Ecological Modelling 495 (2024) 110785

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

The individual-based forest landscape and disturbance model iLand: Overview, progress, and outlook

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A R T I C L E I N F O

Keywords:
Landscape modeling
Agent-based modeling
Simulation modeling
Forest dynamics
Model development
Model initialization
Model parameterization
Model evaluation
Model application

A B S T R A C T

Forest ecosystems are changing rapidly, and landscape-level processes such as disturbance and dispersal are key drivers of change. Consequently, forest landscape models are important tools for studying forest trajectories under changing environmental conditions and their impacts on ecosystem service provisioning. Here, we synthesize 12 years of development and application of the individual-based forest landscape and disturbance model iLand. Specifically, we describe the fundamental model logic and give an overview of model components introduced over the years. Additionally, we outline how to initialize, evaluate and parameterize the model for new applications. iLand is a process-based forest landscape model that simulates forest dynamics at the level of individual trees. It accounts for continuous processes (tree growth, mortality, and regeneration) as well as discontinuous disturbances (wind, wildfire, and biotic agents) and forest management. Simulations span multiple spatial and temporal scales, from individual trees to landscapes of 10^5 hectares, and from hourly disturbance dynamics to centuries of forest development. Environmental conditions are represented by daily climate data and high-resolution soil information. The model was designed for flexibly addressing a wide range of research questions, features a rich graphical user interface and comprehensive scripting support. The model is open source and comes with extensive online model documentation. iLand has hitherto been applied in 50 peer-reviewed simulation studies across three continents. Applications primarily focused on the effects of climate change, disturbances and forest management on forest dynamics, ecosystem service provisioning and forest biodiversity. Future model development could address the representation of belowground processes, biotic interactions, and landscape dynamics beyond forest ecosystems. We conclude that process-based simulation of landscape-scale forest dynamics at the level of individual trees has proven a valuable approach of forest landscape modeling.

1. Introduction

Forests, covering approximately 30 % of the Earth's land surface, play a crucial role in climate regulation (Harris et al., 2021) and harbor a vast proportion of terrestrial biodiversity (*The State of the World's Forests 2020*, 2020). They sustain essential provisioning, regulating, and cultural services and are thus of paramount importance for human well-being. However, forests are increasingly under pressure. Climate change is profoundly altering forest composition, structure, and ecological processes (Calvin et al., 2023). Additionally, forest disturbances are intensifying, with climate change increasing their frequency and severity (McDowell et al., 2020; Senf et al., 2018). At the same time, societal demands on forests are growing: they are expected to provide sustainable resources for industry and the building sector (Churkina et al., 2020), contribute to climate change mitigation through carbon storage (Thom et al., 2017b), offer recreational spaces for an increasingly urban society (Blattert et al., 2017), and maintain biodiversity e.g., in protected areas (Stephens, 2023). The landscape scale is pivotal for managing these growing demands as key factors of forest dynamics like connectivity, disturbance regimes, and spatial heterogeneity unfold across landscapes. Consequently, forest management increasingly prioritizes landscape-scale planning, in order to achieve objectives related to biodiversity, resilience, and multifunctionality. The landscape is thus the critical scale where large-scale climate and biodiversity policies

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https://doi.org/10.1016/j.ecolmodel.2024.110785
Received 29 March 2024; Received in revised form 27 May 2024; Accepted 14 June 2024
Available online 17 July 2024

intersect with their on-the-ground implementation.

Understanding and managing complex landscape dynamics requires specialized tools; these tools need to be spatially explicit and consider landscape-level processes and their dynamic interactions with environmental drivers (Scheller, 2018). Furthermore, these tools should support scenario analyses and the evaluation of how management interventions influence ecosystem dynamics and service provision. Dynamic forest landscape simulation models (henceforth referred to as landscape models for brevity) are particularly well suited for this task. Landscape models make at least three important contributions to the understanding and management of forest landscapes: (1) Studying landscapes experimentally is difficult, as landscape-scale manipulation is expensive, time-consuming (Lindenmayer and Likens, 2010), and near impossible to replicate, as each landscape is shaped by a unique combination of land-use history, topography, soil, and climate (Phillips, 2007). Simulation models support the analysis of landscape dynamics by enabling replicated large-scale experiments *in silico,* e.g., explaining observed landscape patterns (e.g., Peringer et al., 2017), or investigating the effect of particular processes on landscape dynamics (e.g., Seidl et al., 2014b). (2) Landscape models can be used to project the effects of future climate change on landscape dynamics in scenario analyses. Such applications improve our understanding of the potential impacts of climate change, while accounting for interactions with simultaneously changing drivers (Temperli et al., 2013; Thom et al., 2017a). (3) Finally, landscape models can provide important information for decision makers by simulating the outcomes of different management strategies (Holland et al., 2022). They can be used, for instance, to simulate a range of management decisions and inform managers about the expected effects on ecosystem service supply (Albrich et al., 2018). Furthermore, models can be used to communicate potential landscape futures to stakeholders by visualizing different simulated future states of a landscape (Spies et al., 2017).

Because of their utility for landscape research and management, landscape modeling has been an active subfield of ecological modelling since the late 1980s, benefiting strongly from an increasing availability of computing power and spatial data. While a comprehensive review of the development and current state of forest landscape modeling is beyond the scope of this work (but see Bugmann and Seidl, 2022; Keane et al., 2015; Scheller, 2018; Shifley et al., 2017) it is worthwhile to consider important similarities and differences among landscape models. The defining feature of forest landscape models is that they are spatially explicit, i.e. the simulated entities have a unique location in space (Turner and Gardner, 2015). The explicit consideration of space and spatial interactions such as dispersal and disturbance distinguish forest landscape models from other types of models such as stand-level models, gap models, and dynamic global vegetation models (Bugmann and Seidl, 2022; Petter et al., 2020; Shifley et al., 2017). However, the entities being simulated in a landscape models differ widely, ranging from individual trees to cohorts of trees, stands, discrete vegetation states, and ecosystem pools. Furthermore, the level of mechanism incorporated in forest landscape models varies considerably, from highly process-oriented models simulating ecosystems based on first principles of ecology (e.g., Keane et al., 2011) to models capturing the dynamics of interest by means of phenomenological, statistical, or machine learning approaches (Scheller, 2018). Overall, forest landscape models are the most diverse group among all model families of long-term forest dynamics, building on concepts from a wide range of modeling approaches in order to simulate forest landscape dynamics (Bugmann and Seidl, 2022).

Here, we re-visit the individual-based forest landscape and disturbance model iLand to synthesize the state of the model after 12 years of ongoing model development, and discuss its progress and outlook. Our specific objectives were (i) to recap the fundamental ideas behind iLand, (ii) to describe the basic approach to simulating forest landscape dynamics of the current model version (iLand 2.0), (iii) to give an overview of the applications the model has been used in, and (iv) to discuss current limitations and possible ways forward for model development. This overview is intended as a gateway to iLand for prospective users, synthesizing the developments individual authors have contributed to the model over the past 12 years, and highlighting the strengths and limitations of simulating forest landscapes with the current version of iLand.

