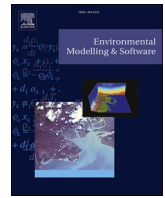




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## From mycelia to mastodons – A general approach for simulating biotic disturbances in forest ecosystems

Juha Honkaniemi<sup>a,b,\*</sup>, Werner Rammer<sup>a,c</sup>, Rupert Seidl<sup>a,c</sup>

<sup>a</sup> University of Natural Resources and Life Sciences (BOKU), Institute of Silviculture, Vienna, Austria

<sup>b</sup> Natural Resources Institute Finland Luke, Forest Health and Biodiversity, Helsinki, Finland

<sup>c</sup> Technical University of Munich, Ecosystem Dynamics and Forest Management Group, Freising, Germany

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### ABSTRACT

Forest disturbance regimes are changing around the globe. Of particular concern are biotic disturbance agents, as they respond strongly to climate warming and invade new ecosystems as alien pests and pathogens. To date, biotic disturbances are either ignored in simulations of vegetation dynamics or only a small number of common agents are considered explicitly. Here we present BITE, a general, process-based approach to simulate biotic forest disturbance agents from fungi to large mammals. BITE considers the processes of agent introduction, dispersal, colonization, population dynamics, and vegetation impact explicitly. Here we parameterize the model for six widely different biotic disturbance agents (*Heterobasidion annosum*, *Hymenoscyphus fraxineus*, *Lymanthia dispar*, *Anoplophora glabripennis*, *Capreolus capreolus*, *Mammut americanum*) and evaluate it using pattern-oriented modeling. BITE enables the inclusion of both established and novel biotic disturbance agents in vegetation models, and is a step towards the comprehensive simulation of forest disturbance regimes in a changing world.

### 1. Introduction

Natural disturbances, i.e. discrete events that disrupt the structure of an ecosystem, shape forests around the world. The disturbance regime of a given area is characterized by a typical frequency, size and severity of disturbance (Turner, 2010). A key determinant of disturbance regimes are the prevailing disturbance agents (i.e., the factors causing disturbance), as they strongly influence the spatial patterns and climate sensitivity of disturbances (Seidl et al., 2020). Ecosystems are generally well-adapted to the prevailing disturbance regime, yet disturbances are changing as a result of climate change. For example, the frequency of wildfires (Schoennagel et al., 2017) and the severity of insect outbreaks (Raffa et al., 2008) is increasing in many parts of the world. These changes are of concern as the ecosystem services forests provide to society are predominately negatively affected by disturbances (Thom and Seidl, 2016). Quantifying and managing the impacts caused by current and potential future disturbance regimes is thus increasingly important.

Investigations of the effects of natural disturbances often focus on severe and abrupt abiotic events, such as large wildfires, flood events or windstorms. However, the impacts of biotic disturbances, i.e., those caused by a variety of organisms from fungi to insects and herbivorous mammals, are rivaling the impacts of their abiotic counterparts (Healey

et al., 2016; Kautz et al., 2017). Furthermore, a warming climate is predicted to benefit many biotic agents significantly (Bentz et al., 2019; La Porta et al., 2008). Compared to abiotic disturbances our understanding of biotic disturbance agents remains limited, not least because of the complex biology of the various life forms that can cause disturbances. Furthermore, biotic disturbances are often modulated by complex interactions with other (abiotic and biotic) disturbance agents (Seidl et al., 2017), which makes their analysis and quantification challenging. Due to the high level of complexity involved, simulation modeling is a particularly important tool for understanding biotic disturbances.

Global change is considerably altering biotic disturbance regimes. Many biotic disturbance agents are, for instance, shifting polewards (Bebber et al., 2013), and species that are benign in their native range can become impactful pests in new systems (Desprez-Loustau et al., 2007; Økland et al., 2019). In addition, new biotic disturbance agents are emerging as global trade accelerates the introduction of non-native pests and pathogens (Chapman et al., 2017; Santini et al., 2013; Seebens et al., 2017). Climate change sometimes benefits the establishment and spread of non-native species, exacerbating the issue of non-native pests and pathogens further (Seidl et al., 2018b; Walther et al., 2009). Invasive pests and pathogens can cause dramatic changes in their new

\* Corresponding author. Latokartanonkaari 9, FI-00790, Helsinki, Finland.

E-mail address: [juha.honkaniemi@luke.fi](mailto:juha.honkaniemi@luke.fi) (J. Honkaniemi).

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environment by diminishing their host population or even driving it into extinction (Lovett et al., 2006; Mack et al., 2000; Wardle et al., 2001). In addition, they can interact with native disturbance agents (Gonthier et al., 2007) or have indirect effects on human health (Donovan et al., 2013).

A common characteristic of all these novel biotic disturbance agents is that the available information on them is limited. This means that strongly data-driven approaches (e.g., empirical models, machine learning, see Rammer and Seidl, 2019) are often not feasible for modeling novel biotic disturbance agents, and rather simple, process-based or theoretical models are needed to provide timely model-based inference for management.

The potential negative impacts of biotic disturbance agents can be mediated through a range of potential management options. These extend from aiming to eradicate a newly introduced agent (Liebhold and Bascompte, 2003) to changing the host population structure and configuration on the landscape (Honkaniemi et al., 2020) and applying chemical or biological control to decrease the abundance of the agent (Holmes and MacQuarrie, 2016). Furthermore, an efficient monitoring of biotic agents is a key element of management, especially in the case of emerging pests and pathogens, as the timing and spatial focus of countermeasures can critically influence management success (Cunniffe et al., 2016; Simberloff, 2003; Simberloff et al., 2005). Simulation models have proven to be valuable tools for informing management on where, when, and which measures to apply in order to optimally contain biotic disturbances.

