In J. Biggins (Ed.), *Progress in photosynthesis research* (pp. 221–224). Springer. https://doi.org/10.1007/978-94-017-0519-6_48

- Barry, S., & Elith, J. (2006). Error and uncertainty in habitat models. *Journal of Applied Ecology*, 43(3), 413–423. <https://doi.org/10.1111/j.1365-2664.2006.01136.x>
- Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis. *Ecology Letters*, 15(5), 393–405. <https://doi.org/10.1111/j.1461-0248.2012.01751.x>
- Bellassen, V., Le Maire, G., Dhôte, J. F., Ciais, P., & Viovy, N. (2010). Modelling forest management within a global vegetation model—Part 1: Model structure and general behaviour. *Ecological Modelling*, 221(20), 2458–2474. <https://doi.org/10.1016/j.ecolmodel.2010.07.008>
- Bertrand, R., Perez, V., & Gégout, J.-C. (2012). Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: The case of *Quercus pubescens* in France. *Global Change Biology*, 18(8), 2648–2660. <https://doi.org/10.1111/j.1365-2486.2012.02679.x>
- Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., & Doughty, C. E. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience*, 1, <https://doi.org/10.1038/s41561-019-0395-6>
- Berzaghi, F., Verbeeck, H., Nielsen, M. R., Doughty, C. E., Bretagnolle, F., Marchetti, M., & Scarascia-Mugnozza, G. (2018). Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential of vegetation models. *Ecography*, 41, 1934–1954. <https://doi.org/10.1111/ecog.03309>
- Bohn, F. J., Frank, K., & Huth, A. (2014). Of climate and its resulting tree growth: Simulating the productivity of temperate forests. *Ecological Modelling*, 278, 9–17. <https://doi.org/10.1016/j.ecolmodel.2014.01.021>
- Bohn, F. J., & Huth, A. (2017). The importance of forest structure to biodiversity–productivity relationships. *Royal Society Open Science*, 4, 160521. <https://doi.org/10.1098/rsos.160521>
- Bohn, F. J., May, F., & Huth, A. (2018). Species composition and forest structure explain the temperature sensitivity patterns of productivity in temperate forests. *Biogeosciences*, 15(6), 1795–1813. <https://doi.org/10.5194/bg-15-1795-2018>
- Bonan, G. B. (2008). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320(5882), 1444–1449. <https://doi.org/10.1126/science.1155121>
- Bonan, G. B., Williams, M., Fisher, R. A., & Oleson, K. W. (2014). Modeling stomatal conductance in the earth system: Linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum. *Geoscientific Model Development*, 7(5), 2193–2222. <https://doi.org/10.5194/gmd-7-2193-2014>
- Bondeau, A., Smith, P. C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-campen, H., Müller, C., Reichstein, M., & Smith, B. (2007). Modelling the role of agriculture for the 20th century global terrestrial carbon balance. *Global Change Biology*, 13, 679–706. <https://doi.org/10.1111/j.1365-2486.2006.01305.x>
- Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20(1), 1–9. <https://doi.org/10.1111/ddi.12144>
- Bossel, H., & Krieger, H. (1991). Simulation model of natural tropical forest dynamics. *Ecological Modelling*, 59(1), 37–71. [https://doi.org/10.1016/0304-3800\(91\)90127-M](https://doi.org/10.1016/0304-3800(91)90127-M)
- Botella, C., Joly, A., Bonnet, P., Monestiez, P., & Munoz, F. (2018). Species distribution modeling based on the automated identification of citizen observations. *Applications in Plant Sciences*, 6(2), e1029. <https://doi.org/10.1002/aps3.1029>
- Botkin, D. B., Janak, J. F., & Wallis, J. R. (1972). Some ecological consequences of a computer model of forest growth. *Journal of Ecology*, 60(3), 849–872. <https://doi.org/10.2307/2258570>
- Boysen, L. R., Lucht, W., Gerten, D., & Heck, V. (2016). Impacts devalue the potential of large-scale terrestrial CO₂ removal through biomass plantations. *Environmental Research Letters*, 11(9), 95010. <https://doi.org/10.1088/1748-9326/11/9/095010>
- Brede, B., Lau, A., Bartholomeus, H., & Kooistra, L. (2017). Comparing RIEGL RiCOPTER UAV LiDAR derived canopy height and DBH with terrestrial LiDAR. *Sensors*, 17, 2371. <https://doi.org/10.3390/s17102371>
- Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S. L., Vásquez Martínez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragão, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., ... Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348. <https://doi.org/10.1038/nature14283>
- Broennimann, O., Treier, U. A., Müller-Schärer, H., Thuiller, W., Peterson, A. T., & Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, 10(8), 701–709. <https://doi.org/10.1111/j.1461-0248.2007.01060.x>
- Brovkin, V., van Bodegom, P. M., Kleinen, T., Wirth, C., Cornwell, W. K., Cornelissen, J. H. C., & Kattge, J. (2012). Plant-driven variation in decomposition rates improves projections of global litter stock distribution. *Biogeosciences*, 9, 565–576. <https://doi.org/10.5194/bg-9-565-2012>
- Bruelheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S. M., Chytrý, M., Pillar, V. D., Jansen, F., Kattge, J., Sandel, B., Aubin, I., Biurrun, I., Field, R., Haider, S., Jandt, U., Lenoir, J., Peet, R. K., Peyre, G., Sabatini, F. M., ... Zverev, A. (2019). sPlot – a new tool for global vegetation analyses. *Journal of Vegetation Science*, 30(2), 161–186. <https://doi.org/10.1111/jvs.12710>
- Bugmann, H. K. M. (1996). A simplified forest model to study species composition along climate gradients. *Ecology*, 77(7), 2055–2074. <https://doi.org/10.2307/2265700>
- Bugmann, H. (2001). A review of forest gap models. *Climatic Change*, 51(3–4), 259–305. <https://doi.org/10.1023/A:1012525626267>
- Bugmann, H. (2014). Forests in a greenhouse atmosphere: Predicting the unpredictable? In D. A. Coomes, D. F. R. P. Burslem, & W. D. Simonson (Eds.), *Forests and Global Change* (pp. 195–238).
- Bugmann, H., & Bigler, C. (2011). Will the CO₂ fertilization effect in forests be offset by reduced tree longevity? *Oecologia*, 165(2), 533–544. <https://doi.org/10.1007/s00442-010-1837-4>
- Bugmann, H., & Fischlin, A. (1996). Simulating forest dynamics in a complex topography using gridded climatic data. *Climatic Change*, 34(2), 201–211. <https://doi.org/10.1007/BF00224631>
- Bugmann, H., & Pfister, C. (2000). Impacts of interannual climate variability on past and future forest composition. *Regional Environmental Change*, 1(3), 112–125. <https://doi.org/10.1007/s101130000015>
- Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Bruna, J., Caillet, M., François, L., Heinke, J., Henrot, A.-J., Hickler, T., Hülsmann, L., Huth, A., Jacquemin, I., Kollas, C., Lasch-Born, P., Lexer, M. J., Merganič, J., Merganičová, K., Mette, T., ... Reyer, C. P. O. (2019). Tree mortality submodels drive simulated long-term forest dynamics: Assessing 15 models from the stand to global scale. *Ecosphere*, 10(2), e02616. <https://doi.org/10.1002/ecs2.2616>
- Bugmann, H. K. M., Yan, X., Sykes, M. T., Martin, P., Lindner, M., Desanker, P. V., & Cumming, S. G. (1996). A comparison of forest gap models: Model structure and behaviour. *Climatic Change*, 34(2), 289–313. <https://doi.org/10.1007/BF00224640>
- Bussotti, F., Pollastrini, M., Gessler, A., & Luo, Z.-B. (2018). Experiments with trees: From seedlings to ecosystems. *Environmental and Experimental Botany, Experiments with Trees: From Seedlings to Ecosystems*, 152, 1–6. <https://doi.org/10.1016/j.envexpbot.2018.04.012>
- Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno,

- J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., ... Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, 328(5982), 1164–1168. <https://doi.org/10.1126/science.1187512>
- Bykova, O., Chuine, I., Morin, X., & Higgins, S. I. (2012). Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography*, 39(2), 2191–2200. <https://doi.org/10.1111/j.1365-2699.2012.02764.x>
- Chauvet, M., Kunstler, G., Roy, J., & Morin, X. (2017). Using a forest dynamics model to link community assembly processes and traits structure. *Functional Ecology*, 31(7), 1452–1461. <https://doi.org/10.1111/1365-2435.12847>
- Chave, J. (1999). Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling*, 124(2–3), 233–254. [https://doi.org/10.1016/S0304-3800\(99\)00171-4](https://doi.org/10.1016/S0304-3800(99)00171-4)
- Chave, J. (2013). The problem of pattern and scale in ecology: What have we learned in 20 years? *Ecology Letters*, 16, 4–16. <https://doi.org/10.1111/ele.12048>
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., & Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145(1), 87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Cheab, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrière, E., François, C., Gritti, E. S., Legay, M., Pagé, C., Thuiller, W., Viovy, N., & Leadley, P. (2012). Climate change impacts on tree ranges: Model intercomparison facilitates understanding and quantification of uncertainty. *Ecology Letters*, 15, 533–544. <https://doi.org/10.1111/j.1461-0248.2012.01764.x>
- Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., ... Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491(7426), 752–755. <https://doi.org/10.1038/nature11688>
- Chuine, I., & Beaubien, E. G. (2001). Phenology is a major determinant of tree species range. *Ecology Letters*, 4, 500–510. <https://doi.org/10.1046/j.1461-0248.2001.00261.x>
- Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation*. Carnegie Institution of Washington.