2. Fundamental design principles of iLand

2.1. Individual-based modeling

Individual-based models or agent-based models represent the variation of the system at the level of individuals. In the case of iLand, the principal simulated entities are individual trees. The model accounts for dynamic interaction between individual trees (e.g., via competition for light) and captures the unique history of the response of individuals to their environment (e.g., via local differences in tree growth, manifested by locally varying tree diameter and height) (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). An important advantage of simulating individual trees at the landscapes scale is that forest structure and composition are emergent properties of the simulation. A second strength of individual tree resolution is that the legacy of forest disturbances can be simulated with high fidelity (e.g., with regard to surviving individuals), which in turn is crucial for realistically capturing forest resilience in simulations (Albrich et al., 2020; Seidl et al., 2014b). A third important advantage is that the wealth of tree-level forest data being available around the globe (e.g., with regard to tree growth and mortality) can be used directly for model evaluation (e.g., Seidl et al., 2017). Simulating millions of trees on the landscape and their interaction also comes with disadvantages, however, one being high computational demand, limiting the applicability of iLand in its current form across very large landscapes.

2.2. Process-based modeling

iLand is a process-based forest model. This means that rather than modeling, e.g., tree growth as an empirical function fit to observational data, the model simulates the underlying mechanisms such as photosynthesis and carbon allocation explicitly. Simulating ecosystem dynamics based on first principles of ecology increases the robustness of simulations in a changing world, as it also allows inferences under novel driver combinations (Gustafson, 2013). It is important to note, however, that process-based models often trade off lower precision for higher realism relative to empirical models (Guisan and Zimmermann, 2000). Furthermore, as process-based models are not per se fit to data, evaluating their behavior via pattern-oriented modelling is crucial to determine their utility for a given application (Grimm et al., 2005). Lastly, what constitutes a process in simulating ecosystems is inherently determined by the scale of analysis. iLand, for instance, being a tree-level model, does not explicitly consider processes at the sub-tree level, instead simulating them in a data-driven manner (e.g., the carbon allocation to foliage and root compartments being driven by empirically-derived allometric ratios). While much more detailed models of trees exist (Bongers, 2020), iLand aims to capture processes at an intermediate level of complexity, also referred to as the Medawar zone (Grimm et al., 2005).

2.3. Multi-scale modeling

iLand explicitly considers a wide range of processes at multiple spatial and temporal scales. Temporal scales range from minutes (e.g., the uprooting and breakage of individual trees in a wind event), days (e.g., the influence of weather conditions), years (e.g., the growth of individual trees), to multiples thereof (e.g., the reoccurrence of mast years). Spatial scales range from square meters (e.g., simulating the spatial variation in forest floor light conditions and the resulting response of tree regeneration) to hundreds of square meters (e.g., simulating the spread of disturbances such as wildfire) and hectares (i.e., units of homogeneous climate and resource availability, called “resource units”, RUs, in iLand). The individual spatial and temporal scales are hierarchically linked, with large-scale processes forming constraints for processes at finer scales, and the dynamics at fine scales feeding into processes at higher scales (see Mäkelä, 2003). An example is stand-level radiation interception, constraining the photosynthetic activity of individual trees within a stand, with individual-tree foliage contributing to stand-level leaf area and hence radiation interception.

2.4. Modeling for application

Each model has its purpose and domain of application, and so does iLand. Within this domain, however, iLand was designed for high flexibility in applications, acknowledging that no two scientific studies are alike, and enabling a quick adaptation of the model to new research questions. This is achieved by a number of design decisions when developing the model: (1) providing the user with a choice of a wide range of model outputs across spatio-temporal scales that can be individually selected, as well as customized outputs that make the large amounts of data generated by the model accessible for the user; (2) detailed control over individual processes (e.g., by enabling or disabling them) for efficient simulation experiments; (3) a built-in scripting interface (using the JavaScript scripting language) that can be used to interact with the simulation (e.g., creating generic, user-defined disturbances) and to design flexible and reproducible scenarios, e.g. with regard to forest management interventions (Rammer and Seidl, 2015). (4) iLand can further be linked with other models to extend its applicability beyond explicitly simulated entities and processes. Simulated forest structure under climate change can, for instance, directly be linked with species distribution models to project changes in the occurrence of forest floor plants (Braziunas et al., 2024a).

2.5. Transparent and efficient software design

Performance and applicability guide the development of iLand, ensuring that model design decisions balance scientific rigor (process resolution and empirical evidence), computational efficiency (runtime and memory requirements), and practical applicability (data availability for drivers and parameters). The iLand model adopts a monolithic approach to software architecture, where core components and processes are tightly integrated, prioritizing computational efficiency over modularity. At a higher level, the model design contains elements of modularity (e.g., with regard to simulated disturbance agents and forest management regimes), allowing for customization and flexibility in these domains. Developed in C++, iLand was one of the first forest models that were developed as being fully open source, adhering to the GNU GPL license (Free Software Foundation, 2007), and leveraging the open-source software stack *Qt framework* and its development tools (Qt, 2024). The model can be executed on various operating systems and comes in two distinct implementations: one featuring a graphical user interface for interactive use and comprehensive visualization of simulation outputs in real time, and the other optimized for automated simulations on high-performance computing infrastructure. Recognizing that comprehensive documentation is essential for effective model application and further development, iLand offers an extensive online wiki (https://iland-model.org, currently approximately 175 pages) encompassing both conceptual and technical aspects.

3. iLand model overview

In the following section we give an overview of the main processes simulated in iLand. The text is intended as a synopsis of *what* is simulated in iLand, while the *how* (including the detailed equations governing model behavior) is covered by more the in-depth model description available at https://iland-model.org. We structure our model description into four parts: Simulated entities, physical environment, continuous processes and discontinuous processes, all of which are described in detail below.

3.1. Entities

The primary entities simulated in iLand are individual trees, saplings (here defined as cohorts of trees < 4 m height) as well as above- and belowground carbon pools (Fig. 1). All trees >4 m in height are simulated as separate individuals in a spatially explicitly manner (with tree coordinates discretized to a grid with a resolution of 2 m). Trees are described by 16 state variables, including tree dimensions (i.e., stem diameter at breast height, tree height), biomass pools (i.e., biomass in stems, branches, foliage, coarse roots, and fine roots), and other indicators describing the current situation of the tree as a function of its recent history, such as nonstructural carbohydrate reserves and stress level. There is no hard limit as to how many individual trees can be simulated in iLand. For simulating saplings, iLand employs a cohort approach for the sake of computational efficiency. Sapling cohorts of a species share a common height and age and are simulated at a level of 2 $\times$ 2 m grid cells, i.e., a maximum of 2500 distinct cohorts (of varying size and age) of a single species are tracked for every simulated hectare of forest. In each 2 $\times$ 2 m grid cell, sapling cohorts of up to five species can co-exist, limiting the maximum total number of simulated sapling cohorts per hectare to 12,500. Each cohort is defined by a number of state variables, including cohort height and cohort age. For simulating ecosystem carbon pools, we distinguish between live and dead carbon. Live carbon pools are simulated at the level of individual trees and sapling cohorts as described above, assuming a carbon content of 0.5 per unit live biomass. Dead carbon pools above and below ground are simulated at the level of resource units (100 $\times$ 100 m grid). They include deadwood (standing woody debris in three size classes as well as one pool for downed woody debris), litter and soil organic matter.