Computer simulations of ecosystem dynamics have developed rapidly in recent years (Seidl, 2017). The increase in computational capacity, for instance, has enabled a shift from modeling forest stands to focusing on their larger spatial context at the landscape scale (Shifley et al., 2017). This development is important especially in the context of simulating biotic disturbances, as they can spread from stand to stand, occur across relatively large extents, and are driven by factors across multiple spatial scales (Cushman and Meentemeyer, 2008; Seidl et al., 2016). Nonetheless, most studies simulating the potential risk from pests and pathogens have to date focused on the potential for introduction and spread of an agent (de la Fuente et al., 2018; Ferrari et al., 2014), with considerably less attention on simulating the potential impacts of biotic agents (Seidl et al., 2018b). Process-based models of biotic disturbances operating at different scales (Cushman and Meentemeyer, 2008) and coupled with dynamic vegetation models (Cunniffe et al., 2015) remain still rare to date. One reason is that process-based models often require detailed information on agent biology, that often is not available. Simplified models, such as SIR-models borrowed from epidemiology (Kermack and McKendrick, 1927), have been successfully applied to pests and pathogens in agricultural crops (Whish et al., 2015) and livestock (Keeling, 2005). However, generally applicable biotic disturbance models in forest ecosystems remain scarce to date (but see Kriticos et al., 2013; Lustig et al., 2017; Sturtevant et al., 2004; Tonini et al., 2018; Wildemeersch et al., 2019).

Here, we present BITE (the Biotic disTurbance Engine), a general model to simulate biotic disturbances in forest ecosystems. Our objective was to develop a modeling framework that is general enough to simulate a wide range of biotic disturbance agents, from fungi to insects and large mammals. Further objectives were to keep the framework simple and modular (in order to also be applicable in situations where knowledge about an agent is limited, as is the case with new invaders). Coupled with a forest landscape simulation model, BITE allows the quantification of the impacts of emerging pests and pathogens on forests in time and space. Here we present the BITE modeling framework and illustrate its generality by applying it to six widely different biotic disturbance agents: two pathogens (an ascomycete and a basidiomycete), two insects (a defoliator and a bark beetle), and two mammals (browsers of different size and life history strategy). We analyzed the different patterns produced by BITE for this wide variety of agents following the principles of pattern-oriented modeling (Grimm et al., 2005).

## 2. Materials and methods

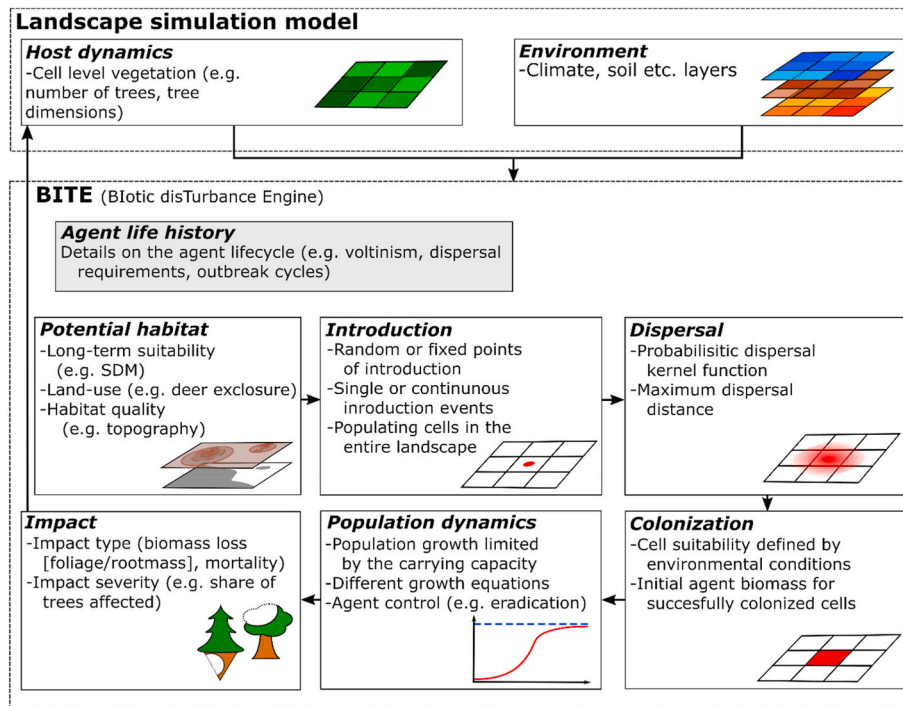
### 2.1. Model overview

BITE is a general model to simulate the dynamics of biotic disturbance agents, with a special focus on being able to accommodate also emerging pests and pathogens. BITE was designed to be easily adaptable to different agents and conditions and allows the flexible assimilation of emerging knowledge on agent dynamics due to its modular structure. The key design elements of our modeling approach are:

- 1) Agents are simulated on a regular grid with an agent specific resolution (between 10 m–1000 m grid cells); while agent-specific variables are homogeneous within a grid-cell, vegetation (i.e., availability of host trees) and environment (e.g., climatic indicators) can vary within a grid cell.
- 2) Biomass is used as a common currency for simulating the abundance of agents in a grid cell, but also for simulating the impact of biotic disturbance agents on forest vegetation. An individual-based modeling approach (Railsback and Grimm, 2019) was considered but was not deemed suitable for the simulation of very small organism such as fungal spores across large spatial extents.
- 3) The movement of individual agents in a given time step is approximated by probabilistic dispersal kernels.
- 4) Agent population dynamics within a grid cell is modeled via empirical growth equations. The growth rate of the population is limited by a carrying capacity determined by the host availability within a cell.
- 5) The impact of biotic disturbance agents on vegetation can be generalized into the consumption of foliage biomass, the consumption of root biomass, or tree mortality (e.g., by disrupting physiological processes such as phloem conductivity).