- Coffin, D. P., & Lauenroth, W. K. (1990). A gap dynamics simulation model of succession in a semiarid grassland. *Ecological Modelling*, 49(3), 229–266. [https://doi.org/10.1016/0304-3800\(90\)90029-G](https://doi.org/10.1016/0304-3800(90)90029-G)
- Collalti, A., Ibrom, A., Stockmarr, A., Cescatti, A., Alkama, R., Fernández-Martínez, M., Matteucci, G., Sitch, S., Friedlingstein, P., Ciais, P., Goll, D. S., Nabel, J. E. M. S., Pongratz, J., Arneeth, A., Haverd, V., & Prentice, I. C. (2020). Forest production efficiency increases with growth temperature. *Nature Communications*, 11(1), 5322. <https://doi.org/10.1038/s41467-020-19187-w>
- Collalti, A., & Prentice, I. C. (2019). Is NPP proportional to GPP? Waring's hypothesis 20 years on. *Tree Physiology*, 39(8), 1473–1483. <https://doi.org/10.1093/treephys/tpz034>
- Collalti, A., Thornton, P. E., Cescatti, A., Rita, A., Borghetti, M., Nolè, A., Trotta, C., Ciais, P., & Matteucci, G. (2019). The sensitivity of the forest carbon budget shifts across processes along with stand development and climate change. *Ecological Applications*, 29, e01837. <https://doi.org/10.1002/eap.1837>
- Collalti, A., Tjoelker, M. G., Hoch, G., Mäkelä, A., Guidolotti, G., Heskell, M., Petit, G., Ryan, M. G., Battipaglia, G., Matteucci, G., & Prentice, I. C. (2020). Plant respiration: Controlled by photosynthesis or biomass? *Global Change Biology*, 26(3), 1739–1753. <https://doi.org/10.1111/gcb.14857>
- Collalti, A., Trotta, C., Keenan, T. F., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C. P. O., Migliavacca, M., Veroustraete, F., Anav, A., Campioli, M., Scoccimarro, E., Šigut, L., Grieco, E., Cescatti, A., & Matteucci, G. (2018). Thinning can reduce losses in carbon use efficiency and carbon stocks in managed forests under warmer climate. *Journal of Advances in Modeling Earth Systems*, 10(10), 2427–2452. <https://doi.org/10.1029/2018MS001275>
- Collatz, G. J., Ball, J. T., Grivet, C., & Berry, J. A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, 54(2–4), 107–136. [https://doi.org/10.1016/0168-1923\(91\)90002-8](https://doi.org/10.1016/0168-1923(91)90002-8)
- Collier, N., Hoffman, F. M., Lawrence, D. M., Keppel-Aleks, G., Koven, C. D., Riley, W. J., Mu, M., & Randerson, J. T. (2018). The International Land Model Benchmarking (ILAMB) system: Design, theory, and implementation. *Journal of Advances in Modeling Earth Systems*, 10(11), 2731–2754. <https://doi.org/10.1029/2018MS001354>
- Courbaud, B., Goreaud, F., Dreyfus, P. H., & Bonnet, F. R. (2001). Evaluating thinning strategies using a tree distance dependent growth model: Some examples based on the CAPSIS software “uneven-aged spruce forests” module. *Forest Ecology and Management*, 145(1), 15–28. [https://doi.org/10.1016/S0378-1127\(00\)00571-5](https://doi.org/10.1016/S0378-1127(00)00571-5)
- Courchamp, F., Dunne, J. A., Le Maho, Y., May, R. M., Thébaud, C., & Hochberg, M. E. (2015). Fundamental ecology is fundamental. *Trends in Ecology & Evolution*, 30(1), 9–16. <https://doi.org/10.1016/j.tree.2014.11.005>
- Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., & Young-Molling, C. (2001). Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models. *Global Change Biology*, 7(4), 357–373. <https://doi.org/10.1046/j.1365-2486.2001.00383.x>
- Dantas de Paula, M., Groeneveld, J., Fischer, R., Taubert, F., Martins, V. F., & Huth, A. (2018). Defaunation impacts on seed survival and its effect on the biomass of future tropical forests. *Oikos*, 127(10), 1526–1538. <https://doi.org/10.1111/oik.05084>
- Dantas de Paula, M., Groeneveld, J., & Huth, A. (2015). Tropical forest degradation and recovery in fragmented landscapes – Simulating changes in tree community, forest hydrology and carbon balance. *Global Ecology and Conservation*, 3, 664–677. <https://doi.org/10.1016/j.gecco.2015.03.004>
- Davis, M. B., & Zabinski, C. (1992). Changes in geographical range from greenhouse warming: effects on biodiversity in forests. In R. L. Peters, & T. E. Lovejoy (eds.) *Global Warming and Biological Diversity* (pp. 297–309). : Yale University Press.
- Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: Biodiversity conservation in a changing climate. *Science*, 332, 53–58. <https://doi.org/10.1126/science.1200303>
- DeAngelis, D. L., & Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36, 147–168. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152644>
- de Groot, R. S., Wilson, M. A. & Boumans, R. M. J. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, 41, 393–408.
- Didion, M., Kupferschmid, A. D., Zingg, A., Fahse, L., & Bugmann, H. (2009). Gaining local accuracy while not losing generality

- extending the range of gap model applications. *Canadian Journal of Forest Research*, 39(6), 1092–1107. <https://doi.org/10.1139/X09-041>
- Dietrich, J. P., Bodirsky, B. L., Humpenöder, F., Weindl, I., Stevanović, M., Karstens, K., & Popp, A. (2019). MAgPIE 4 – a modular open-source framework for modeling global land systems. *Geoscientific Model Development*, 12(4), 1299–1317. <https://doi.org/10.5194/gmd-12-1299-2019>
- Dietze, M. C., Serbin, S. P., Davidson, C., Desai, A. R., Feng, X., Kelly, R., Kooper, R., LeBauer, D., Mantooh, J., McHenry, K., & Wang, D. (2014). A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes. *Journal of Geophysical Research: Biogeosciences*, 119, (3), 286–300. <https://doi.org/10.1002/2013JG002392>
- Disney, M. (2018). Terrestrial LiDAR: A three-dimensional revolution in how we look at trees. *New Phytologist*, 222, (4), 1736–1741. <https://doi.org/10.1111/nph.15517>
- Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19(9), 1172–1185. <https://doi.org/10.1111/ele.12648>
- Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16, 421–429. <https://doi.org/10.1111/ele.12086>
- Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., Moretti, M. D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S., Steinbauer, M. J., Zeuss, D., & Kraan, C. (2018). Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, 27(9), 1004–1016. <https://doi.org/10.1111/geb.12759>
- Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, 39(12), 2119–2131. <https://doi.org/10.1111/j.1365-2699.2011.02659.x>
- Doyle, T. W. (1981). The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. In D. C. West, H. H. Shugart, & D. B. Botkin (Eds.), *Forest Succession: Concepts and Application* (pp. 56–73). Springer. https://doi.org/10.1007/978-1-4612-5950-3_6
- Dufour-Kowalski, S., Courbaud, B., Dreyfus, P., Meredieu, C., & de Coligny, F. (2012). Capsis: An open software framework and community for forest growth modelling. *Annals of Forest Science*, 69(6), 221–233. <https://doi.org/10.1007/s13595-011-0140-9>
- Dunford, R., Harrison, P. A., & Rounsevell, M. D. A. (2015). Exploring scenario and model uncertainty in cross-sectoral integrated assessment approaches to climate change impacts. *Climatic Change*, 132(3), 417–432. <https://doi.org/10.1007/s10584-014-1211-3>
- Duputié, A., Rutschmann, A., Ronce, O., & Chuine, I. (2015). Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, 21, 3062–3073. <https://doi.org/10.1111/gcb.12914>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elkin, C., Gutiérrez, A. G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., & Bugmann, H. (2013). A 2°C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biology*, 19(6), 1827–1840. <https://doi.org/10.1111/gcb.12156>
- Estes, L., Elsen, P. R., Treuer, T., Ahmed, L., Caylor, K., Chang, J., Choi, J. J., & Ellis, E. C. (2018). The spatial and temporal domains of modern ecology. *Nature Ecology & Evolution*, 1, <https://doi.org/10.1038/s41559-018-0524-4>
- Evans, T. G., Diamond, S. E., & Kelly, M. W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. *Conservation Physiology*, 3(1), cov056. <https://doi.org/10.1093/conphys/cov056>
- F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30(5), 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K. J., Elbers, J. A., Goldstein, A. H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A. S., Katul, G., Law, B. E., ... Wofsy, S. (2002). Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, 113(1-4), 53–74. [https://doi.org/10.1016/S0168-1923\(02\)00102-8](https://doi.org/10.1016/S0168-1923(02)00102-8)
- Falster, D. S., Brännström, A., Westoby, M., & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, 114, E2719–E2728. <https://doi.org/10.1073/pnas.1610206114>
- Famiglietti, C. A., Smallman, T. L., Levine, P. A., Flack-Prain, S., Quetin, G. R., Meyer, V., Parazoo, N. C., Stettz, S. G., Yang, Y., Bonal, D., Bloom, A. A., Williams, M., & Konings, A. G. (2020). Optimal model complexity for terrestrial carbon cycle prediction. *Biogeosciences Discussions*, 1–42. <https://doi.org/10.5194/bg-2020-478>. [Epub ahead of print].
- Fedrigo, M., Stewart, S. B., Roxburgh, S. H., Kasel, S., Bennett, L. T., Vickers, H., & Nitschke, C. R. (2019). Predictive ecosystem mapping of South-Eastern Australian temperate forests using lidar-derived structural profiles and species distribution models. *Remote Sensing*, 11, 93. <https://doi.org/10.3390/rs11010093>
- Felton, A. J., & Smith, M. D. (2017). Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160142. <https://doi.org/10.1098/rstb.2016.0142>
- Fernandes, R. F., Scherrer, D., & Guisan, A. (2018). How much should one sample to accurately predict the distribution of species assemblages? A virtual community approach. *Ecological Informatics*, 48, 125–134. <https://doi.org/10.1016/j.ecoinf.2018.09.002>
- Ferraz, A., Saatchi, S., Mallet, C., & Meyer, V. (2016). Lidar detection of individual tree size in tropical forests. *Remote Sensing of Environment*, 183, 318–333. <https://doi.org/10.1016/j.rse.2016.05.028>
- Ferrier, S. (2002). Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? *Systematic Biology*, 51(2), 331–363. <https://doi.org/10.1080/10635150252899806>
- Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, 43, 393–404. <https://doi.org/10.1111/j.1365-2664.2006.01149.x>
- Field, C. B., V. Barros, T. F. Stocker, & Q. Dahe (Eds.) (2012). *Managing the risks of extreme events and disasters to advance climate change adaptation*. Cambridge University Press.