3.2. Environment

Forest ecosystem dynamics is driven by climate and the availability of energy, water, and nutrients. iLand utilizes daily-resolution climate data (minimum and maximum temperature, precipitation, radiation, vapor pressure deficit) as model input to represent climate conditions. The spatial resolution for climate data is the resource unit, enabling the simulation of highly variable climatic conditions across forest landscapes (e.g., in mountain regions). However, for the sake of computational efficiency several resource units can be grouped into homogeneous climate zones within the landscape. iLand also includes a microclimate module simulating temperatures close to the forest floor based on local topography as well as canopy structure and composition (Braziunas et al., 2024b).

Radiation interception is a main driver of individual-tree competition in the model, and the intercepted radiation directly drives primary production in the simulation. The approach to simulate competition for light is inspired by ecological field theory (Wu et al., 1985) and the field-of-neighborhood approach (Berger and Hildenbrandt, 2000): Each tree has a spatially discrete area in which it influences its surrounding via shading, and is in turn influenced by the accumulated shading effect that its neighboring trees have on its position. However, since a tree’s influence on its neighborhood changes with daily and seasonal variation in sun position, direct calculations (e.g., via ray tracing) are computationally challenging at the landscape scale (i.e., tracking millions of trees simultaneously). To address this issue iLand decouples the calculation of a tree’s shading potential from the dynamic simulation. Specifically, we calculate patterns of influence for individual trees in a 3D space around a virtual tree (spatial resolution of 2 $\times$ 2 $\times$ 2 m) prior to the dynamic simulation. We perform these calculations for a large number of possible tree sizes and species at a given latitude and proportion of direct

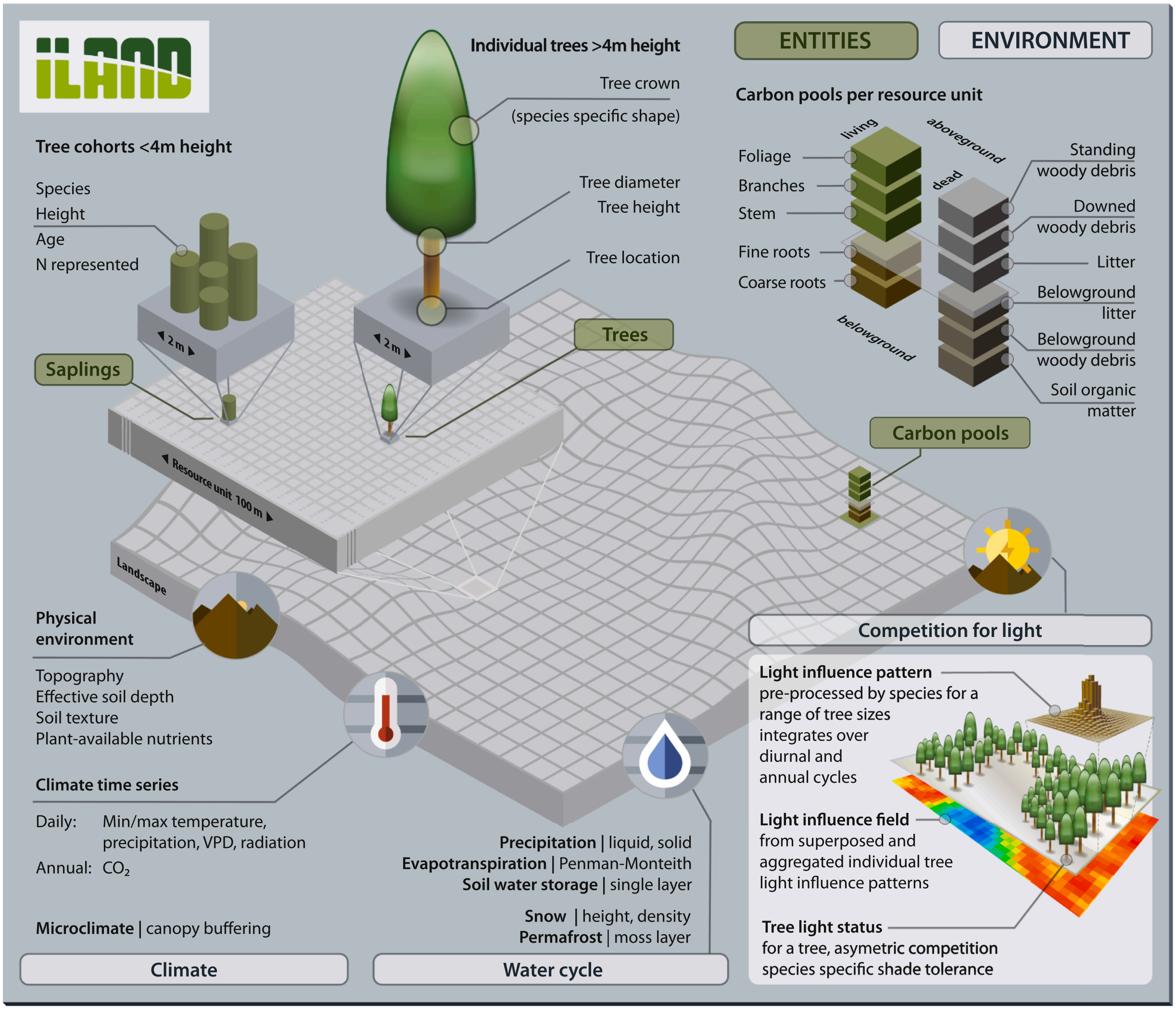

Fig. 1. Overview of the main entities and environmental drivers simulated in iLand. The figure highlights the hierarchically nested spatial organization of iLand (landscape, resource unit, 2 × 2 m cell), and the key entities simulated (i.e., individual trees, sapling cohorts for trees < 4 m height, live and dead carbon pools) within the simulated physical environment (with key components being light, climate and water).

radiation using a global light index approach (Canham, 1988), and store the resultant light influence patterns (LIPs) in a library (Fig. 1, box "Competition for Light"). Once this pre-processing is completed, the LIPs are assigned to all individual trees on the landscape based on their height, diameter, and species, and their transmissivity is calculated based on a tree's crown shape and foliage biomass. The individual LIPs are subsequently aggregated by accounting for local differences in tree height, resulting in a continuous light interference field simulated at 2 × 2 m spatial resolution and updated annually in the simulation (Seidl et al., 2012a).