An important design strategy for achieving general applicability across a wide range of biotic disturbance agents is modularity. BITE models biotic disturbance agents in six distinct modules, i) potential habitat, ii) introduction, iii) dispersal, iv) colonization, v) population dynamics, and vi) impact (Fig. 1). Each module represents an important aspect of agent biology and provides specific options in the parameterization of a specific agent (e.g. different dispersal kernel functions) to accurately characterize agent behavior. The level of detail implemented in each module can vary from simple to complex, and computations in each module can potentially use state variables such as agent biomass in the previous time step, vegetation structure and composition, and environmental conditions. Modules can also be bypassed for selected agents if they are not applicable or if not enough information for their parameterization is available.

BITE is a general framework that can be coupled with a wide variety of dynamic vegetation models. Conceptually, any model that provides gridded host biomass for the agents to consume could be coupled with BITE. However, specific implementations of the BITE framework can be tailored to a model's representation of vegetation and environment, such as the specific rendering of stand structure, tree dimensions and available climate variables in a given model. In the current implementation, the framework is coupled with the individual-based forest landscape and disturbance model iLand (Seidl et al., 2012a; Thom et al., 2017). Consequently, we here focus on the dynamics of biotic disturbance agents in forest ecosystems at the landscape scale (i.e., an extent of  $10^3$ – $10^5$  ha). iLand is a process-based model simulating forest landscape dynamics at the spatial grain of individual trees (see <http://iland.boku.ac.at/> for a technical model documentation). Disturbances can have long-term impacts on forest structure and composition (Johnstone et al., 2016), with regeneration and growth processes being key determinants of ecosystem resilience and the persistence of disturbance impacts. In iLand, these processes are simulated in detail based on first principles of ecology, e.g. spatio-temporal dispersal in combination



**Fig. 1.** The overall structure of the BITE framework for simulating biotic disturbance agents, consisting of six core modules of agent dynamics, and a coupling to a landscape model for simulating feedbacks between biotic disturbance agents and forest vegetation.

with local light availability and environmental filters determines the establishment of new trees after a disturbance. A radiation use efficiency approach (Landsberg and Waring, 1997) is used to calculate gross primary production from daily weather data and local water and nutrient availability. The assimilated carbon is subsequently allocated to different tree compartments based on species-specific allometric ratios between compartments. In BITE these compartments are consumed by the simulated agents leading to single tree mortality, which is related to carbon starvation. Thus, mortality increases if stressors, such as the biotic agents simulated in BITE, lead to the depletion of a trees carbohydrate reserves. In addition, an age- and size-related background mortality rate is calculated. The spatial grain of simulations in iLand varies, with local light environment being simulated on 2 m grid cells while heterogeneity in climate and soil is considered at the resolution of 100 m. iLand was successfully evaluated and applied in Central Europe (Silva Pedro et al., 2015; Thom et al., 2018) and the Western US (Braziunas et al., 2018; Seidl et al., 2012b). In the current implementation of BITE, relevant elements of vegetation (e.g., host tree biomass) and climate (e.g., growing degree days) are provided dynamically from the iLand simulation environment. In turn, vegetation impacts from BITE disturbance agent activity (e.g., trees killed, biomass consumed) are dynamically fed back into iLand, where they change the simulated vegetation state. BITE is thus fully integrated within iLand, with dynamic feedbacks between vegetation and biotic disturbance agents.

2.2. Detailed model description

2.2.1. Technical implementation

Besides general applicability across a wide range of biotic disturbance agents important design principles of BITE were flexibility in the application (in order to allow tailoring the model to emerging research questions) and computational efficiency (to accommodate a potential large number of simulations in scenario analyses). Therefore, agents in BITE are defined in JavaScript (granting ease of use and flexibility) and executed with an engine written in C++ (ensuring its computational efficiency). The agent code is mostly declarative (i.e., describing the

“what” rather than the “how”), but can be augmented by imperative code for more complex agent behavior (see Supplementary material S1 and JavaScript files for the agents in Figshare).

Multiple agents can be active within a single simulation run, and events such as agent introductions or management interventions can be triggered at any time during a simulation. Technical details and example code are provided in Supplementary Material S1. Full source code and documentation is available under a GNU General Public License (GNU GPL [www.gnu.org/licenses/gpl-3.0.html](http://www.gnu.org/licenses/gpl-3.0.html)) from <http://iland.boku.ac.at/bite/#/>.

The implementation of BITE is generally model-agnostic and provides a clear technical interface between BITE and the vegetation model. Coupling BITE with a new vegetation model is fairly straightforward via this interface. However, since the structure of vegetation models differ from each other (e.g., represented biomass pools, spatial resolution, different environmental drivers), coupling a new model might also require an adaptation of BITE processes and functions. The following description is based on the current implementation of BITE within the iLand landscape and disturbance modeling framework.

2.2.2. Agent life history

Important information on the life history of the simulated agent(s) need to be provided to the model. These include information on voltinism (i.e. univoltine, bivoltine, multivoltine), the frequency of dispersal (number of dispersal sequences per timestep and generation), and prerequisites for initiating dispersal after colonization (i.e. possible delay due to inoculum accumulation). In addition, in case of cyclic agents (e.g. insect or vole outbreaks), the outbreak duration and time between outbreaks are specified.

2.2.3. Potential habitat

This module determines the general habitat suitability of an agent for the simulated landscape. It uses binary raster files of long-term climate suitability (e.g., derived from species distribution models), land-use (e.g. deer exclosures) or other environmental filters of relevance (e.g. elevation, water bodies). All these filters are not calculated dynamically

in BITE but are provided as external input to the model simulation. Essentially, the provided rasters identify the potential spatial domain of simulation for each agent within the landscape. Please note that filters can change over time (e.g., when habitat suitability changes in response to climate change).

#### 2.2.4. Introduction

This module simulates the introduction of a new biotic disturbance agent into the simulated landscape. In BITE an agent can be introduced at time  $t$  in  $n$  cells of the landscape either randomly or in predefined locations. Grids with introduction probability can also be provided (e.g. increased probability of introduction closer to roads or human settlements).