- Fischer, F. J., Maréchaux, I., & Chave, J. (2019). Improving plant allometry by fusing forest models and remote sensing. *New Phytologist*, 223(3), 1159–1165. <https://doi.org/10.1111/nph.15810>
- Fischer, R., Armstrong, A., Shugart, H. H., & Huth, A. (2014). Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest. *Environmental Modelling & Software*, 52, 200–206. <https://doi.org/10.1016/j.envsoft.2013.10.026>
- Fischer, R., Bohn, F., Dantas de Paula, M., Dislich, C., Groeneveld, J., Gutiérrez, A. G., Kazmierczak, M., Knapp, N., Lehmann, S., Paulick, S., Pütz, S., Rödig, E., Taubert, F., Köhler, P., & Huth, A. (2016). Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. *Ecological Modelling, next Generation Ecological Modelling, Concepts, and Theory*:

- Structural Realism, Emergence, and Predictions*, 326, 124–133. <https://doi.org/10.1016/j.ecolmodel.2015.11.018>
- Fischer, R., Ensslin, A., Rutten, G., Fischer, M., Schellenberger Costa, D., Kleyer, M., Hemp, A., Paulick, S., & Huth, A. (2015). Simulating carbon stocks and fluxes of an African tropical montane forest with an individual-based forest model. *PLoS One*, 10, e0123300. <https://doi.org/10.1371/journal.pone.0123300>
- Fischer, R., Knapp, N., Bohn, F., Shugart, H. H., & Huth, A. (2019). The relevance of forest structure for biomass and productivity in temperate forests: New perspectives for remote sensing. *Surveys in Geophysics*, 40, 709–734. <https://doi.org/10.1007/s10712-019-09519-x>
- Fischer, R., Rödig, E., & Huth, A. (2018). Consequences of a reduced number of plant functional types for the simulation of forest productivity. *Forests*, 9(8), 460. <https://doi.org/10.3390/f9080460>
- Fisher, R. A., & Koven, C. D. (2020). Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems*, 12(4), e2018MS001453. <https://doi.org/10.1029/2018MS001453>
- Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farnier, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., ... Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, 24(1), 35–54. <https://doi.org/10.1111/gcb.13910>
- Fisher, R. A., Williams, M., Do Vale, R. L., Da Costa, A. L., & Meir, P. (2006). Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant, Cell & Environment*, 29(2), 151–165. <https://doi.org/10.1111/j.1365-3040.2005.01407.x>
- Fischer, R. (2013). *Modellierung der Dynamik afrikanischer Tropenwälder*. Analyse des Einflusses von Störungen auf tropische Wälder mit Hilfe des Waldmodells FORMIND (Dissertation, Universität Osnabrück). Retrieved from <https://repositorium.ub.uni-osnabrueck.de/handle/urn:nbn:de:gbv:700-2014032112302>
- Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., Garcia, S., Goll, D. S., Grandis, A., Jiang, M., Haverd, V., Hofhansl, F., Holm, J. A., Kruijt, B., Leung, F., Medlyn, B. E., Mercado, L. M., Norby, R. J., Pak, B., ... Lapola, D. M. (2019). Amazon forest response to CO₂ fertilization dependent on plant phosphorus acquisition. *Nature Geoscience*, 12(9), 736–741. <https://doi.org/10.1038/s41561-019-0404-9>
- Fontes, L., Bontemps, J. D., Bugmann, H., van Oijen, M., Gracia, C., Kramer, K., & Skovsgaard, J. P. (2010). Models for supporting forest management in a changing environment. *Forest Systems*, 19, 8–29.
- Forkel, M., Andela, N., Harrison, S. P., Lasslop, G., van Marle, M., Chuvieco, E., Dorigo, W., Forrest, M., Hantson, S., Heil, A., Li, F., Melton, J., Sitch, S., Yue, C., & Arneeth, A. (2019). Emergent relationships with respect to burned area in global satellite observations and fire-enabled vegetation models. *Biogeosciences*, 16(1), 57–76. <https://doi.org/10.5194/bg-16-57-2019>
- Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, 27(2), 245–256. <https://doi.org/10.1111/geb.12684>
- Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, 16(3), 321–330. <https://doi.org/10.1111/j.1472-4642.2010.00641.x>
- Franklin, O., Harrison, S. P., Dewar, R., Farnier, C. E., Brännström, Å., Dieckmann, U., Pietsch, S., Falster, D., Cramer, W., Loreau, M., Wang, H., Mäkelä, A., Rebel, K. T., Meron, E., Schymanski, S. J., Rovenskaya, E., Stocker, B. D., Zaehle, S., Manzoni, S., ... Prentice, I. C. (2020). Organizing principles for vegetation dynamics. *Nature Plants*, 6(5), 444–453. <https://doi.org/10.1038/s41477-020-0655-x>
- Frieler, K., Lange, S., Piontek, F., Reyer, C., Schewe, J., Warszawski, L., Yamagata, Y. (2017). Assessing the impacts of 1.5 °C global warming – simulation protocol of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2b). Geoscientific Model Development. <https://doi.org/10.5194/gmd-10-4321-11312017>
- Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., & Woodward, F. I. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. *Proceedings of National Academy of Science USA*, 111(9), 3280–3285. <https://doi.org/10.1073/pnas.1222477110>
- Fyllas, N. M., Bentley, L. P., Shenkin, A., Asner, G. P., Atkin, O. K., Díaz, S., Enquist, B. J., Farfan-Rios, W., Gloor, E., Guerrieri, R., Huasco, W. H., Ishida, Y., Martin, R. E., Meir, P., Phillips, O., Salinas, N., Silman, M., Weerasinghe, L. K., Zaragoza-Castells, J., & Malhi, Y. (2017). Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. *Ecology Letters*, 20(6), 730–740. <https://doi.org/10.1111/ele.12771>
- García-Valdés, R., Bugmann, H., & Morin, X. (2018). Climate change-driven extinctions of tree species affect forest functioning more than random extinctions. *Diversity and Distributions*, 24(7), 906–918. <https://doi.org/10.1111/ddi.12744>
- García-Valdés, R., Estrada, A., Early, R., Lehsten, V., & Morin, X. (2020). Climate change impacts on long-term forest productivity might be driven by species turnover rather than by changes in tree growth. *Global Ecology and Biogeography*, 29(8), 1360–1372. <https://doi.org/10.1111/geb.13112>
- Gibbs, H. K., Brown, S., Niles, J. O., & Foley, J. A. (2007). Monitoring and estimating tropical forest carbon stocks: Making REDD a reality. *Environmental Research Letters*, 2(4), 45023. <https://doi.org/10.1088/1748-9326/2/4/045023>
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53(1), 7–26. <https://doi.org/10.2307/2479933>
- Goetz, S., & Dubayah, R. (2011). Advances in remote sensing technology and implications for measuring and monitoring forest carbon stocks and change. *Carbon Management*, 2(3), 231–244. <https://doi.org/10.4155/cmt.11.18>
- Goll, D. S., Vuichard, N., Maignan, F., Jornet-Puig, A., Sardans, J., Violette, A., & Ciais, P. (2017). A representation of the phosphorus cycle for ORCHIDEE (revision 4520). *Geoscientific Model Development*, 10(10), 3745–3770. <https://doi.org/10.5194/gmd-10-3745-2017>
- Grisebach, A. (1872). *Die Vegetation der Erde nach ihrer klimatischen Anordnung: Ein Abriss der vergleichenden Geographie der Pflanzen*. Bd. I und II. Verlag von Wilhelm Engelmann.
- Groeneveld, J., Alves, L. F., Bernacci, L. C., Catharino, E., Knogge, C., Metzger, J. P., Pütz, S., & Huth, A. (2009). The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. *Ecological Modelling*, 220(19), 2450–2459. <https://doi.org/10.1016/j.ecolmodel.2009.06.015>
- Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R. E., Pockman, W. T., Salmon, Y., Zweifel, R., & McDowell, N. G. (2018). Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. *Environmental and Experimental Botany, Experiments with Trees: From Seedlings to Ecosystems*, 152, 19–27. <https://doi.org/10.1016/j.envexpbot.2017.12.010>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A.,

- Broennimann, O., Austin, M., ... Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16(12), 1424–1435. <https://doi.org/10.1111/ele.12189>
- Hantson, S., Arneith, A., Harrison, S. P., Kelley, D. I., Prentice, I. C., Rabin, S. S., Archibald, S., Mouillot, F., Arnold, S. R., Artaxo, P., Bachelet, D., Ciais, P., Forrest, M., Friedlingstein, P., Hickler, T., Kaplan, J. O., Kloster, S., Knorr, W., Lasslop, G., ... Yue, C. (2016). The status and challenge of global fire modelling. *Biogeosciences*, 13(11), 3359–3375. <https://doi.org/10.5194/bg-13-3359-2016>
- Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. *Ecology Letters*, 19(8), 825–838. <https://doi.org/10.1111/ele.12618>
- Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T., & Huth, A. (2011). Statistical inference for stochastic simulation models – theory and application. *Ecology Letters*, 14(8), 816–827. <https://doi.org/10.1111/j.1461-0248.2011.01640.x>
- Hartig, F., Dislich, C., Wiegand, T., & Huth, A. (2014). Technical Note: Approximate Bayesian parameterization of a process-based tropical forest model. *Biogeosciences*, 11(4), 1261–1272. <https://doi.org/10.5194/bg-11-1261-2014>
- Hartmann, H., Moura, C. F., Anderegg, W. R. L., Ruehr, N. K., Salmon, Y., Allen, C. D., Arndt, S. K., Breshears, D. D., Davi, H., Galbraith, D., Ruthrof, K. X., Wunder, J., Adams, H. D., Bloemen, J., Cailleret, M., Cobb, R., Gessler, A., Grams, T. E. E., Jansen, S., ... O'Brien, M. (2018). Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist*, 218(1), 15–28. <https://doi.org/10.1111/nph.15048>
- Heiri, C., Bugmann, H., Tinner, W., Heiri, O., & Lischke, H. (2006). A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. *Journal of Ecology*, 94(1), 206–216. <https://doi.org/10.1111/j.1365-2745.2005.01072.x>
- Hickler, T., Prentice, I. C., Smith, B., Sykes, M. T., & Zaehle, S. (2006). Implementing plant hydraulic architecture within the LPJ Dynamic Global Vegetation Model. *Global Ecology and Biogeography*, 15(6), 567–577. <https://doi.org/10.1111/j.1466-8238.2006.00254.x>
- Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R., Cramer, W., Kühn, I., & Sykes, M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, 21(1), 50–63. <https://doi.org/10.1111/j.1466-8238.2010.00613.x>
- Hiltner, U., Huth, A., Bräuning, A., Hérault, B., & Fischer, R. (2018). Simulation of succession in a neotropical forest: High selective logging intensities prolong the recovery times of ecosystem functions. *Forest Ecology and Management*, 430, 517–525. <https://doi.org/10.1016/j.foreco.2018.08.042>
- Holzwarth, F., Kahl, A., Bauhus, J., & Wirth, C. (2013). Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology*, 101(1), 220–230. <https://doi.org/10.1111/1365-2745.12015>
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Humpenöder, F., Popp, A., Bodirsky, B. L., Weindl, I., Biewald, A., Lotze-Campen, H., Dietrich, J. P., Klein, D., Kreidenweis, U., Müller, C., Rolinski, S., & Stevanovic, M. (2018). Large-scale bioenergy production: How to resolve sustainability trade-offs? *Environmental Research Letters*, 13(2), 24011. <https://doi.org/10.1088/1748-9326/aa9e3b>
- Huston, M., DeAngelis, D., & Post, W. (1988). New computer models unify ecological theory. *BioScience*, 38(10), 682–691. <https://doi.org/10.2307/1310870>
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- Huth, A., & Ditzer, T. (2001). Long-term impacts of logging in a tropical rain forest – a simulation study. *Forest Ecology and Management*, 142(1), 33–51. [https://doi.org/10.1016/S0378-1127\(00\)00338-8](https://doi.org/10.1016/S0378-1127(00)00338-8)
- Huth, A., Drechsler, M., & Köhler, P. (2005). Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in Dipterocarp lowland rain 1250 forests. *Forest Ecology and Management*, 207(1), 215–232. <https://doi.org/10.1016/j.foreco.2004.10.028>
- IPBES. (2016). *Summary for policymakers of the methodological assessment of scenarios and models of biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Iverson, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M., & Violle, C. (2017). A Global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, 215(1), 15–26. <https://doi.org/10.1111/nph.14486>
- Iverson, L. R., Schwartz, M. W., & Prasad, A. M. (2004). Potential colonization of newly available tree-species habitat under climate change: An analysis for five eastern US species. *Landscape Ecology*, 19(7), 787–799. <https://doi.org/10.1007/s10980-005-3990-5>
- Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, 317(5834), 58–62. <https://doi.org/10.1126/science.1133258>
- Jägermeyr, J., Gerten, D., Heinke, J., Schaphoff, S., Kummu, M., & Lucht, W. (2015). Water savings potentials of irrigation systems: Global simulation of processes and linkages. *Hydrology and Earth System Sciences*, 19(7), 3073–3091. <https://doi.org/10.5194/hess-19-3073-2015>
- Jarvis, P. G. (Ed.). (1998). *European forests and global change: The likely impacts of rising CO₂ and temperature*. Cambridge University Press, Cambridge, U.K.
- Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences*, 110(28), E2602–E2610. <https://doi.org/10.1073/pnas.1302251110>
- Joetzer, E., Pillet, M., Ciais, P., Barbier, N., Chave, J., Schlund, M., & Poulter, B. (2017). Assimilating satellite-based canopy height within an ecosystem model to estimate aboveground forest biomass. *Geophysical Research Letters*, 44(13), 6823–6832. <https://doi.org/10.1002/2017GL074150>
- Johnson, M. O., Galbraith, D., Gloor, M., De Deurwaerder, H., Guimberteau, M., Rammig, A., Thonicke, K., Verbeeck, H., von Randow, C., Monteagudo, A., Phillips, O. L., Brien, R. J. W., Feldpausch, T. R., Lopez Gonzalez, G., Fauset, S., Quesada, C. A., Christoffersen, B., Ciais, P., Sampaio, G., ... Baker, T. R. (2016). Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: Implications for dynamic global vegetation models. *Global Change Biology*, 22(12), 3996–4013. <https://doi.org/10.1111/gcb.13315>
- Journé, V., Barnagaud, J.-Y., Bernard, C., Crochet, P.-A., & Morin, X. (2020). Correlative climatic niche models predict real and virtual species distributions equally well. *Ecology*, 101(1), e02912. <https://doi.org/10.1002/ecy.2912>
- Jucker, T., Bongalov, B., Burslem, D. F. R. P., Nilus, R., Dalponte, M., Lewis, S. L., Phillips, O. L., Qie, L., & Coomes, D. A. (2018). Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters*, 21(7), 989–1000. <https://doi.org/10.1111/ele.12964>
- Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., Dalponte, M., van Ewijk, K. Y., Forrester, D. I., Haeni, M., Higgins, S. I., Holdaway, R. J., Iida, Y., Lorimer, C., Marshall, P. L., Momo, S., Moncrieff, G. R., Ploton, P., Poorter, L., ... Coomes, D. A. (2017). Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Global Change Biology*, 23(1), 177–190. <https://doi.org/10.1111/gcb.13388>
- Jung, M., Reichstein, M., & Bondeau, A. (2009). Towards global empirical upscaling of FLUXNET eddy covariance observations:

- Validation of a model tree ensemble approach using a biosphere model. *Biogeosciences*, 6(10), 2001–2013. <https://doi.org/10.5194/bg-6-2001-2009>
- Justice, C. O., Townshend, J. R. G., Vermote, E. F., Masuoka, E., Wolfe, R. E., Saleous, N., Morisette, J. T. (2002). An overview of MODIS Land data processing and product status. *Remote Sensing of Environment, the Moderate Resolution Imaging Spectroradiometer (MODIS): a New Generation of Land Surface Monitoring*, 83(1), 3–15. [https://doi.org/10.1016/S0034-1306-4257\(02\)00084-6](https://doi.org/10.1016/S0034-1306-4257(02)00084-6)
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. <https://doi.org/10.1111/gcb.14904>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van BODEGOM, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., ... Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, 17(9), 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Keane, R. E., Austin, M., Field, C., Huth, A., Lexer, M. J., Peters, D., & Wyckoff, P. (2001). Tree mortality in gap models: Application to climate change. *Climatic Change*, 51(3–4), 509–540. <https://doi.org/10.1023/A:1012539409854>
- Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12(4), 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
- Keenan, T., Niinemets, Ü., Sabate, S., Gracia, C., & Peñuelas, J. (2009a). Process based inventory of isoprenoid emissions from European forests: Model comparisons, current knowledge and uncertainties. *Atmospheric Chemistry and Physics*, 9(12), 4053–4076. <https://doi.org/10.5194/acp-9-4053-2009>
- Keenan, T., Niinemets, Ü., Sabate, S., Gracia, C., & Peñuelas, J. (2009b). Seasonality of monoterpene emission potentials in *Quercus ilex* and *Pinus pinea*: Implications for regional VOC emissions modeling. *Journal of Geophysical Research: Atmospheres*, 114(D22202), <https://doi.org/10.1029/2009JD011904>
- Keenan, T., Sabaté, S., & Gracia, C. (2008). Forest eco-physiological models and carbon sequestration. In: F. Bravo, R. Jandl, V. LeMay, & K. von Gadow (Eds.) *Managing Forest Ecosystems: The Challenge of Climate Change* (pp. 83–102). : Springer. https://doi.org/10.1007/978-1-4020-8343-3_5
- Keenan, T., Serra, J. M., Lloret, F., Ninyerola, M., & Sabate, S. (2011). Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters!. *Global Change Biology*, 17(1), 565–579. <https://doi.org/10.1111/j.1365-2486.2010.02254.x>
- Kercher, J. R., & Axelrod, M. C. (1984). Analysis of silva: A model for forecasting the effects of SO2 pollution and fire on western coniferous forests. *Ecological Modelling*, 23(1), 165–184. [https://doi.org/10.1016/0304-3800\(84\)90124-8](https://doi.org/10.1016/0304-3800(84)90124-8)
- Kienast, F. (1987). FORECE: A forest succession model for southern Central Europe (No. ORNL/TM-10575). Oak Ridge National Lab., TN (USA) website: <https://www.osti.gov/biblio/5729437>
- Kleidon, A., & Mooney, H. A. (2000). A global distribution of biodiversity inferred from climatic constraints: Results from a process-based modelling study. *Global Change Biology*, 6(5), 507–523. <https://doi.org/10.1046/j.1365-2486.2000.00332.x>
- Knapp, N., Fischer, R., & Huth, A. (2018). Linking lidar and forest modeling to assess biomass estimation across scales and disturbance states. *Remote Sensing of Environment*, 205, 199–209. <https://doi.org/10.1016/j.rse.2017.11.018>
- Köhler, P., & Huth, A. (1998). The effects of tree species grouping in tropical rainforest modelling: Simulations with the individual-based model Formind. *Ecological Modelling*, 109(3), 301–321. [https://doi.org/10.1016/S0304-3800\(98\)00066-0](https://doi.org/10.1016/S0304-3800(98)00066-0)
- Kramer, K., Leinonen, I., Bartelink, H. H., Berbigier, P., Borghetti, M., Bernhofer, C., & Vesala, T. (2002). Evaluation of six process-based forest growth models using eddy-covariance measurements of CO2 and H2O fluxes at six forest sites in Europe. *Global Change Biology*, 8(3), 213–230. doi: 10.1046/j.1365-2486.2002.00471.x (2002). Evaluation of six process-based forest growth models using eddy-covariance measurements of CO2 and H2O fluxes at six forest sites in Europe. *Global Change Biology*, 8, 213–230.
- Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S., & Prentice, I. C. (2005). A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, 19(1), GB1015. <https://doi.org/10.1029/2003GB002199>
- Kunstler, G., Allen, R. B., Coomes, D. A., Canham, C. D., & Wright, E. F. (2013). Sustainable management, earthquake disturbances, and transient dynamics: Modelling timber harvesting impacts in mixed-species forests. *Annals of Forest Science*, 70(3), 287–298. <https://doi.org/10.1007/s13595-012-0256-6>
- Kunstler, G., Coomes, D. A., & Canham, C. D. (2009). Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *Journal of Ecology*, 97(4), 685–695. <https://doi.org/10.1111/j.1365-2745.2009.01482.x>
- Kurzweil, R. (2005). *The singularity is near: When humans transcend biology*. Penguin Books.
- Lafond, V., Lagarrigues, G., Cordonnier, T., & Courbaud, B. (2014). Uneven-aged management options to promote forest resilience for climate change adaptation: Effects of group selection and harvesting intensity. *Annals of Forest Science*, 71(2), 173–186. <https://doi.org/10.1007/s13595-013-0291-y>
- Langan, L., Higgins, S. I., & Scheiter, S. (2017). Climate-biomes, pedo-biomes or pyro-biomes: Which world view explains the tropical forest-savanna boundary in South America? *Journal of Biogeography*, 44(10), 2319–2330. <https://doi.org/10.1111/jbi.13018>
- Langerwisch, F., Václavík, T., von Bloh, W., Vetter, T., & Thonicke, K. (2017). Combined effects of climate and land-use change on the provision of ecosystem services in rice agro-ecosystems. *Environmental Research Letters*, 13(1), 15003. <https://doi.org/10.1088/1748-9326/aa954d>
- Lasslop, G., Thonicke, K., & Kloster, S. (2014). SPITFIRE within the MPI Earth system model: Model development and evaluation. *Journal of Advances in Modeling Earth Systems*, 6(3), 740–755. <https://doi.org/10.1002/2013MS000284>
- Leathwick, J. R., & Austin, M. P. (2001). Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology*, 82(9), 2560–2573. [https://doi.org/10.1890/0012-9658\(2001\)082\[2560:CIBTSI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2560:CIBTSI]2.0.CO;2)
- LeBauer, D. S., Wang, D., Richter, K. T., Davidson, C. C., & Dietze, M. C. (2013). Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs*, 83(2), 133–154. <https://doi.org/10.1890/12-0137.1>
- Leemans, R., & Prentice, I. C. (1989). FORSKA - a general forest succession model. Meddelanden Fraan Vaextbiologiska Institutionen: Retrieved from. <http://agris.fao.org/agris-search/search.do?recordID=SE19890116521>
- Lehmann, S., & Huth, A. (2015). Fast calibration of a dynamic vegetation model with minimum observation data. *Ecological Modelling*, 301, 98–105. <https://doi.org/10.1016/j.ecolmodel.2015.01.013>
- Lehsten, V., Mischurov, M., Lindström, E., Lehsten, D., & Lischke, H. (2019). LPJ-GM 1.0: Simulating migration efficiently in a dynamic vegetation model. *Geoscientific Model Development*, 12(3), 893–908. <https://doi.org/10.5194/gmd-12-893-2019>
- Lenihan, J. M., Daly, C., Bachelet, D., & Neilson, R. P. (1998). Simulating broad-scale fire severity in a Dynamic Global Vegetation Model. *Northwest Science*, 72, 91–103.

- Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*, 73(6), 1943–1967. <https://doi.org/10.2307/1941447>
- Lischke, H. (2005). Modeling tree species migration in the Alps during the Holocene: What creates complexity? *Ecological Complexity*, 2(2), 159–174. <https://doi.org/10.1016/j.ecocom.2004.11.009>
- Lischke, H., & Löffler, T. J. (2006). Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. *Ecological Modelling*, 198(3–4), 341–361. <https://doi.org/10.1016/j.ecolmodel.2006.05.005>
- Lischke, H., von Grafenstein, U., & Ammann, B. (2013). Forest dynamics during the transition from the Oldest Dryas to the Bølling-Allerød at Gerzensee—A simulation study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 391, 60–73. <https://doi.org/10.1016/j.palaeo.2012.12.001>
- Lischke, H., Zimmermann, N. E., Bolliger, J., Rickebusch, S., & Löffler, T. J. (2006). TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, 199(4), 409–420. <https://doi.org/10.1016/j.ecolmodel.2005.11.046>
- Liu, J., & Ashton, P. S. (1995). Individual-based simulation models for forest succession and management. *Forest Ecology and Management*, 73(1), 157–175. [https://doi.org/10.1016/0378-1127\(94\)03490-N](https://doi.org/10.1016/0378-1127(94)03490-N)
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., & Wardle, D. A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294(5543), 804–808. <https://doi.org/10.1126/science.1064088>
- Lovenduski, N. S., & Bonan, G. B. (2017). Reducing uncertainty in projections of terrestrial carbon uptake. *Environmental Research Letters*, 12(4), 44020. <https://doi.org/10.1088/1748-1412-9326/aa66b8>
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385. <https://doi.org/10.1086/282505>
- Makela, A., Landsberg, J., Ek, A. R., Burk, T. E., Ter-Mikaelian, M., Agren, G. I., Oliver, C. D., & Puttonen, P. (2000). Process-based models for forest ecosystem management: Current state of the art and challenges for practical implementation. *Tree Physiology*, 20(5–6), 289–298. <https://doi.org/10.1093/treephys/20.5-6.289>
- Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., del Aguila-Pasquel, J., Aragão, L. E. O. C., Araujo-Murakami, A., Brando, P., da Costa, A. C. L., Silva-Espejo, J. E., Farfán Amézquita, F., Galbraith, D. R., Quesada, C. A., Rocha, W., Salinas-Revilla, N., Silvério, D., Meir, P., & Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, 21(6), 2283–2295. <https://doi.org/10.1111/gcb.12859>
- Maréchaux, I., & Chave, J. (2017). An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: Description and applications. *Ecological Monographs*, 87(4), 632–664. <https://doi.org/10.1002/ecm.1271>
- Maris, V., Huneman, P., Coreau, A., Kéfi, S., Pradel, R., & Devictor, V. (2018). Prediction in ecology: Promises, obstacles and clarifications. *Oikos*, 127(2), 171–183. <https://doi.org/10.1111/oik.04655>
- Maroschek, M., Rammer, W., & Lexer, M. J. (2015). Using a novel assessment framework to evaluate protective functions and timber production in Austrian mountain forests under climate change. *Regional Environmental Change*, 15(8), 1543–1555. <https://doi.org/10.1007/s10113-014-0691-z>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- McMahon, S. M., Harrison, S. P., Armbruster, W. S., Bartlein, P. J., Beale, C. M., Edwards, M. E., Kattge, J., Midgley, G., Morin, X., & Prentice, I. C. (2011). Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution*, 26(5), 249–259. <https://doi.org/10.1016/j.tree.2011.02.012>
- Medlyn, B. E., De Kauwe, M. G., Zaehle, S., Walker, A. P., Duursma, R. A., Luus, K., Mishurov, M., Pak, B., Smith, B., Wang, Y.-P., Yang, X., Crous, K. Y., Drake, J. E., Gimeno, T. E., Macdonald, C. A., Norby, R. J., Power, S. A., Tjoelker, M. G., & Ellsworth, D. S. (2016). Using models to guide field experiments: A priori predictions for the CO₂ response of a nutrient- and water-limited native Eucalypt woodland. *Global Change Biology*, 22(8), 2834–2851. <https://doi.org/10.1111/gcb.13268>
- Medlyn, B. E., Duursma, R. A., & Zeppel, M. J. B. (2011). Forest productivity under climate change: A checklist for evaluating model studies. *Wires Clim Change*, 2(3), 332–355. <https://doi.org/10.1002/wcc.108>
- Medlyn, B. E., Pepper, D. A., O'Grady, A. P., & Keith, H. (2007). Linking leaf and tree water use with an individual-tree model. *Tree Physiology*, 27(12), 1687–1699. <https://doi.org/10.1093/treephys/27.12.1687>
- Medvigy, D., Wang, G., Zhu, Q., Riley, W. J., Trierweiler, A. M., Waring, B. G., Xu, X., & Powers, J. S. (2019). Observed variation in soil properties can drive large variation in modelled forest functioning and composition during tropical forest secondary succession. *New Phytologist*, 223(4), 1820–1833. <https://doi.org/10.1111/nph.15848>
- Meier, E. S., Edwards Jr, T. C., Kienast, F., Dobbertin, M., & Zimmermann, N. E. (2011). Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, 38(2), 371–382. <https://doi.org/10.1111/j.1365-2699.2010.02405.x>
- Meir, P., Wood, T. E., Galbraith, D. R., Brando, P. M., Costa, A. C. L. D., Rowland, L., & Ferreira, L. V. (2015). Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: Insights from field experiments. *BioScience*, 65(9), 882–892. <https://doi.org/10.1093/biosci/biv107>
- Merganičová, K., Merganič, J., Lehtonen, A., Vacchiano, G., Sever, M. Z. O., Augustynczyk, A. L. D., Grote, R., Kyselová, I., Mäkelä, A., Yousefpour, R., Krejza, J., Collalti, A., & Reyer, C. P. O. (2019). Forest carbon allocation modelling under climate change. *Tree Physiology*, 39(12), 1937–1960. <https://doi.org/10.1093/treephys/tpz105>
- Millennium Ecosystem Assessment. (2005). *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Mina, M., Bugmann, H., Cordonnier, T., Irauschek, F., Klopčič, M., Pardos, M., & Cailletet, M. (2017). Future ecosystem services from European mountain forests under climate change. *Journal of Applied Ecology*, 54(2), 389–401. <https://doi.org/10.1111/1365-2664.12772>
- Mohren, G. M. J., K. Kramer, & S. Sabaté (Eds.) (1997). *Impacts of Global Change on Tree Physiology and Forest Ecosystems: Proceedings of the International Conference on Impacts of Global Change on Tree Physiology and Forest Ecosystems, held 26–29 November 1996, Wageningen, The Netherlands*. Kluwer Academic Publishers.
- Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling vegetation dynamics: the ecosystem demography model (ed). *Ecological Monographs*, 71(4), 1478–1486. [https://doi.org/10.1890/0012-9615\(2001\)071\[0557:AMFSVD\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2)
- Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., & Ogee, J. (2005). Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. *Global Change Biology*, 11(12), 2211–2233. <https://doi.org/10.1111/j.1365-2486.2005.01036.x>
- Mori, A. S. (2017). Biodiversity and ecosystem services in forests: Management and restoration founded on ecological theory. *Journal of Applied Ecology*, 54(1), 7–11. <https://doi.org/10.1111/1365-2664.12854>
- Morin, X., Bugmann, H., Coligny, F., Martin-StPaul, N., Cailletet, M., Limousin, J.-M., Ourcival, J.-M., Prevosto, B., Simioni, G., Toigo, M., Vennetier, M., Catteau, E., & Guillemot, J. (2021). Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology*, <https://doi.org/10.1111/1365-2435.13760>

- Morin, X., Damestoy, T., Toigo, M., Castagneyrol, B., Jactel, H., de Coligny, F., & Meredieu, C. (2020). Using forest gap models and experimental data to explore long-term effects of tree diversity on the productivity of mixed planted forests. *Annals of Forest Science*, 77(2), 50. <https://doi.org/10.1007/s13595-020-00954-0>
- Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M., & Bugmann, H. (2014). Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters*, 17(12), 1526–1535. <https://doi.org/10.1111/ele.12357>
- Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, 8(1), 5627. <https://doi.org/10.1038/s41598-018-23763-y>
- Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14(12), 1211–1219. <https://doi.org/10.1111/j.1461-0248.2011.01691.x>
- Morin, X., & Lechowicz, M. J. (2008). Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters*, 4(5), 573–576. <https://doi.org/10.1098/rsbl.2008.0181>
- Morin, X., & Thuiller, W. (2009). Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, 90(5), 1301–1313. <https://doi.org/10.1890/08-0134.1>
- Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G. J., Lavorel, S., Le Gall, L., Meslin, L., ... Loreau, M. (2015). REVIEW: Predictive ecology in a changing world. *Journal of Applied Ecology*, 52(5), 1293–1310. <https://doi.org/10.1111/1365-2664.12482>
- Muller-Landau, H. C., Wright, S. J., Calderón, O., Condit, R., & Hubbell, S. P. (2008). Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology*, 96(4), 653–667. <https://doi.org/10.1111/j.1365-2745.2008.01399.x>
- Nabuurs, G.-J., Delacote, P., Ellison, D., Hanewinkel, M., Hetemäki, L., & Lindner, M. (2017). By 2050 the Mitigation Effects of EU Forests Could Nearly Double through Climate Smart Forestry. *Forests*, 8(12), 484. <https://doi.org/10.3390/f8120484>
- Naeem, S., Bunker, D. E., Hector, A., Loreau, M., & Perrings, C. (2009). *Biodiversity, ecosystem functioning, and human wellbeing: An ecological and economic perspective*. Oxford University Press.