The water cycle in iLand is simulated daily at the resource unit level. Key processes include precipitation, interception in the canopy and subsequent evaporation, snow storage and melt-off, soil water storage, runoff, and evapotranspiration. Canopy interception of precipitation depends on leaf area index and leaf type (conifer or broadleaved) (Seidl et al., 2005). Snow is modeled as a simple pool that accumulates precipitation on days with mean temperature below 0 °C, and loses water with a thaw rate of 0.7 mm/ °C/day (Running and Hunt, 1993). A module simulating detailed permafrost dynamics as a result of climate-vegetation feedbacks is also available (Hansen et al., 2023). iLand uses a one-layer soil model to characterize soil water storage. Storage capacity is calculated from effective rock-free soil depth and soil texture as the difference between field capacity and minimum plant-available soil water potential (Schwalm and Ek, 2004). Evapotranspiration is based on the Penman–Monteith equation as implemented in 3-PG (Landsberg and Waring, 1997). It is driven by net energy input and the dryness of the air (represented by solar radiation and vapor pressure deficit) and considers the physiological response of trees in regulating their canopy conductance to water. iLand assumes a species-dependent maximum conductance for closed canopies (i.e., leaf area index above three). Actual daily conductance is calculated based on the species-specific responses to vapor pressure deficit and soil water potential, simulating a species-specific down-regulation of canopy water loss under both atmospheric and soil drought.

3.3. *Continuous processes*

Continuous processes are active within every time step of the simulation. The central continuous processes in iLand pertain to the three main demographic processes in tree populations, i.e., growth, mortality, and regeneration (Fig. 2). Primary production is simulated based on a light use efficiency approach (Landsberg and Waring, 1997). It is computed monthly at the level of resource units, deriving GPP as the product of utilizable absorbed photosynthetically active radiation (*uAPAR*, MJ) and effective radiation use efficiency (ε_{eff}, g MJ^{-1}). To derive *uAPAR*, the absorbed photosynthetically active radiation (*APAR*)

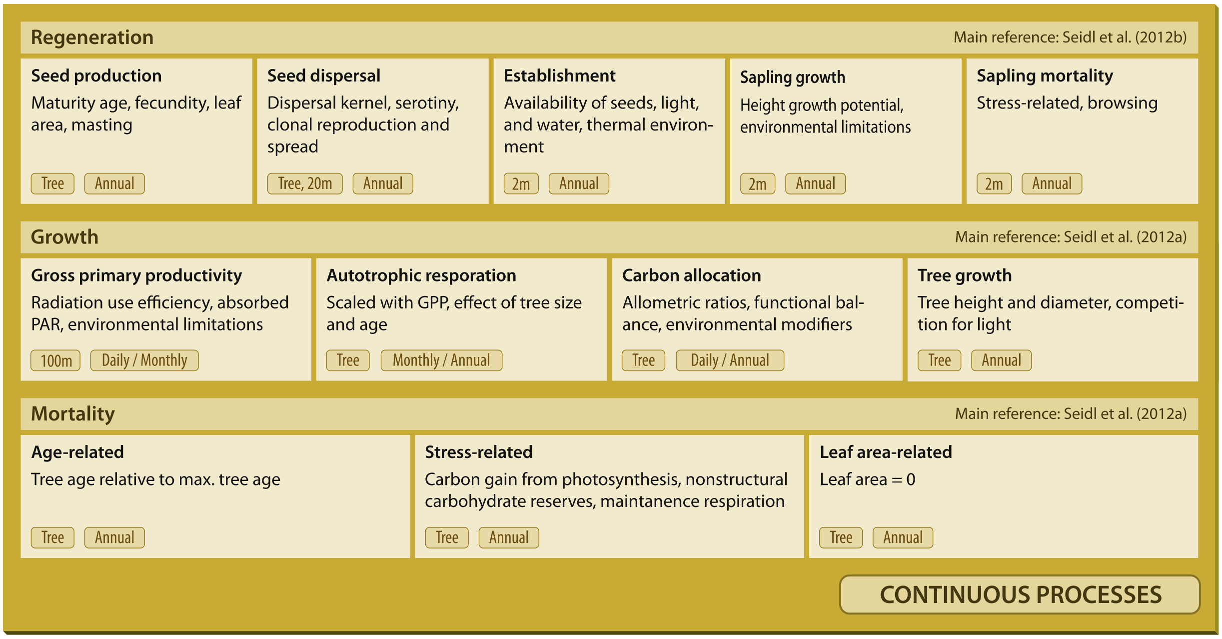

Fig. 2. Continuous processes simulated in iLand. Rows represent major demographic processes with main sub-processes and their drivers in cells. The tags in each cell indicate the main entity or spatial resolution and the primary time-step of the respective process.

is calculated via the leaf area of trees at RU-level, considering light attenuation within the canopy (Beers Law) as well as environmental limitations to photosynthesis at daily time step (via species-specific scalar response functions accounting for leaf phenology and the effects of air temperature, soil water availability and vapor pressure deficit). ε_{eff} is derived by modifying a biome-specific optimum radiation use efficiency for the effects of nutrient availability and ambient CO_2 concentration. The thus derived stand-level GPP is decomposed to the level of individual trees via the contribution of each individual to the product of *uAPAR* and ε_{eff}. Autotrophic respiration is initially derived as a fixed fraction of GPP (Waring et al., 1998), but also considers a reduced carbon use efficiency of tall and/ or old trees. The allocation of the thus derived net primary production (NPP) to tree compartments is calculated based on allometric ratios, assuming that foliage and fine roots take priority over stem compartments, and considering a higher allocation to roots under harsh environmental conditions. Finally, annual increments in stem diameter and tree height are calculated based on updated stem biomass and a species- and size-specific height-to-diameter ratio for stem increment that varies with competitive status of the tree, favoring height growth over diameter growth if an individual experiences strong competition for light (Bossel, 1996).

Individual tree mortality (for mortality from disturbances see below) is modeled probabilistically, with both maximum tree age and stress contributing to the probability of individual tree death. Age-related (intrinsic) mortality probability is calculated from species-specific maximum age, assuming that only a certain fraction of the population reaches this maximum age. Note that due to the probabilistic implementation of mortality, maximum age is no hard limit and can actually be exceeded by individuals. Stress in iLand is modeled based on a tree's carbon balance, assuming that a tree is stressed when it cannot meet the carbon demands from turnover in root and foliage compartments with the carbon gains from photosynthesis plus the carbon available from non-structural carbohydrate reserves. The risk of stress-related mortality increases if a tree is increasingly unable to maintain a positive carbon balance. Additionally, when a tree has lost all live foliage biomass, it dies.