#### 2.2.5. Dispersal

The dispersal module is responsible for simulating the movement of the agent across the landscape. Dispersal is simulated in a probabilistic way in BITE, calculating the spatiotemporal establishment probability of an agent at a new location. A species-specific dispersal kernel (indicating the probability that a cell is the target of dispersal from a focal cell, as determined by the distance from the focal cell) and a maximum dispersal distance determine agent movement in space and time. BITE first calculates dispersal individually for all cells where the agent is present, and subsequently combines dispersal probabilities for cells that can be reached from multiple source cells of the agent population.

#### 2.2.6. Colonization

The colonization module calculates whether an agent is actually able to colonize a previously uninhabited cell. Successful colonization is contingent on several conditions: First, the agent must be able to successfully disperse into the cell. Dispersal success is calculated from the dispersal probability derived in the dispersal module, by either invoking a fixed threshold or by drawing a random number [user parameter]. In addition, the successful colonization of a cell depends on the vegetation of a cell, e.g., the presence of host trees of the agent. Furthermore, environmental conditions can limit colonization of a cell, e.g. the need to exceed certain temperature sums indicating the thermal ability to complete a full development cycle for insects. Both vegetation and environmental conditions are implemented as Boolean filters, i.e., colonization is successful only when all conditions are met. Successfully colonized cells are simulated to have an initial agent biomass, which serves as the basis for further calculations of population dynamics [user parameter].

#### 2.2.7. Population dynamics

Once an agent has successfully colonized a cell, its biomass in the cell ( $BM_A$ ) can grow, with growth being limited by the relevant host biomass (e.g. canopy biomass, root biomass - depending on the compartment that is affected by the agent) that is available at a cell as well as environmental conditions (e.g. temperature, soil moisture). Population growth is simulated with a growth equation that can be provided by the user for each specific case. By default, a logistic growth equation is used, incorporating a relative maximum growth rate  $r$ , the agent biomass  $M$  in the previous time step, and the carrying capacity of a cell  $K$  (see Supplementary Material S1 Eq. S2). The carrying capacity is calculated as a function of the targeted host biomass in the cell and the potential annual biomass consumption per biomass unit of the agent. The output of the population dynamics module is the agent biomass  $BM_A$  in each cell at timestep  $t$ . Although the default function for population dynamics in BITE is a simple logistic growth equation, any other type of function (e.g. second order equations, Lotka-Volterra) to describe population dynamics could be used. The use of more complex growth equations depends on improved data availability for parametrization, but equations can also be used experimentally to test the effect of different assumptions of agent growth on simulated disturbance dynamics.

#### 2.2.8. Impact

The Impact module calculates the effect of biotic agent activity on vegetation and provides a feedback to the simulated vegetation dynamics in the cell. In BITE, impact is calculated as the host biomass loss due to agent activity. This information is subsequently fed back to the vegetation simulator, where impacts alter the simulated vegetation structure and composition. Impacts in BITE either affect a specified host compartment (with a maximum annual consumption rate per unit agent biomass), or an entire tree (in the case of direct mortality). In iLand, the consumption of different tree compartments (foliage or roots) increases the probability of mortality, as it changes the physiological abilities of a tree, increases maintenance respiration and can lead to carbon starvation. Possible impact types for trees  $>4$  m in height are consumption of foliage or root biomass, and tree mortality. For saplings (height  $< 4$  m) the simulated impacts are either tree mortality or consumption of the leader shoot (by browsing). Impacts can be stratified by tree dimension, and agent preferences can be considered (e.g. shortest trees are targeted first). For example, an agent can be parameterized to affect only trees  $<15$  m in height or have varying impact rates between diameter classes. Agents can also impact different tree compartments at the same time. In a simplified implementation of BITE, where agent biomass dynamics are not simulated explicitly due to data limitations, the impact of an agent can be simulated phenomenologically by specifying the share of trees affected per cell or the share of compartment consumed in affected trees. Trees in iLand also die from other causes of mortality such as self-thinning, harvesting and abiotic stress. These causes of mortality are computed independently from biotic disturbance mortality, but do interact with each other indirectly, as they all modify forest structure and composition, which in turn influences mortality.

### 2.3. Model evaluation

#### 2.3.1. Biotic agents

To demonstrate the utility and versatility of BITE we parameterized and tested it for six widely different biotic disturbance agents, i.e. Heterobasidion root rot (*Heterobasidion annosum* Fr. (Bref)), European gypsy moth (*Lymantria dispar* L.), roe deer (*Capreolus capreolus* L.), ash dieback (*Hymenoscyphus fraxineus* Baral et al. (2014)), Asian long-horned beetle (*Anolophora glabripennis* Motchulsky), and mastodon (*Mammuth americanus* Kerr) (Table 1, see Figshare folder for BiteAgent JavaScript codes). The agents were chosen to cover a wide variety of biota (from fungi to insects and large mammals), differing strongly in their life history and impact on tree vegetation. In addition, the agents represent a wide variety of information available, from organisms that have been studied in depth (Heterobasidion root rot, gypsy moth, roe deer) to those for which less information is available (ash dieback, Asian long-horned beetle, mastodon), in order to test the robustness of the model also in situations where information is limited (such as is often the case with a newly invading pest species). All species were parameterized based on available information from the literature. We also want to highlight that while some of the simulated example agents are invasive alien species, we do not aim to capture invasion dynamics with BITE and iLand, as this would require a much larger spatial scope for the simulations. We here explicitly focus on the dynamics of biotic agents and their impacts on vegetation in the landscape scale.

*Heterobasidion annosum* is one of the most destructive forest pathogens in the northern hemisphere, causing root rot specifically on conifers (Garbelotto and Gonthier, 2013). Different species of the group are well established in many regions of Eurasia and North America, but it is currently also spreading into new areas (e.g. Bérubé et al., 2018). *Heterobasidion* sp. spread via spore infections through fresh stumps, e.g. created by tree harvesting. Within the stand the fungus spreads vegetatively via mycelia (Garbelotto and Gonthier, 2013). While *Heterobasidion* sp. spreads only over short distances (Kallio, 1970; Mõykkynen et al., 1997) it can endure at a site for several tree generations (Stenlid and Redfern, 1998). 99.5% of the spores land within a few hundred

**Table 1**

BITE agent parameters. NA indicates that the parameter was not available from the literature and the respective BITE module was not used in the simulations.