- Nakashizuka, T. (2001). Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology & Evolution*, 16(4), 205–210. [https://doi.org/10.1016/S0169-5347\(01\)02117-6](https://doi.org/10.1016/S0169-5347(01)02117-6)
- Neilson, R. P., Pitelka, L. F., Solomon, A. M., Nathan, R., Midgley, G. F., Fragoso, J. M. V., & Thompson, K. (2005). Forecasting regional to global plant migration in response to climate change. *BioScience*, 55(9), 749–759. [https://doi.org/10.1641/0006-3568\(2005\)055\[0749:FRTGP M\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0749:FRTGP M]2.0.CO;2)
- Nobis, M. P., & Normand, S. (2014). KISSMig – a simple model for R to account for limited migration in analyses of species distributions. *Ecography*, 37(12), 1282–1287. <https://doi.org/10.1111/ecog.00930>
- Noce, S., Collalti, A., & Santini, M. (2017). Likelihood of changes in forest species suitability, distribution, and diversity under future climate: The case of Southern Europe. *Ecology and Evolution*, 7(22), 9358–9375. <https://doi.org/10.1002/ece3.3427>
- Norby, R. J., De Kauwe, M. G., Domingues, T. F., Duursma, R. A., Ellsworth, D. S., Goll, D. S., & Zaehle, S. (2016). Model–data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytologist*, 209(1), 17–28. <https://doi.org/10.1111/nph.13593>
- Overpeck, J. T., Rind, D., & Goldberg, R. (1990). Climate-induced changes in forest disturbance and vegetation. *Nature*, 343(6253), 51–53. <https://doi.org/10.1038/343051a0>
- Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., & Ribbens, E. (1996). Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs*, 66(1), 1–43. <https://doi.org/10.2307/2963479>
- Pachzelt, A., Rammig, A., Higgins, S., & Hickler, T. (2013). Coupling a physiological grazer population model with a generalized model for vegetation dynamics. *Ecological Modelling*, 263, 92–102. <https://doi.org/10.1016/j.ecolmodel.2013.04.025>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>
- Park, J. Y., Muller-Landau, H. C., Lichstein, J. W., Rifai, S. W., Dandois, J. P., & Bohlman, S. A. (2019). Quantifying leaf phenology of individual trees and species in a tropical forest using unmanned aerial vehicle (UAV) images. *Remote Sensing*, 11(13), 1534. <https://doi.org/10.3390/rs11131534>
- Pastor, J., & Post, W. M. (1986). Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry*, 2(1), 3–27. <https://doi.org/10.1007/BF02186962>
- Pastor, J., & Post, W. M. (1988). Response of northern forests to CO₂-induced climate change. *Nature*, 334(6177), 55–58. <https://doi.org/10.1038/334055a0>
- Pastorello, G., Trotta, C., Canfora, E., Chu, H., Christianson, D., Cheah, Y.-W., Poindexter, C., Chen, J., Elbashandy, A., Humphrey, M., Isaac, P., Polidori, D., Reichstein, M., Ribeca, A., van Ingen, C., Vuichard, N., Zhang, L., Amiro, B., Ammann, C., ... Papale, D. (2020). The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. *Scientific Data*, 7(1), 225. <https://doi.org/10.1038/s41597-020-0534-3>
- Pausas, J. G. (1999). Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach. *Journal of Vegetation Science*, 10(5), 717–722. <https://doi.org/10.2307/3237086>
- Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., & Kleidon, A. (2013). The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): A diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences*, 10(6), 4137–4177. <https://doi.org/10.5194/bg-10-4137-2013>
- Pérez-Méndez, N., Jordano, P., García, C., & Valido, A. (2016). The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. *Scientific Reports*, 6, 24820. <https://doi.org/10.1038/srep24820>
- Petter, G., Mairota, P., Albrich, K., Bebi, P., Bruna, J., Bugmann, H., Haffenden, A., Scheller, R. M., Schmatz, D. R., Seidl, R., Speich, M., Vacchiano, G., & Lischke, H. (2020). How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environmental Modelling & Software*, 134, 104844. <https://doi.org/10.1016/j.envsoft.2020.104844>
- Ploton, P., Mortier, F., Barbier, N., Cornu, G., Réjou-Méchain, M., Rossi, V., Alonso, A., Bastin, J.-F., Bayol, N., Bénédet, F., Bissengou, P., Chuyong, G., Demarquez, B., Doucet, J.-L., Droissart, V., Kamdem, N. G., Kenfack, D., Memiaghe, H., Moses, L., ... Gourlet-Fleury, S. (2020). A map of African humid tropical forest aboveground biomass derived from management inventories. *Scientific Data*, 7(1), 221. <https://doi.org/10.1038/s41597-020-0561-0>
- Ploton, P., Mortier, F., Réjou-Méchain, M., Barbier, N., Picard, N., Rossi, V., Dormann, C., Cornu, G., Viennois, G., Bayol, N., Lyapustin, A., Gourlet-Fleury, S., & Pélissier, R. (2020). Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nature Communications*, 11(1), 4540. <https://doi.org/10.1038/s41467-020-18321-y>

- Porté, A., & Bartelink, H. H. (2002). Modelling mixed forest growth: A review of models for forest management. *Ecological Modelling*, 150(1–2), 141–188. [https://doi.org/10.1016/S0304-3800\(01\)00476-8](https://doi.org/10.1016/S0304-3800(01)00476-8)
- Porcia e Brugnera, M., Meunier, F., Longo, M., Krishna Moorthy, S. M., De Deurwaerder, H., Schnitzer, S. A., Bonal, D., Faybisenko, B., & Verbeeck, H. (2019). Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests. *Global Change Biology*, 25, 3767–3780. <https://doi.org/10.1111/gcb.14769>
- Poyatos, R., Granda, V., Molowny-Horas, R., Mencuccini, M., Steppe, K., & Martínez-Vilalta, J. (2016). SAPFLUXNET: Towards a global database of sap flow measurements. *Tree Physiology*, 36(12), 1449–1455. <https://doi.org/10.1093/treephys/tpw110>
- Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., & Sykes, M., (2007). Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to Large-Scale environmental change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (pp. 175–192). : Springer Science & Business Media. Retrieved from http://link.springer.com/chapter/10.1007/978-3-540-32730-1_15
- Prentice, I. C., Liang, X., Medlyn, B. E., & Wang, Y.-P. (2015). Reliable, robust and realistic: The three R's of next-generation land-surface modelling. *Atmospheric Chemistry and Physics*, 15(10), 5987–6005. <https://doi.org/10.5194/acp-15-5987-2015>
- Pretzsch, H., Biber, P., & Ďurský, J. (2002). The single tree-based stand simulator SILVA: Construction, application and evaluation. *Forest Ecology and Management, National and Regional Climate Change Impact Assessments in the Forestry Sector*, 62(1), 3–21. [https://doi.org/10.1016/S0378-1127\(02\)00047-6](https://doi.org/10.1016/S0378-1127(02)00047-6)
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T., & Seifert, S. (2008). Models for forest ecosystem management: A European perspective. *Annals of Botany*, 62(1), 3–21. [https://doi.org/10.1016/S0378-1127\(02\)00047-6](https://doi.org/10.1016/S0378-1127(02)00047-6)
- Pütz, S., Groeneveld, J., Alves, L. F., Metzger, J. P., & Huth, A. (2011). Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. *Ecological Modelling*, 222(12), 1986–1997. <https://doi.org/10.1016/j.ecolmodel.2011.03.038>
- Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A. C., Metz, M., Metzger, J. P., Ribeiro, M. C., de Paula, M. D., & Huth, A. (2014). Long-term carbon loss in fragmented Neotropical forests. *Nature Communications*, 5, 5037. <https://doi.org/10.1038/ncomms6037>
- Quillet, A., Peng, C., & Garneau, M. (2010). Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: Recent developments, limitations, and future challenges. *Environmental Reviews*, 18(NA), 333–353. <https://doi.org/10.1139/A10-016>
- Radchuk, V., Laender, F. D., Cabral, J. S., Boulangeat, I., Crawford, M., Bohn, F., Raedt, J. D., Scherer, C., Svenning, J.-C., Thonicke, K., Schurr, F. M., Grimm, V., & Kramer-Schadt, S. (2019). The dimensionality of stability depends on disturbance type. *Ecology Letters*, 22(4), 674–684. <https://doi.org/10.1111/ele.13226>
- Raiho, A., Dietze, M., Dawson, A., Rollinson, C. R., Tipton, J., & McLachlan, J. (2020). Towards understanding predictability in ecology: A forest gap model case study. *BioRxiv*, 2020.05.05.079871. <https://doi.org/10.1101/2020.05.05.079871>
- Ram, K. (2013). Git can facilitate greater reproducibility and increased transparency in science. *Source Code for Biology and Medicine*, 8(1), 7. <https://doi.org/10.1186/1751-0473-8-7>
- Ramage, M. H., Burridge, H., Busse-Wicher, M., Fereday, G., Reynolds, T., Shah, D. U., Wu, G., Yu, L. I., Fleming, P., Densley-Tingley, D., Allwood, J., Dupree, P., Linden, P. F., & Scherman, O. (2017). The wood from the trees: The use of timber in construction. *Renewable and Sustainable Energy Reviews*, 68, 333–359. <https://doi.org/10.1016/j.rser.2016.09.107>
- Rammer, W., & Seidl, R. (2019). A scalable model of vegetation transitions using deep neural networks. *Methods in Ecology and Evolution*, 10(6), 879–890. <https://doi.org/10.1111/2041-210X.13171>
- Rasche, L., Fahse, L., Zingg, A., & Bugmann, H. (2011). Getting a virtual forester fit for the challenge of climatic change. *Journal of Applied Ecology*, 48(5), 1174–1186. <https://doi.org/10.1111/j.1365-2664.2011.02014.x>
- Reed, S. C., Yang, X., & Thornton, P. E. (2015). Incorporating phosphorus cycling into global modeling efforts: A worthwhile, tractable endeavor. *New Phytologist*, 208(2), 324–329. <https://doi.org/10.1111/nph.13521>
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., & Wattenbach, M. (2013). Climate extremes and the carbon cycle. *Nature*, 500(7462), 287–295. <https://doi.org/10.1038/nature12350>
- Reichstein, M., Camps-Valls, G., Stevens, B., Jung, M., Denzler, J., Carvalhais, N., & Prabhat, Xxx. (2019). Deep learning and process understanding for data-driven Earth system science. *Nature*, 566(7743), 195. <https://doi.org/10.1038/s41586-019-0912-1>
- Réjou-Méchain, M., Barbier, N., Couteron, P., Ploton, P., Vincent, G., Herold, M., Mermoz, S., Saatchi, S., Chave, J., de Boissieu, F., Féret, J.-B., Takoudjou, S. M., & Pélissier, R. (2019). Upscaling forest biomass from field to satellite measurements: Sources of errors and ways to reduce them. *Surveys in Geophysics*, 40(4), 881–911. <https://doi.org/10.1007/s10712-019-09532-0>
- Reyer, C. (2015). Forest Productivity under environmental change—a Review of Stand-Scale modeling studies. *Current Forestry Report*, 1(2), 53–68. <https://doi.org/10.1007/s40725-1632-015-0009-5>
- Reyer, C. P. O., Bugmann, H., Nabuurs, G.-J., & Hanewinkel, M. (2015). Models for adaptive forest management. *Regional Environmental Change*, 15(8), 1483–1487. <https://doi.org/10.1007/s10113-015-0861-7>
- Reyer, C. P. O., Silveyra Gonzalez, R., Dolos, K., Hartig, F., Hauf, Y., Noack, M., Lasch-Born, P., Rötzer, T., Pretzsch, H., Meesenburg, H., Fleck, S., Wagner, M., Bolte, A., Sanders, T. G. M., Kolari, P., Mäkelä, A., Vesala, T., Mammarella, I., Pumpanen, J., ... Frieler, K. (2020). The PROFOUND Database for evaluating vegetation models and simulating climate impacts on European forests. *Earth System Science Data*, 12(2), 1295–1320. <https://doi.org/10.5194/essd-12-1295-2020>
- Richter, S., Kipfer, T., Wohlgemuth, T., Calderón Guerrero, C., Ghazoul, J., & Moser, B. (2012). Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia*, 169(1), 269–279. <https://doi.org/10.1007/s00442-011-2191-x>
- Rödig, E., Cuntz, M., Heinke, J., Rammig, A., & Huth, A. (2017). Spatial heterogeneity of biomass and forest structure of the Amazon rain forest: Linking remote sensing, forest modelling and field inventory. *Global Ecology and Biogeography*, 26(11), 1292–1302. <https://doi.org/10.1111/geb.12639>
- Rödig, E., Cuntz, M., Rammig, A., Fischer, R., Taubert, F., & Huth, A. (2018). The importance of forest structure for carbon fluxes of the Amazon rainforest. *Environmental Research Letters*, 13(5), 54013. <https://doi.org/10.1088/1748-9326/aabc61>
- Rogers, A., Medlyn, B. E., Dukes, J. S., Bonan, G., von Caemmerer, S., Dietze, M. C., Kattge, J., Leakey, A. D. B., Mercado, L. M., Niinemets, Ü., Prentice, I. C., Serbin, S. P., Sitch, S., Way, D. A., & Zaehle, S. (2017). A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytologist*, 213(1), 22–42. <https://doi.org/10.1111/nph.14283>
- Rogers, B. M., Soja, A. J., Goulden, M. L., & Randerson, J. T. (2015). Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience*, 8(3), 228–234. <https://doi.org/10.1038/ngeo2352>
- Rolinski, S., Müller, C., Heinke, J., Weindl, I., Biewald, A., Bodirsky, B. L., Bondeau, A., Boons-Prins, E. R., Bouwman, A. F., Leffelaar, P. A., te

- Roller, J. A., Schaphoff, S., & Thonicke, K. (2018). Modeling vegetation and carbon dynamics of managed grasslands at the global scale with LPJmL 3.6. *Geoscientific Model Development*, 11(1), 429–451. <https://doi.org/10.5194/gmd-11-429-2018>