Regeneration is simulated based on the complex interactions of processes from the local scale (2 × 2 m cell) to the landscape scale in iLand (Seidl et al., 2012b). Trees older than a species-specific maturity age produce seeds (at distinctly different quantities for mast years and non-mast years in the case of masting species). Subsequently, seeds of each species are dispersed using two-part exponential dispersal kernels (Lischke et al., 2006), and aggregated to an annual seed pool per species on a 20×20 m grid. Serotiny (i.e., the development of a canopy seed bank released by fire) and resprouting after tree mortality can also be simulated in iLand (Hansen et al., 2018). For trees to establish at a given 2 × 2 m cell seeds need to be there (probabilistically determined via the seed pool generated from individual dispersal kernels), a number of abiotic filters need to be passed (e.g., frost, available water, growing degree day thresholds, chilling requirements) and sufficient light needs to be available (derived from the light inference field on the forest floor). Upon successful establishment, a cohort of trees grows in height following a species-specific height growth potential, which is reduced to account for suboptimal environmental conditions applying the same environmental response functions as in calculating stand-level GPP. If a cohort fails to exceed a minimum height growth threshold for a number of years its mortality probability increases. Multiple species can establish on a 2 × 2 m cell, yet they do not directly interact with each other in the simulation (e.g., by shading each other). Competition in the sapling stage is only implicitly simulated, as only one cohort (i.e., the first to exceed 4 m in height) recruits as individual trees, while all other cohorts on the cell die.

3.4. *Discontinuous processes*

Discontinuous processes, i.e., processes that are spatially and temporally discrete and do not occur regularly and everywhere on the landscape, are important drivers of forest landscape dynamics. In iLand, the two major groups of discontinuous processes simulated are natural disturbances and management interventions (Fig. 3). iLand currently simulates disturbances by wind, wildfire, and a diverse set of biotic disturbance agents. The occurrence of strong winds that can break or uproot trees is triggered by external information on the occurrence and intensity of storms, accounting for the modifying effects of topography on local wind speed at the spatial scale of 100 m grid cells. The impacts of wind are simulated with a dose-response model, accounting for the vertical wind profile and resulting turning moment (Gardiner et al., 2000), as well as for local sheltering by neighboring trees and the size of

Fig. 3. Discontinuous processes simulated in iLand. Each row represents a discontinuous process caused by natural (top four) or human (bottom two) agents, with sub-processes and their main drivers in cells. The tags in each cell indicate the main entity or spatial resolution and the primary time-step of the process.

upwind gaps. Calculations are initially performed for areas where discontinuities in the canopy exist (i.e., forest edges, identified at a horizontal resolution of 10 m), and if trees fall or are broken, new trees are exposed to wind. Calculations are repeated at the time scale of minutes throughout the duration of a wind event, iteratively deriving wind impacts as an emerging property of the simulation (Seidl et al., 2014a).

Wildfires require ignitions, which depend on fuel availability, fire weather, fire suppression, and historical fire probability in iLand (Seidl et al., 2014b). A location-specific base ignition probability is modified for the effects of fire weather (represented by the Keetch Byram Drought Index, Keane et al. (2011)) and fire suppression efforts. Once a fire is ignited it spreads to neighboring cells (20 m spatial resolution) accounting for the effects of wind, slope, and fuel availability using a modified cellular automaton approach. Fires stop burning either when no further spread is predicted, or when the maximum fire size (drawn from an empirically parameterized maximum fire size distribution) is reached. Fire severity is simulated based on available fuel (here represented by the litter and downed woody debris pools), fuel moisture, as well as tree size and bark thickness, which are used to calculate the percent of crown volume affected and trees killed by fire. All seedlings and saplings are assumed to be killed in a fire. Fire effects on carbon pools are derived from pool-specific consumption factors.

A variety of biotic disturbance agents can affect forest ecosystems. To account for this diversity, iLand includes a general framework for simulating biotic disturbance agents, from fungi to insects and large mammals (BITE, the BIotic disTurbance Engine) (Honkaniemi et al., 2021). For each agent, biotic disturbance dynamics is simulated by accounting for the potential habitat of the agent, its introduction, dispersal, and colonization, as well as the population dynamics of the agent and its impact on vegetation. Each of these processes can be parameterized based on available data, and agents can flexibly be added and modified via the JavaScript interface of iLand. In addition to the flexible BITE framework iLand also includes a detailed submodule for the most important biotic disturbance agent in Europe's forests, the European spruce bark beetle (*Ips typographus* L.) (Seidl and Rammer, 2016). Outbreaks are initiated based on a region-specific background probability, modified by the effect of climate. Beetle development is simulated using a phenology-based process model (Baier et al., 2007), accounting for life-stage specific thermal requirements for development, and determining the number of generations and sister broods the insect can complete per year. Beetle dispersal is simulated at 10 m resolution, and is done spatially explicitly for each beetle generation and sister brood completed per year. It assumes two stages, first passive flight (simulated with a symmetrical dispersal kernel) and second active flight where beetles look for suitable host trees (i.e., Norway spruce trees above a user-defined diameter threshold) within a 30 × 30 m search window. Host colonization success depends on the defense capacity of the host tree (a function of its non-structural carbohydrate reserves). If a tree is successfully colonized it dies at the end of the year. Beetle overwintering depends on life stage and winter minimum temperatures, and beetle fitness decreases with duration of an outbreak, leading to increasing mortality and the local collapse of populations after some years.

A wide range of management interventions can be simulated in iLand. These include the planting of trees, the removal of trees in tending and thinning operations, and the final harvesting of trees. All operations can be targeted to happen at a specific time, and to affect only a specified area of the simulation and/ or cohort of trees (species, size, social status, etc.). To simulate complex forest management regimes and account for the dynamic interactions between management decisions and forest development iLand includes an agent-based model of forest management (ABE - the Agent Based management Engine) (Rammer and Seidl, 2015). In ABE, different management agents can be specified for parts of the landscape, with agents following different stand treatment programs and adaptive responses to the effects of global change and disturbance. Stand treatment programs of agents follow a sequence of activities executed over the course of stand development, but are dynamically responding to the emergent changes in the environment (e.g., decreased harvest because of growth losses due to simulated drought effects). In addition to silvicultural decision making at the stand level agents are also able to consider landscape-level aspects such as minimum or maximum harvest levels, neighborhood relationships between stands, and different management priorities, which feed back to individual stand-level decisions. ABE thus simulates both tactical and strategic management decisions and their interactions (Fig. 3).