Agent	Type	Host	Host requirements and affected compartment	Dispersal distance	Population dynamics	Impact
Root rot ( <i>Heterobasidion annosum</i> )	Fungus	Scots pine ( <i>Pinus sylvestris</i> )	Trees of all sizes; root biomass	Short, fat-tailed	Low initial agent biomass, fast growth	Root biomass loss
Gypsy moth ( <i>Lymanthia dispar</i> )	Insect	Pedunculate oak ( <i>Quercus robur</i> )	Trees of all sizes; foliage biomass	Short	Moderate initial agent biomass, moderate growth	Defoliation
Roe deer ( <i>Capreolus capreolus</i> )	Mammal	Silver fir ( <i>Abies alba</i> )	Trees with height < 1.3 m; leader shoot	NA (assumed present everywhere)	High initial agent biomass, stable population	Browsing
Ash dieback ( <i>Hymenoscyphus fraxineus</i> )	Fungus	European ash ( <i>Fraxinus excelsior</i> )	Trees of all sizes; foliage biomass	Long	NA	Defoliation
Asian long-horned beetle ( <i>Anoplophora glabripennis</i> )	Insect	Sycamore ( <i>Acer pseudoplatanus</i> )	Trees with dbh>7.5 cm; stems	Moderate	NA	Tree mortality
Mastodon ( <i>Mammot americanum</i> )	Mammal	Norway spruce ( <i>Picea abies</i> )	Trees with height < 4 m; foliage biomass	NA (assumed present everywhere)	High initial agent biomass, slow growth	Browsing and tree mortality

meters, with the remaining 0.5% being responsible for the long distance dispersal of the pathogen (Kallio, 1970). In BITE, dispersal was simulated with a power law function (Kallio, 1970; Möykkynen et al., 1997), and the colonization was restricted to cells where fresh stump surfaces were available for spore germination (Rishbeth, 1951). Population dynamics were simulated based on a logistic growth model, with consumption and growth rate parameters derived from Honkaniemi et al. (2017b). The impact on infested trees is simulated as a reduction in root biomass.

European gypsy moth (hereafter referred to as gypsy moth) is a defoliator native to Europe where it causes substantial disturbance especially on oaks (Mcmanus and Csóka, 2007). In 1869 it was also introduced to North America, where it became an invasive pest seriously threatening oak forests in the Northeastern USA (Elkinton and Liebhold, 1990). Adult gypsy moths are poor dispersers, but the first instar larvae spread passively over short distances via wind (Hunter and Elkinton, 2000). However, human-aided long distance dispersal is driving the invasion in North America (Liebhold et al., 1992). The development of a gypsy moth from egg to adult takes one season and during that development, each larvae consume about 3–4 g of foliage (Sharov and Colbert, 1996). Outbreaks of gypsy moth typically last for several years and occur both in Europe and North America in 8–12 year intervals (Johnson et al., 2005). Gypsy moth dispersal was approximated with a Gaussian dispersal kernel in BITE (Elder et al., 2013), and its population dynamics was simulated with a logistic growth equation based on growth rates modified from Lustig et al. (2017). The simulated impact was consumption of foliage biomass, with preference for small over large trees.

Roe deer is a species of deer native to Europe. It is widespread throughout the whole continent from southern Europe to the Nordic countries, and is expanding its range due to warming climate and changes in land-use (Danilov et al., 2017; Valente et al., 2014). Roe deer is a relatively small deer species with an average body mass of ~20–30 kg (Andersen et al., 1998; Pettorelli et al., 2002). They are territorial animals and their habitat can range from agricultural landscapes to woodlands (Tixier and Duncan, 1996). Roe deer graze fresh grass, but a significant part of the diet consists also of sapling shoots (Tixier and Duncan, 1996). Silver fir (*Abies alba*) is one of the most favored tree species for browsing. In many areas browsing rates on the species are substantial, and can even lead to regeneration failure of Silver fir (Senn and Suter, 2003). In BITE, we assumed roe deer to populate the entire landscape with a constant density of 14 individuals per 100 ha (Senn and Suter, 2003). The consumption was derived by combining daily diet preferences and consumption rates reported from different environments (Drozd and Osiecki, 1973; Tixier and Duncan, 1996). The

simulated impact was a loss of the leader shoot (and thus a loss of current year height growth) for saplings with a height of <1.3 m.

*Hymenoscyphus fraxineus* is the causal agent of ash dieback, a non-native disease that has affected Europe's forests over the past three decades (Kowalski and Holdenrieder, 2009; McKinney et al., 2014), and is currently threatening ash (primarily *Fraxinus excelsior* L.) populations all over the continent (Pautasso et al., 2013). Environmental factors such as soil moisture and temperature as well as stand variables like stand age and density have been linked to the epidemiology of the fungus (Skovsgaard et al., 2017). In BITE, its dispersal was simulated with an inverse power law dispersal kernel (Grosdidier et al., 2018). As recent results show a decrease of the disease with decreasing host density (Bakys et al., 2013), we assumed that only cells with a host tree density of  $\geq 100$  stems  $\text{ha}^{-1}$  over more than 3 years were susceptible to ash dieback. As we could not gather enough information to build a reliable agent population dynamics module we omitted this aspect in simulations. We assumed that if the pathogen is present, it causes heavy defoliation (50–100% of foliage mass removed) for a maximum of 30% of the host trees of a cell (Timmermann et al., 2017). In addition, we assumed that 1% of the trees are resistant to the disease (Kjaer et al., 2012; Wohlmuth et al., 2018).