- Roşca, S., Suomalainen, J., Bartholomeus, H., & Herold, M. (2018). Comparing terrestrial laser scanning and unmanned aerial vehicle structure from motion to assess top of canopy structure in tropical forests. *Interface Focus*, 8(2), 20170038. <https://doi.org/10.1098/rsfs.2017.0038>
- Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., & Fariori, C. E. (2019). Demographic tradeoffs predict tropical forest dynamics. *BioRxiv*, 808865. <https://doi.org/10.1101/808865>
- Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *BioScience*, 54(6), 547–560. [https://doi.org/10.1641/0006-1666-3568\(2004\)054\[0547:ACSMO G\]2.0.CO;2](https://doi.org/10.1641/0006-1666-3568(2004)054[0547:ACSMO G]2.0.CO;2)
- Rykiel, E. J. Jr (1996). Testing ecological models: The meaning of validation. *Ecological Modelling*, 90(3), 229–244. [https://doi.org/10.1016/0304-3800\(95\)00152-2](https://doi.org/10.1016/0304-3800(95)00152-2)
- Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., & Morel, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, 108(24), 9899–9904. <https://doi.org/10.1073/pnas.1019576108>
- Sabaté, S., Gracia, C. A., & Sánchez, A. (2002). Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management, National and Regional Climate Change Impact Assessments in the Forestry Sector*, 162(1), 23–37. [https://doi.org/10.1016/S0378-1127\(02\)00048-8](https://doi.org/10.1016/S0378-1127(02)00048-8)
- Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., & Thonicke, K. (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*, 6(11), 1032–1036. <https://doi.org/10.1038/nclimate3109>
- Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J., & Thonicke, K. (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, 21(7), 2711–2725. <https://doi.org/10.1111/gcb.12870>
- Saltelli, A. (2019). A short comment on statistical versus mathematical modelling. *Nature Communications*, 10(1), 3870. <https://doi.org/10.1038/s41467-019-11865-8>
- Sato, H., Itoh, A., & Kohyama, T. (2007). SEIB-DGVM: A new dynamic global vegetation model using a spatially explicit individual-based approach. *Ecological Modelling*, 200(3–4), 279–307. <https://doi.org/10.1016/j.ecolmodel.2006.09.006>
- Savage, M., Sawhill, B., & Askenazi, M. (2000). Community dynamics: What happens when we rerun the tape? *Journal of Theoretical Biology*, 205(4), 515–526. <https://doi.org/10.1006/jtbi.2000.2055>
- Schaphoff, S., von Bloh, W., Rammig, A., Thonicke, K., Biemans, H., Forkel, M., & Waha, K. (2018). LPJmL4 – A dynamic global vegetation model with managed land – Part 1: Model description. *Geoscientific Model Development*, 11(4), 1343–1375. <https://doi.org/10.5194/gmd-11-1343-2018>
- Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytologist*, 198(3), 957–969. <https://doi.org/10.1111/nph.12210>
- Scherer-Lorenzen, M. (2014). The functional role of biodiversity in the context of global change. In D. A. Coomes, D. F. R. P. Burslem, & W. D. Simonson (Eds.), *Forests and Global Change* (pp. 195–238). : Cambridge University Press.
- Scherstjanoi, M., Kaplan, J. O., Poulter, B., & Lischke, H. (2014). Challenges in developing a computationally efficient plant physiological height-class-structured forest model. *Ecological Complexity*, 19, 96–110. <https://doi.org/10.1016/j.ecocom.2014.05.009>
- Schmid, J. S., Huth, A., & Taubert, F. (2021). Influences of traits and processes on productivity and functional composition in grasslands: A modeling study. *Ecological Modelling*, 440, 109395. <https://doi.org/10.1016/j.ecolmodel.2020.109395>
- Schmitt, S., Maréchaux, I., Chave, J., Fischer, F. J., Piponiot, C., Traissac, S., & Hérault, B. (2020). Functional diversity improves tropical forest resilience: Insights from a long-term virtual experiment. *Journal of Ecology*, 108(3), 831–843. <https://doi.org/10.1111/1365-2745.13320>
- Schnitzer, S. A., & Carson, W. P. (2016). Would ecology fail the repeatability test? *BioScience*, 66(2), 98–99. <https://doi.org/10.1093/biosci/biv176>
- Schwörer, C., Henne, P. D., & Tinner, W. (2014). A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Global Change Biology*, 20(5), 1512–1526. <https://doi.org/10.1111/gcb.12456>
- Seagle, S. W., & Liang, S.-Y. (2001). Application of a forest gap model for prediction of browsing effects on riparian forest succession. *Ecological Modelling*, 144(2), 213–229. [https://doi.org/10.1016/S0304-3800\(01\)00373-8](https://doi.org/10.1016/S0304-3800(01)00373-8)
- Seidl, R., Albrich, K., Thom, D., & Rammer, W. (2018). Harnessing landscape heterogeneity for managing future disturbance risks in forest ecosystems. *Journal of Environmental Management*, 209, 46–56. <https://doi.org/10.1016/j.jenvman.2017.12.014>
- Seidl, R., Fernandes, P. M., Fonseca, T. F., Gillet, F., Jönsson, A. M., Merganičová, K., Netherer, S., Arpacı, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J. R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., & Mohren, F. (2011). Modelling natural disturbances in forest ecosystems: A review. *Ecological Modelling*, 222(4), 903–924. <https://doi.org/10.1016/j.ecolmodel.2010.09.040>
- Seidl, R., Rammer, W., & Blennow, K. (2014). Simulating wind disturbance impacts on forest landscapes: Tree-level heterogeneity matters. *Environmental Modelling & Software*, 51, 1–11. <https://doi.org/10.1016/j.envsoft.2013.09.018>
- Seidl, R., Rammer, W., Scheller, R. M., & Spies, T. A. (2012). An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling*, 231, 87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>
- Seidl, R., Schelhaas, M.-J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4(9), 806–810. <https://doi.org/10.1038/nclimate2318>
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402. <https://doi.org/10.1038/nclimate3303>
- Serra-Diaz, J. M., Keenan, T. F., Ninyerola, M., Sabaté, S., Gracia, C., & Lloret, F. (2013). Geographical patterns of congruence and incongruence between correlative species distribution models and a process-based ecophysiological growth model. *Journal of Biogeography*, 40(10), 1928–1938. <https://doi.org/10.1111/jbi.12142>
- Shifley, S. R., He, H. S., Lischke, H., Wang, W. J., Jin, W., Gustafson, E. J., & Yang, J. (2017). The past and future of modeling forest dynamics: From growth and yield curves to forest landscape models. *Landscape Ecology*, 32(7), 1307–1325. <https://doi.org/10.1007/s10980-017-0540-9>
- Shugart, H. H. (1984). A theory of forest dynamics. Retrieved from <http://www.osti.gov/scitech/biblio/5642300>
- Shugart, H. H., Asner, G. P., Fischer, R., Huth, A., Knapp, N., Le Toan, T., & Shuman, J. K. (2015). Computer and remote-sensing infrastructure to enhance large-scale testing of individual-based forest models. *Frontiers in Ecology and the Environment*, 13(9), 503–511. <https://doi.org/10.1890/140327>

- Shugart, H. H., & Noble, I. R. (1981). A computer model of succession and fire response of the high-altitude Eucalyptus forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology*, 6(2), 149–164. <https://doi.org/10.1111/j.1442-9993.1981.tb01286.x>
- Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., Huth, A., & Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. *Environmental Research Letters*, 13(3), 33001. <https://doi.org/10.1088/1748-9326/aaaacc>
- Shugart, H. H. J., & West, D. C. (1977). Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *Journal of Environmental Management*, 5, 161–179.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C., & Woodward, F. I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14(9), 2015–2039. <https://doi.org/10.1111/j.1365-2486.2008.01626.x>
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., & Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9(2), 161–185. <https://doi.org/10.1046/j.1365-2486.2003.00569.x>
- Smith, B., Prentice, I. C., & Sykes, M. T. (2001). Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, 10(6), 621–637. <https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x>
- Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, 11(7), 2027–2054. <https://doi.org/10.5194/bg-11-2027-2014>
- Snell, R. S. (2014). Simulating long-distance seed dispersal in a dynamic vegetation model. *Global Ecology and Biogeography*, 23(1), 89–98. <https://doi.org/10.1111/geb.12106>
- Snell, R. S., & Cowling, S. A. (2015). Consideration of dispersal processes and northern refugia can improve our understanding of past plant migration rates in North America. *Journal of Biogeography*, 42(9), 1677–1688. <https://doi.org/10.1111/jbi.1254>
- Snell, R. S., Huth, A., Nabel, J. E. M. S., Bocedi, G., Travis, J. M. J., Gravel, D., Bugmann, H., Gutiérrez, A. G., Hickler, T., Higgins, S. I., Reineking, B., Scherstjanoi, M., Zurbriggen, N., & Lischke, H. (2014). Using dynamic vegetation models to simulate plant range shifts. *Ecography*, 37(12), 1184–1197. <https://doi.org/10.1111/ecog.00580>
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Sofaer, H. R., Jarnevich, C. S., & Flather, C. H. (2018). Misleading prioritizations from modelling range shifts under climate change. *Global Ecology and Biogeography*, 27(6), 658–666. <https://doi.org/10.1111/geb.12726>
- Solomon, A. M. (1986). Transient response of forests to CO₂-induced climate change: Simulation modeling experiments in eastern North America. *Oecologia*, 68(4), 567–579. <https://doi.org/10.1007/BF00378773>
- Stephenson, N. L. (1990). Climatic control of vegetation distribution: The role of the water balance. *The American Naturalist*, 135(5), 649–670. <https://doi.org/10.1086/285067>
- Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., ... Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101(1), 58–67. <https://doi.org/10.1111/1365-2745.12025>
- Svenning, J.-C., & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecology Letters*, 7(7), 565–573. <https://doi.org/10.1111/j.1461-0248.2004.00614.x>
- Takoudjou, S. M., Ploton, P., Sonké, B., Hackenberg, J., Griffon, S., de Coligny, F., & Barbier, N. (2018). Using terrestrial laser scanning data to estimate large tropical trees biomass and calibrate allometric models: A comparison with traditional destructive approach. *Methods in Ecology and Evolution*, 9(4), 905–916. <https://doi.org/10.1111/2041-210X.12933>
- Taubert, F., Hetzer, J., Schmid, J. S., & Huth, A. (2020). Confronting an individual-based simulation model with empirical community patterns of grasslands. *PLoS One*, 15(7), e0236546. <https://doi.org/10.1371/journal.pone.0236546>
- Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., & Seidl, R. (2017). The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology*, 54(1), 28–38. <https://doi.org/10.1111/1365-2664.12644>
- Thonicke, K., Venevsky, S., Sitch, S., & Cramer, W. (2001). The role of fire disturbance for global vegetation dynamics: Coupling fire into a Dynamic Global Vegetation Model. *Global Ecology and Biogeography*, 10(6), 661–677. <https://doi.org/10.1046/j.1466-822X.2001.00175.x>
- Thuiller, W. (2003). BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9(10), 1353–1362. <https://doi.org/10.1046/j.1365-2486.2003.00666.x>
- Thuiller, W. (2004). Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, 10(12), 2020–2027. <https://doi.org/10.1111/j.1365-2486.2004.00859.x>
- Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G. F., Paterson, J., Schurr, F. M., Sykes, M. T., & Zimmermann, N. E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9(3–4), 137–152. <https://doi.org/10.1016/j.ppees.2007.09.004>
- Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O., & Rouget, M. (2005). Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, 11(12), 2234–2250. <https://doi.org/10.1111/j.1365-2486.2005.001018.x>
- Thuiller, W., Vayreda, J., Pino, J., Sabate, S., Lavorel, S., & Gracia, C. (2003). Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). *Global Ecology and Biogeography*, 12(4), 313–325. <https://doi.org/10.1046/j.1466-822X.2003.00033.x>
- Treydte, K., Frank, D., Esper, J., Andreu, L., Bednarz, Z., Berninger, F., Boettger, T., D'Alessandro, C. M., Etien, N., Filot, M., Grabner, M., Guillemin, M. T., Gutierrez, E., Haupt, M., Helle, G., Hilasvuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., ... Schleser, G. H. (2007). Signal strength and climate calibration of a European tree-ring isotope network. *Geophysical Research Letters*, 34(24), <https://doi.org/10.1029/2007GL031106>
- United Nations. (2014). *New York Declaration on Forests*. United Nations.