4. Using iLand

In the following section we briefly describe typical steps for applying iLand to a new study system. This is intended to give new and prospective model users an overview and general understanding of the initial efforts and data needed before the model can be applied. Model initialization involves specifying the landscape extent and forest cover, geospatial data on biophysical drivers, and initial vegetation conditions. The evaluation phase consists of a series of simulation experiments to test iLands ability to realistically simulate important patterns within the landscape (e.g., growth, mortality and regeneration). Finally, species parameterization is required either when focal species are not yet included in iLand, or when the evaluation has revealed shortcomings of the current parameterization. See Box 1 for additional resources on using iLand.

4.1. Model initialization

The first step for model initialization is to define the simulation extent and the forested or potentially forested (i.e., stockable) area within the study area. The total extent of a landscape often aligns with property boundaries, natural barriers such as ridgetops or large water bodies, or edges between forests and other land cover types. Stockable area in iLand applications typically ranges from 1000 s to 10,000 s of ha, although the overall landscape extent can often be larger if there are extensive areas of non-forest land cover. Note that iLand is not limited to applications in real-world locations, but can also be applied to simulate (large numbers of) individual stands (Hansen et al., 2018; Kobayashi et al., 2023) or hypothetical landscapes designed to address specific research questions (Braziunas et al., 2021). Landscape size strongly affects computation time and memory requirements of the model. Landscapes with a size between 5000 and 50,000 ha run well on recent consumer hardware, with computation taking minutes to one hour per century of simulation.

Spatially explicit biophysical drivers include topography, daily climate data, and soil properties, ideally at the same spatial resolution as an iLand resource unit (1 ha) or finer (Fig. 1). Daily climate data (historical or future) is often available at regional to global scales (e.g., Karger et al., 2017), though resolution and availability of specific future climate trajectories may vary locally. Downscaling daily climate data to match iLand's spatial resolution of 100 × 100 m grid cells (Thom et al., 2017c), or generating daily timeseries from coarser temporal resolutions (Thom et al., 2022) may be needed. Soil properties (effective soil depth, soil texture, plant-available nitrogen, and – if of interest for a given research objective – carbon pools) tend to be more challenging to obtain than climate data. Categorical soil type maps, along with ancillary data (soil profile data from soil samples, forest type, productivity), help estimate important properties per stratum. Global soil databases offer increasing potential, but regional accuracy and variable availability may be limited. A spinup process can help to derive initial carbon pools that are consistent with live vegetation dynamics.

Initial vegetation consists of species- and size-specific data on individual trees and regeneration cohorts, frequently derived from forest inventory data or a spinup process. Combining forest inventories with data such as canopy height from LiDAR and imputation methods (e.g., Thom et al., 2022) allows for a detailed representation of current forest structure and composition in model initialization. A customizable spinup process provides an alternative means to assimilate field data. Spinups start from bare ground and run the model for centuries, potentially incorporating historical disturbance and management. A specific form to initialize the model and assimilate available empirical data into simulations are directed spinups, using aggregated target values from observations (age and size distribution, species composition) and iterating the treatments simulated in the spinup (e.g., disturbance, management) until simulated conditions align with targets (Thom et al., 2018).

4.2. Model evaluation

Model evaluation typically follows a pattern-oriented approach (Grimm et al., 2005), testing iLands ability to realistically reproduce different patterns observed in the simulated ecosystem. Evaluation

Box 1
Additional online resources for model users.

- Homepage and extensive model documentation: https://iland-model.org
- User guide with technical documentation and practical tips for different modeling tasks: https://iland-model.org/iland-book
- Full model source code: https://github.com/edfm-tum/iland-model
- Community channel for interaction and collaboration among iLand users: https://tinyurl.com/iland-model-discord

exercises vary among landscapes due to varying data availability, but typically include both tests of stand-level patterns over short time frames and assessments of landscape-level patterns over long time frames.

Stand-level tests assess iLand's ability to simulate structural trajectories and variability, such as stem density, basal area, and tree height (Braziunas et al., 2018), but also basal area increment (Kobayashi et al., 2023), or site index (Thom et al., 2022). The available reference data for evaluation dictate the design of the evaluation exercise, with the most basic evaluations consisting of simulating monospecific stands in the absence of disturbances under historical climate conditions along a representative environmental gradient (e.g., Seidl et al., 2012a). Simulated data is then compared with reference data, which can include statistical goodness-of-fit tests. A powerful means of evaluating specific processes is by comparing simulations with experimental data, e.g., observed and simulated diameter increments from stem density trials (Seidl et al., 2017). If no local reference data exist on a given process, theoretical concepts can also be used to test model behavior (e.g., self-thinning in the context of individual-tree mortality (Reineke, 1933)).

An important landscape-level test examines the model's ability to simulate species succession and the emergence of a realistic late-seral tree species composition. Typical reference data are species-level cover type maps (Braziunas et al., 2018), inventory data (Kobayashi et al., 2023; Thom et al., 2017a), or descriptive accounts of potential natural vegetation composition based on expert assessments and vegetation mapping (Albrich et al., 2018). Simulations frequently start from bare ground, include external seed inputs, and run for millennia under static historical climate with or without disturbances. Analyses focus on how well iLand reproduces expected successional patterns and late-seral species composition (as an indicator of competitive strength of species in an area, i.e., the long-term integral over growth, mortality and regeneration processes), over the environmental gradients in the landscape under study. Further landscape-scale evaluations include the comparison of individual disturbance modules against available remote sensing products (Thom et al., 2022), and of simulated management strategies with data reported for the study area (Albrich et al., 2018).

4.3. Species parameterization

Species parameterization is a critical component of forest simulation modeling, determining the behavior of individual tree species and their interactions in the simulation. iLand uses 65 parameters to characterize a species. Parameters describe stem and crown shape as well as wood traits, the response to the environment, characteristics of seed production and distribution, establishment and growth in the sapling stage, as well as maximum age and other mortality-related parameters.

Compiling all relevant parameters needed to simulate a new tree species in iLand is a considerable effort; while some parameters can be easily measured in the field or extracted from the literature (e.g., existing trait databases, Kattge et al., 2020), others are more challenging to obtain. Parameterizing a new species is thus an iterative and step-wise process strongly intertwined with model evaluation. The first tier of parameters, describing tree allometry, growth, and environmental responses, can usually be determined from the literature (Burns, and Honkala, 1990; Schütt, 2006). These can then be evaluated by conducting stand-level simulations solely focusing on growth, while disregarding regeneration and mortality processes. The second tier of parameters describe tree mortality and aging. These include a number of life history parameters that often are available from the literature (e.g., maximum tree age, maximum tree height), but also parameters that are difficult to determine empirically and require iterative estimation (e.g., the increase of mortality probability with increasing carbon starvation of a tree). For this, a second set of stand-level evaluation exercises can be conducted, focusing on the reproduction of stand density patterns over time (self thinning) as well as on simulated maximum tree properties (maximum tree age, diameter, and height). The third tier of parameters characterize seed production/dispersal, tree establishment and sapling growth. These include a number of empirically derived estimates, e.g. describing the seed dispersal kernel and the height growth potential of saplings, but also some parameters that are more difficult to obtain from available data (e.g., fecundity, here the number of seeds produced per m^2 of canopy area of a species, used to scale seed dispersal kernels). If regeneration data for evaluation are available, specific evaluation tests can be set up to assess these parameters (Hansen et al., 2018). If not, a coarse filter approach is to simulate landscape-scale potential natural vegetation development over long time frames and evaluate whether (i) stem densities and diameter distributions are realistic, (ii) simulated basal area and biomass pools are close to observed values, (iii) the species that dominate immediately after disturbance are the early-seral species expected for the area, and (iv) the species dominating after centuries of undisturbed forest development are the ones expected for the landscape. These expected patterns will only emerge from the simulation if the parameters related to all three demographic processes – growth, mortality, and regeneration – have been well specified.