Asian long-horned beetle (ALB) is an insect species native to China and Korea, attacking the stems of multiple deciduous tree species. Its larvae consume the wood, which can eventually lead to tree mortality (Haack et al., 1997; Hérard et al., 2006). Global trade has resulted in the introduction of ALB to many areas outside its native range (Eyre and Haack, 2017), as the species effectively disperses in wood packaging material. ALB is a moderate disperser, and we here used a general leptokurtic dispersal kernel (Shatz et al., 2016). We assumed that to colonize a cell, the presence of a host with dbh>7.5 cm was needed (Dodds and Orwig, 2011). Even though the life cycle of the agent is generally well-known (Haack et al., 2009), we didn't find enough reliable quantitative information to parameterize the detailed agent population dynamics module of BITE. There are several different estimates of the potential impact of ALB, with reported mortality rates varying from ~3 to 30% (Faccoli and Gatto, 2016; Nowak et al., 2001). Impact data often stem from poplar plantations in the native habitat of the beetle in China (see Hu et al., 2009 and the references therein). However, quick eradication measures at infested sites interfere with the quantification of the true impacts ALB could cause on host populations. Dodds and Orwig (2011) studied the only large-scale infestation outside the native range in a non-urban environment in Massachusetts, USA and found that tree mortality and growth losses were extremely rare even more than 5 years after an infestation. We here assumed a linearly increasing mortality rate from 0 to 2% over a 10-year period to simulate the protracted mortality

caused by ALB.

Mastodons were large mammals distantly related to elephants, inhabiting the forests of North America and Eurasia until their extinction ~10–11,000 years ago. Compared to mammoths (*Mammuthus* sp.), which were grazers, mastodons were forest-dwelling browsers with *Picea* spp. forming a significant part of their diet (Birks et al., 2018; Teale and Miller, 2012). Their estimated body mass was ~8000 kg, mastodons were thus slightly heavier than modern elephants although their shoulder height was roughly comparable (Larramendi, 2015). We assumed mastodons to inhabit the whole test landscape with an initial density of 1.5 individuals per 100 ha, corresponding to the estimated densities of Pleistocene megaherbivores (120 kg ha<sup>-1</sup>) (Bakker et al., 2016). Mastodon population growth rate was assumed to be 1% yr<sup>-1</sup> using a logistic growth model. We assumed that mastodons were able to browse trees up to 4 m height, with a preference for trees between 0 and 2 m (Guy, 1976) and the occasional uprooting of trees, similar to modern elephants (Scheiter and Higgins, 2012; Shannon et al., 2008). The diet was assumed to consist of 20% Norway spruce (*Picea abies* (L.) Karst.).

### 2.3.2. Simulation design

To demonstrate the model's utility and evaluate the patterns emerging from simulations we simulated the dynamics of each agent separately in a generic landscape with tree species and climate typical for the temperate biome. We aimed for maximum comparability between agents of different traits, and thus eliminated potential confounding factors such as variability in climate and host tree distribution in our simulations. Specifically, we simulated a rectangular 5 × 5 km forest area solely populated by the main host species of each agent (Table 1). Initial stand age was uniformly distributed on the landscape between 0 and 100 years. Stands were created as Voronoi polygons with an average stand size of 1 ha. Tree dimensions (e.g. tree diameter, tree height, stand density) were derived from yield tables (Marschall, 1975). The environment (i.e. soil, climate) was assumed to be uniform in space, but climate varied over time around a stationary mean temperature of 8.6 °C and annual precipitation of 810 mm. The climate data were derived from a typical temperate forest landscape in Central Europe (see Honkaniemi et al., 2020) by taking the landscape mean and variation of a time series from 1981 to 2010. In the simulations including management (see below) stands were clearcut at a stand age of 100 years, and replanted with the host tree species. Natural regeneration as well as abiotic disturbances (e.g., wind, wildfire) were omitted.

### 2.3.3. Analyses

We analyzed model behavior for the six agents in a pattern-oriented framework (Grimm et al., 2005; Grimm and Railsback, 2012). Specifically, we focused on three patterns produced by BITE, (1) impact on host (mortality or browsing rate), (2) spatial patterns of agent spread from a single point of introduction, and (3) temporal patterns of agent dynamics over time. Impact rates (pattern 1) were simulated assuming that the agent is present in each cell of the landscape and thus controls for differences in colonization times (analyzed separately in pattern 2). The analyzed impact solely relates to the direct effects of the focal agent and excludes other causes of mortality, such as density-dependent mortality or age-related mortality. Simulated impact rates were compared against independent data sources not used for model parameterization (Table 2, Supplementary material S3) except for Asian long-horned beetle and mastodon, where no field data were available. The simulations were run for 50 years. Simulations of pattern 1 excluded forest management to avoid confounding effects between simulated management and disturbance. In addition to mean impact rates, we also analyzed structural effects of tree mortality and compared the diameter distribution of trees killed by a focal agent to background mortality from competition and age-related causes. We also carried out a sensitivity analysis for simulating biotic disturbance impact on varying tree sizes (see Supplementary Material S2).

Spatial patterns of biotic disturbance (pattern 2) were simulated in

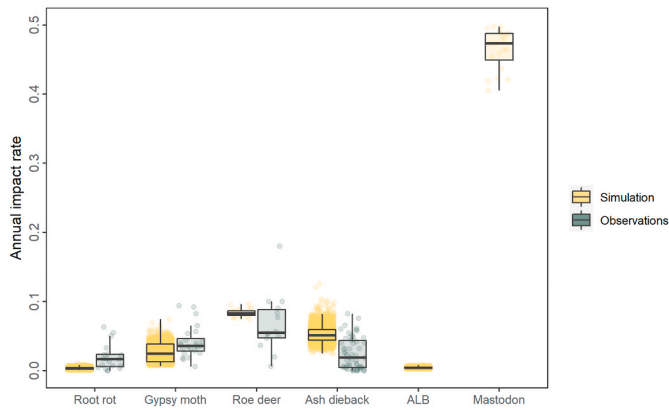
**Table 2**

Expected patterns of biotic disturbance activity.