- Urban, D. L., Bonan, G. B., Smith, T. M., & Shugart, H. H. (1991). Spatial applications of gap models. *Forest Ecology and Management*, 42(1), 95–110. [https://doi.org/10.1016/0378-1127\(91\)90067-6](https://doi.org/10.1016/0378-1127(91)90067-6)
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Peer, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353(6304), aad8466. <https://doi.org/10.1126/science.aad8466>

- Vacchiano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M. E., Caignard, T., Collalti, A., Mairota, P., Palaghianu, C., Reyer, C. P. O., Sanders, T. G. M., Schermer, E., Wohlgenuth, T., & Hackett-Pain, A. (2018). Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological Modelling*, 376, 40–53. <https://doi.org/10.1016/j.ecolmodel.2018.03.004>
- Václavík, T., Kupfer, J. A., & Meentemeyer, R. K. (2012). Accounting for multi-scale spatial autocorrelation improves performance of invasive species distribution modelling (iSDM). *Journal of Biogeography*, 39(1), 42–55. <https://doi.org/10.1111/j.1365-2699.2011.02589.x>
- Václavík, T., & Meentemeyer, R. K. (2012). Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Diversity and Distributions*, 18(1), 73–83. <https://doi.org/10.1111/j.1472-4642.2011.00854.x>
- van der Sande, M. T., Poorter, L., Balvanera, P., Kooistra, L., Thonicke, K., Boit, A., Dutrieux, L. P., Equihua, J., Gerard, F., Herold, M., Kolb, M., Simões, M., & Peña-Claros, M. (2017). The integration of empirical, remote sensing and modelling approaches enhances insight in the role of biodiversity in climate change mitigation by tropical forests. *Current Opinion in Environmental Sustainability*, 26(Supplement C), 69–76. <https://doi.org/10.1016/j.cosust.2017.01.016>
- van Oijen, M., Reyer, C., Bohn, F. J., Cameron, D. R., Deckmyn, G., Flechsig, M., Härkönen, S., Hartig, F., Huth, A., Kiviste, A., Lasch, P., Mäkelä, A., Mette, T., Minunno, F., & Rammer, W. (2013). Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe. *Forest Ecology and Management*, 289, 255–268. <https://doi.org/10.1016/j.foreco.2012.09.043>
- Van Nes, E. H., & Scheffer, M. (2005). A strategy to improve the contribution of complex simulation models to ecological theory. *Ecological Modelling*, 185(2–4), 153–164. <https://doi.org/10.1016/j.ecolmodel.2004.12.001>
- van Oijen, M., Rougier, J., & Smith, R. (2005). Bayesian calibration of process-based forest models: Bridging the gap between models and data. *Tree Physiology*, 25(7), 915–927. <https://doi.org/10.1093/treephys/25.7.915>
- Veloz, S. D., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary: Implications for 21st-century predictions by species distribution models. *Global Change Biology*, 18(5), 1698–1713. <https://doi.org/10.1111/j.1365-2486.2011.02635.x>
- Verbeeck, H., & Kearsley, E. (2016). The importance of including lianas in global vegetation models. *PNAS*, 113(1), E4. <https://doi.org/10.1073/pnas.1521343113>
- Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J., & van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology*, 21(8), 3074–3086. <https://doi.org/10.1111/gcb.12871>
- Vira, B., Wildburger, C., & Mansourian, S. (Eds.). (2015). Forests, trees and landscapes for food security and nutrition a global assessment report. International Union of Forest Research Organizations (IUFRO), Vienna. Retrieved from <http://www.iufro.org/fileadmin/material/publications/iufro-series/ws33/ws33.pdf>
- von Bloh, W., Rost, S., Gerten, D., & Lucht, W. (2010). Efficient parallelization of a dynamic global vegetation model with river routing. *Environmental Modelling & Software*, 25, 685–690. <https://doi.org/10.1016/j.envsoft.2009.11.012>
- von Bloh, W., Schaphoff, S., Müller, C., Rolinski, S., Waha, K., & Zaehle, S. (2018). Implementing the nitrogen cycle into the dynamic global vegetation, hydrology, and crop growth model LPJmL (version 5.0). *Geoscientific Model Development*, 11(7), 2789–2812. <https://doi.org/10.5194/gmd-11-2789-2018>
- von Humboldt, A. (1849). *Aspects of nature, in different lands and different climates; with scientific elucidations*. Lea and Blanchard.xx
- Wang, B., Shuman, J., Shugart, H. H., & Lerda, M. T. (2018). Biodiversity matters in feedbacks between climate change and air quality: A study using an individual-based model. *Ecological Applications*, 28(5), 1223–1231. <https://doi.org/10.1002/eap.1721>
- Wang, Y. P., Law, R. M., & Pak, B. (2010). A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, 7(7), 2261–2282. <https://doi.org/10.5194/bg-7-2261-2010>
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, 35(1/2), 1–22. <https://doi.org/10.2307/2256497>
- Woodward, F. I., & Cramer, W. (1996). Plant functional types and climatic change: Introduction. *Journal of Vegetation Science*, 7(3), 306–308. <https://doi.org/10.1111/j.1654-1103.1996.tb00489.x>
- Wright, J. S. (2002). Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia*, 130(1), 1–14. <https://doi.org/10.1007/s004420100809>
- Xiaodong, Y., & Shugart, H. H. (2005). FAREAST: A forest gap model to simulate dynamics and patterns of eastern Eurasian forests. *Journal of Biogeography*, 32(9), 1641–1658. <https://doi.org/10.1111/j.1365-2699.2005.01293>
- Yousefpour, R., Augustynczyk, A. L. D., Reyer, C. P. O., Lasch-Born, P., Suckow, F., & Hanewinkel, M. (2018). Realizing mitigation efficiency of European commercial forests by climate smart forestry. *Scientific Reports*, 8(1), 345. <https://doi.org/10.1038/s41598-017-18778-w>
- Yue, C., Ciais, P., Cadule, P., Thonicke, K., Archibald, S., Poulter, B., Hao, W. M., Hantson, S., Mouillot, F., Friedlingstein, P., Maignan, F., & Viovy, N. (2014). Modelling the role of fires in the terrestrial carbon balance by incorporating SPITFIRE into the global vegetation model ORCHIDEE – Part 1: Simulating historical global burned area and fire regimes. *Geoscientific Model Development*, 7(6), 2747–2767. <https://doi.org/10.5194/gmd-7-2747-2014>
- Yue, C., Ciais, P., Cadule, P., Thonicke, K., & van Leeuwen, T. T. (2015). Modelling the role of fires in the terrestrial carbon balance by incorporating SPITFIRE into the global vegetation model ORCHIDEE – Part 2: Carbon emissions and the role of fires in the global carbon balance. *Geoscientific Model Development*, 8(5), 1321–1338. <https://doi.org/10.5194/gmd-8-1321-2015>
- Zaehle, S., Sitch, S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., & Smith, B. (2006). The importance of age-related decline in forest NPP for modelling regional carbon balances. *Ecological Applications*, 16(4), 1555–1574. [https://doi.org/10.1890/1051-0761\(2006\)016\[1555:TIOADI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1555:TIOADI]2.0.CO;2)
- Zolkos, S. G., Goetz, S. J., & Dubayah, R. (2013). A meta-analysis of terrestrial aboveground biomass estimation using lidar remote sensing. *Remote Sensing of Environment*, 128, 289–298. <https://doi.org/10.1016/j.rse.2012.10.01>
- Zuidema, P. A., Baker, P. J., Groenendijk, P., Schippers, P., van der Slepen, P., Vlam, M., & Sterck, F. (2013). Tropical forests and global change: Filling knowledge gaps. *Trends in Plant Science*, 18(8), 413–419. <https://doi.org/10.1016/j.tplants.2013.05.006>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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