Following the process-based philosophy of iLand, a parameterization of a species should be valid and applicable over wide geographic and ecological gradients without requiring local adaptation. To date, a total of 150 species have been parameterized in iLand (Thom et al., 2024). We advocate against intensive local tuning of species parameters and suggest to accept trade offs between local precision and broad scale accuracy, as parameter tuning might lead to overfitting and reduce the applicability of the model under no analog environmental conditions. We suggest that before species parameters are changed, the suggested changes should be evaluated against a representative subset of previous applications of the model, ensuring that the changes improve model behavior over a wide range of conditions. In this way, parameters are refined and new information is assimilated into the species parameter set, while ensuring accuracy and general applicability of the model under current and future environmental conditions. To perform this data assimilation and continuous improvement of parameters in iLand a tool to aid the analysis of changes between simulations with different parameter sets against reference data is available for model users (see Box 1).

5. iLand applications

Where and to what end has iLand been applied in the past 12 years? To address this question, we examined all 50 scientific papers using iLand published since the presentation of the model in 2012 (Fig. 4a, see Supplementary Material Table S1 for a full list of publications). Disturbances, climate change, and forest management emerged as the dominant drivers investigated with the model (Fig. 4b). Research questions were diverse, but broadly focused on two areas: One group of studies investigated ecosystem dynamics and forest resilience, focusing on changes in forest composition, structure and functioning in response to disturbances, climate change, and forest management. The other group of studies addressed the impacts of drivers on ecosystem service provisioning, with a specific focus on carbon sequestration, biodiversity and timber production. Study landscapes were located in Europe ($N = 36$), North America ($N = 13$), and Asia ($N = 1$) (Fig. 5). European applications focused on Central Europe. North American applications focused on the Greater Yellowstone Ecosystem and the Pacific Northwest, but also included applications in Alaska and Eastern Canada. The sole Asian study landscape to date lies in northern Japan. Of the landscapes analyzed, 30 % were protected areas and 38 % were managed forest landscapes, with the remainder being generic landscapes or stand-level analyses. The average simulated landscape size in landscape studies was 15,104 ha, with the maximum simulated landscape size to date being 61,000 ha (Hansen et al., 2023).

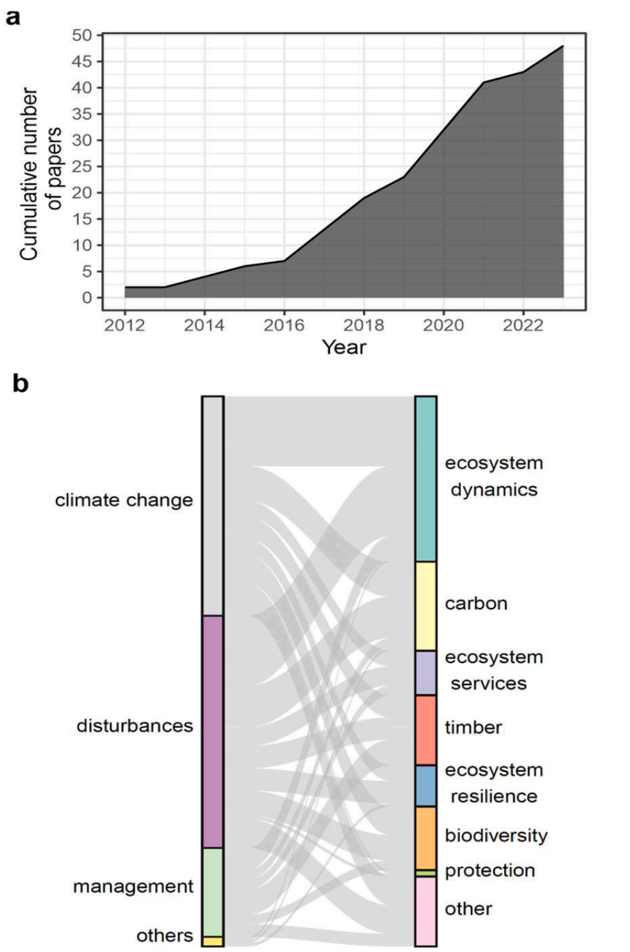

Fig. 4. a) Cumulative number of peer reviewed scientific publications using the model since 2012. b) Relationship of simulated drivers (left) and addressed research topics (right) in studies applying iLand. Note: studies can have investigated multiple drivers and topics.

6. Limitations and outlook

Over the past 12 years, the individual-based forest landscape and disturbance model iLand has matured considerably, and has contributed to a wide variety of scientific questions. Nonetheless, a number of limitations remain with the current model. We here highlight three areas that warrant more attention in future model development: belowground processes, biotic interactions, and landscape dynamics beyond forest ecosystems.

The belowground realm of forest landscapes is captured only in a simplistic manner in the current version of iLand. While iLand simulates aboveground competition for light with considerably higher detail than most other landscape models, a spatially explicit competition for belowground resources between individual trees is not considered, essentially assuming that belowground resource competition is size-symmetrical (Cahill and Casper, 2000). This limitation is potentially important when applying the model under more arid conditions, where competition for water is a stronger driver of ecosystem dynamics than competition for light (Zavala and Bravo De La Parra, 2005). In theory, the field of neighborhood approach adopted in iLand to simulate competition for light could also be applied to simulate belowground competition. This would require the derivation of process-based belowground interaction kernels, representing a trees' ability to locally compete for water and nutrients (Farrior, 2019). A further limitation of iLands current representation of belowground processes is that subsurface water routing throughout the landscape is not considered. Currently, the water balance is simulated for each 100 m grid cell in isolation, without considering water input from cells located higher up in the landscape to cells located in lower portions of the landscape. Depending on landscape topography and bedrock conditions such processes could be important determinants of local water availability (Schoorl et al., 2002), and approaches for simulating subsurface water routing at the landscape scale exist (Tague and Band, 2004) and could be included in the model. Furthermore, nutrient dynamics remain poorly accounted for in iLand. While nitrogen stocks can be simulated in the current model version via fixed stochiometric ratios, the dynamic interactions between belowground nutrient availability and aboveground vegetation dynamics are not accounted for in iLand. Furthermore, nutrients beyond nitrogen – such as phosphorus – are not considered in the model, but have received increasing attention in, e.g., the dynamic