Agent	Impact (pattern 1)	Spatial (pattern 2)	Temporal (pattern 3)
Root rot	Mean annual mortality rate 1.9% (Gibbs et al., 2002; Rönnberg et al., 2006)	Small and distributed area colonized (Gonthier et al., 2012; Piri and Korhonen, 2007)	Large amount of host biomass colonized by the agent. Increase in colonized host biomass is slow, but hosts remain colonized for long period (Garbelotto and Gonthier, 2013). Outbreaks every 8–12 years (Johnston et al., 2005; Liebhold and Kamata, 2000) with tree mortality peaking 2–5 years after agent population peak (Mcmanus and Csóka, 2007)
Gypsy moth	Mean annual mortality rate 4.1% (Gottschalk et al., 1998)	Moderate dispersal and cyclic outbreaks result in patchy colonization and impact (Foster et al., 2013; Townsend et al., 2012).	Time-invariant impact at stable populations and constant forest structure. NA
Roe deer	Browsing rate 6.8% (Senn and Suter, 2003).	NA	NA
Ash dieback	Mean mortality rate 2.5% (Coker et al., 2019)	Long distance dispersal, low mortality via foliage loss results patchy mortality patterns. Moderate to long distance spread; self-limiting due to high impact on host tree population.	Population biomass equal to past megafauna densities decrease the host biomass, which in turn result in agent population decline over time (Bakker et al., 2016)
Asian long-horned beetle	NA	NA	NA
Mastodon	NA	NA	NA

the same agent-specific landscapes, but agents were introduced in a single cell in the center of the landscape, and their spread simulated over a 50-year period. The two browsing mammals (roe deer and mastodon) were excluded from this analysis as they were assumed to be present throughout the landscape. Analysis variables were the infestation pattern emerging from the landscape as well as the impact on the host species. No field data were available for direct comparison, but the emerging infestation patterns were assessed qualitatively against expected patterns (see Table 2). Forest management was simulated in all model runs for testing pattern 2 in order to maintain a comparable landscape state in areas not yet infested by the agent.

Agent dynamics over time (pattern 3) was studied over 50 years for the four agents for which population dynamics was explicitly simulated (i.e. root rot, gypsy moth, roe deer, and mastodon). Root rot and gypsy moth were introduced in the center cell of the landscape as described for pattern 2 above. Roe deer and mastodon were assumed to be present in each simulated cell of the landscape. The output was normalized to the number of cells colonized in each time step to facilitate comparison across agents. The development of agent populations and their impact on host tree vegetation were compared against independent observations from the literature (Table 2).

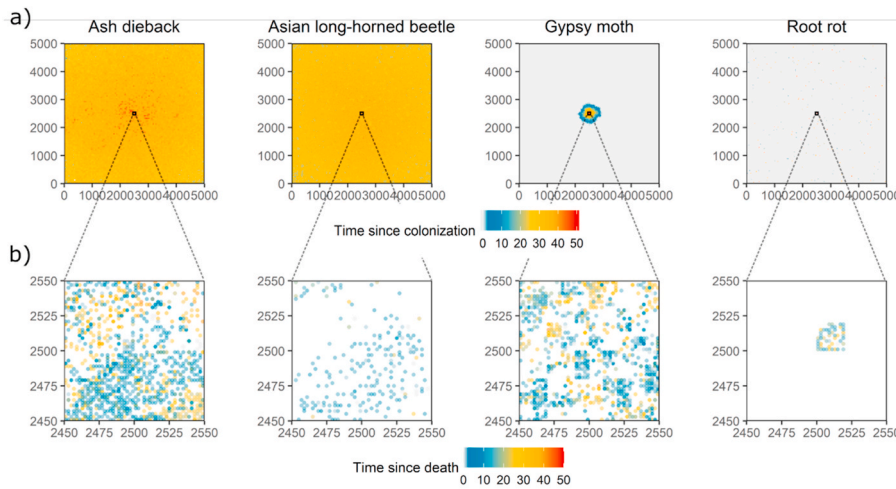


**Fig. 2.** Annual impact rates for the biotic disturbance agents. For root rot, gypsy moth, ash dieback and Asian long-horned beetle, tree mortality rate is reported as the fraction of stems that died per year. For roe deer and mastodon, browsing rate is reported as the fraction of saplings browsed per year. Each dot for observations is a single data point from the literature (see Supplementary material S3). Each dot for simulations is a mean annual impact rate over the 50-year simulation period for each simulated cell in the landscape. Mortality rates only refer to mortality from the respective agent and do not include background mortality (e.g. from competition or age-related causes).

background mortality was higher than mortality caused by root rot and ALB in our simulations (agent induced mortality 0.3% and 0.5%, respectively, compared to background mortality of 1.8% and 1.5%, respectively). The diameter distributions of trees affected by biotic agents reflected the different size preferences of agents well (see Supplementary material S2).

**3.2. Spatial patterns of agent spread (pattern 2)**

Spatial patterns of spread varied widely between the simulated agents. After 50 simulation years, ash dieback was active in 100% of the landscape, ALB in 25.6%, gypsy moth in 1.7% and Heterobasidion root rot in 0.3%. In line with expectations, ash dieback spread throughout the landscape (Table 2, Fig. 3a) and caused mortality over the entire simulation period, but affected trees in a scattered pattern (Fig. 3b). Asian long-horned beetle behaved similarly to Ash dieback by spreading throughout the landscape (100%). The relatively low mortality rate kept the infestation going throughout the entire simulation period as host trees remained available for infestation (see Supplementary material S2 for a management-related eradication experiment). The impact patterns of ALB were generally patchier, with synchronous mortality occurring in larger areas (Fig. 3b). Gypsy moth only dispersed to a small area (1.7%) of the landscape over 50 years of simulation, and cells were frequently