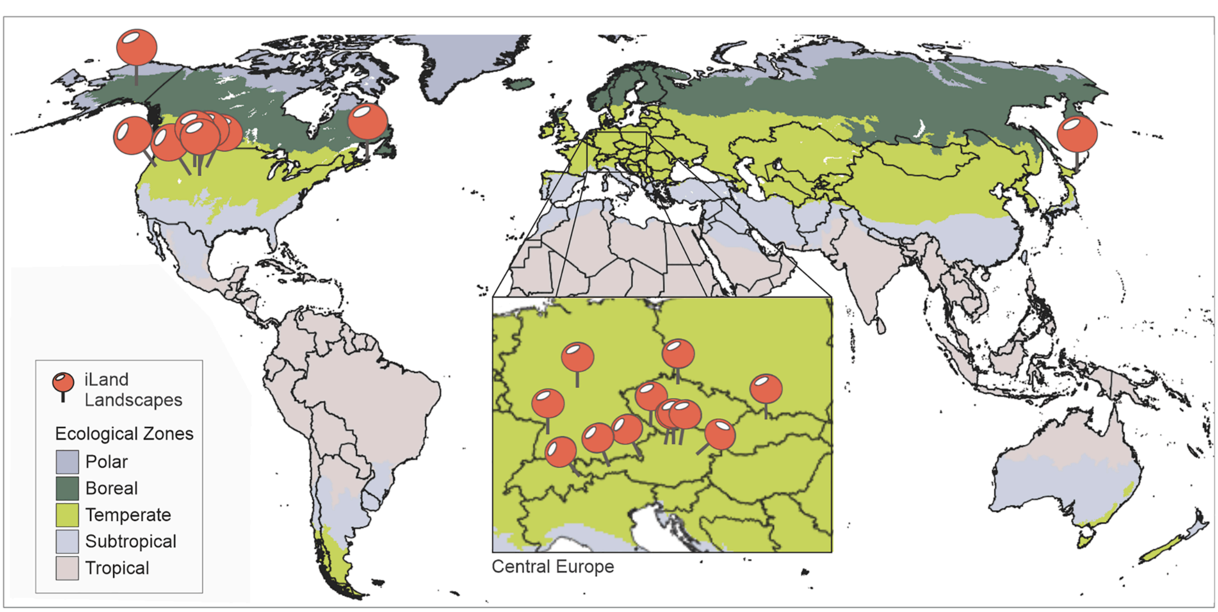

Fig. 5. iLand has been applied across three continents. Pins show the location of study landscapes simulated with iLand, derived from the published peer-reviewed literature (ecological zones according to FAO, 2012).

global vegetation modeling community (Nakhavali et al., 2022; Reed et al., 2015).

An important hallmark of iLand is the dynamic simulation of the interactions between individual trees at the landscape scale. However, this simulation currently focuses on competition for resources, and does not explicitly consider facilitation between trees. Furthermore, interactions between trees are currently determined by traits that remain constant throughout the lifetime of a tree (e.g., shade tolerance), and that do not vary between the individuals of the same species. Future work could consider more dynamic traits, allowing changes with ontogeny as well as intra-specific variation in traits and their inheritance between tree generations (Kramer et al., 2010; Purves and Pacala, 2008; Scheiter et al., 2013). Beyond interactions between trees, other biotic interactions are important in forest ecosystems. One example is the simulation of forest floor vegetation, which harbors the large majority of plant diversity in temperate forest ecosystems (Gilliam, 2007) and is highly responsive to changes in climate and disturbance regimes (Braziunas et al., 2024a). Future work could focus on a more dynamic consideration of forest floor plant communities, consider interactions between vegetation cover and tree establishment, and simulate its implications for forest landscape dynamics (Thrippleton et al., 2016). Lastly, interactions of trees with other biota such as mycorrhiza or ungulates could be potential avenues for future model development (Bennett et al., 2017). More broadly, while currently only the forested part of landscapes is simulated in iLand, interactions with the portions of the landscape not forested could be of interest, e.g., in the context of forest loss (Parks et al., 2019), the expansion of forest tree lines (Rotbarth et al., 2023), or approaches of integrated landscape management (Schirpke et al., 2023).

A key element that has constrained the inclusion of further processes in iLand is data availability. However, the advent of new approaches to automated data collection (Wilmers et al., 2015) and remote sensing (Senf, 2022) are opening up new avenues, providing unprecedented information for model development, parameterization, initialization and evaluation. When we started the development of iLand more than 15 years ago, we anticipated the wide availability of individual-tree information from remote sensing, and included these data streams in our considerations of model design. Likewise, the next wave of model development should anticipate the potential of big data (Hampton et al., 2013) and artificial intelligence (Perry et al., 2022) to leverage new avenues for forest landscape modeling. One such avenue is harnessing artificial intelligence to upscale detailed process information available from simulations with high resolution models such as iLand to large spatial extents (Rammer and Seidl, 2019). Such bottom-up approaches to scaling hold considerable potential to improve our understanding of large-scale vegetation dynamics, as they are better able to account for landscape-scale processes such as dispersal and disturbance compared to current top-down approaches to large-scale vegetation modeling (Fisher et al., 2018).

We conclude that simulating landscape-scale forest dynamics at the level of individual trees and with intermediate process resolution has improved our understanding of the impacts of global change on forest landscapes worldwide. The current paper takes stock of the state and contributions of the model iLand, synthesizing its development over the past 12 years, and serving as a gateway to the growing body of literature and code for prospective model users (see Box 1 for additional resources). While we here have highlighted the applications and limitations of the model we also note that modeling inherently means simplification. Consequently, whether a model (and its intrinsic simplifications) are useful always need to be assessed carefully in the context of the research question at hand. We conclude that long-term model development is important to harness the power of simulation models for improved understanding and management of dynamic forest landscapes.

CRediT authorship contribution statement

Werner Rammer: Writing – review & editing, Writing – original draft, Software, Resources, Project administration, Methodology, Conceptualization. **Dominik Thom:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Martin Baumann:** Writing – review & editing, Software, Investigation. **Kristin Braziunas:** Writing – review & editing, Methodology, Investigation. **Christina Dollinger:** Writing – review & editing, Investigation. **Jonas Kerber:** Writing – review & editing, Investigation. **Johannes Mohr:** Writing – review & editing, Investigation. **Rupert Seidl:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

A technical model description and full source code are available online (see Box 1 for details).

Acknowledgements

W.R., R.S., K.B., C.D., M.B., and J.M. acknowledge support by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 101001905, FORWARD). W.R., J.K., J.M. were further supported by the German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection (grant no. 67KI21002A).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2024.110785.

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