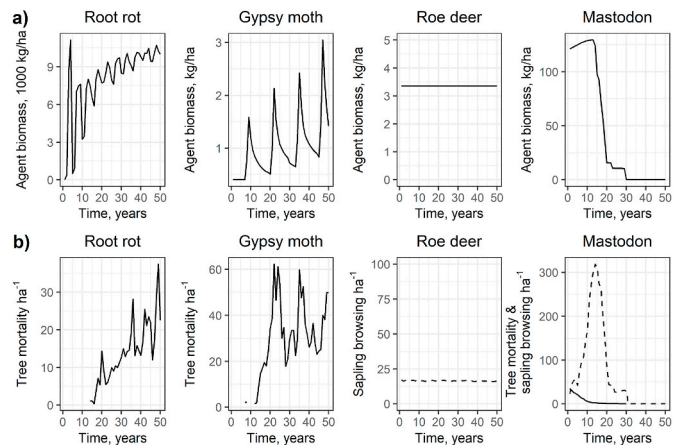
**Fig. 3.** Spatial patterns of dispersal 50 years after the initial introduction of the agent in the center of the landscape. a) Cells colonized since the initial introduction and time since each cell was colonized for the first time. b) Example of 1 ha showing the individual trees killed by the agent and their time since death.

**3. Results**

**3.1. Impact (pattern 1)**

Simulated annual mortality rates corresponded well with independent observations for well-described agents (i.e. root rot and gypsy moth) (Fig. 2), although BITE on average underestimated the impact of these agents slightly. Browsing rates for roe deer were also well in line with expectations, though slightly higher than those reported in the literature. BITE simulations overestimated the annual mortality from ash dieback, although the variation on the landscape was high. Asian long-horned beetle and mastodon presented the extreme ends of the range in terms of impact on vegetation, which was consistent with the model-internal logic and parameterization. Field data for evaluation were, unfortunately, not available for these two species.

Tree mortality caused by gypsy moth and ash dieback were higher than background mortality (i.e. mortality caused by other reasons than the agent, such as competition or age-related causes), and amounted to 2.5% and 5.3% of mortality per year, respectively (compared to 0.6% and 1.3% of background mortality, respectively). Conversely,



**Fig. 4.** Temporal development of a) agent biomass and b) impact on host (solid line = number of dead trees, dashed line = number of saplings browsed) caused by the agent in the landscape.

infested only once (Fig. 3a). We note that human-aided long-distance dispersal of gypsy moth was not considered here. Due to the periodicity of outbreaks, gypsy moth impact occurred synchronous in small patches (Fig. 3b). Heterobasidion was a poor disperser, being only able to colonize 0.3% of the landscape in our simulation. Its pronounced long-distance dispersal in combination with the establishment requirement of fresh stumps resulted in an almost random pattern of infested cells on the landscape (Fig. 3a). The resulting impact pattern of small mortality centers in stands corresponds well with expectations from the literature (Table 2, Fig. 3b).

### 3.3. Temporal patterns of agent dynamics (pattern 3)

The four agents for which population dynamics was explicitly simulated showed widely varying development over time. The relatively fast growth rate of Heterobasidion root rot together with a high carrying capacity (as determined by the root biomass of both fresh stumps and live trees) enabled the agent biomass to increase to high levels (Fig. 4a). Because root rot is introduced via stumps and only after a considerable lag colonizes live trees, tree mortality lagged behind infestation and increased only towards the end of the simulation period (Fig. 4b). Gypsy moth outbreaks followed the periodicity as specified in the species' parameters, with population biomass fluctuating strongly over time (Fig. 4a). The overall biomass affected increased over time with the expanding colonized area. Host mortality due to defoliation reached its peak 1–3 years after the gypsy moth population peak, which is well in line with independent observations (Table 2, Fig. 4b). Roe deer consumed its host at a steady rate over time. In contrast, mastodon populations consumed high levels of host biomass in a short period of time, with negative feedbacks on habitat suitability and agent population levels. This indicates that they would have had to either shift their diet to other plants or migrate to another landscape, also suggesting that megaherbivore levels as in the Pleistocene could not be sustained in modern landscapes.

## 4. Discussion and conclusions

Biotic disturbances are an integral part of forest ecosystems and are particularly sensitive to climate change (Seidl et al., 2017; Turner, 2010). In the past, the impacts of biotic disturbances have been modeled using predominately statistical approaches, correlating disturbance presence/abundance and impact (Seidl et al., 2011). However, the no-analog conditions expected for the future (Steffen et al., 2018) require alternative approaches, as it is unlikely that future ecosystem dynamics can be faithfully predicted from the past (Gustafson, 2013). Data-driven theoretical models, e.g. based on approaches developed in epidemiology, are a possible alternative to traditional empirical models (e.g., Jeger et al., 2007; Wildemeersch et al., 2019). Also novel machine learning approaches such as deep neural networks (e.g. Rammer and Seidl, 2019; Reichstein et al., 2019) are better able to deal with extrapolation than traditional correlative models. Yet, both of these approaches thrive on the availability of large amounts of data, and are thus of limited use in situations where information is scarce (as is the case e.g., for the invasion of pests and pathogens into new areas). Process-based models, i.e., approaches focusing on the underlying mechanisms and modeling the system based on first principles of ecology, are important tools in this regard. They are also better suited to address unprecedented future changes (e.g. climate change, novel agent interactions). In developing BITE as a general framework that should be applicable to both established and novel biotic disturbance agents, we have chosen a modular, process-oriented framework. We here demonstrate the generality of our framework by simulating six widely different biotic disturbance agents, ranging from fungi to large mammals. A key question with all process-based models is whether the relevant processes have been addressed, and whether their interactions have been faithfully represented in the model. Pattern-oriented modeling (Grimm et al.,

2005; Grimm and Railsback, 2012) offers a consistent pathway for testing whether key patterns of the system are emerging from the simulation. Here we applied a pattern-oriented approach, assessing the behavior of the newly developed model, and demonstrating that the model can handle a wide range of different types of agents. We document that realistic patterns of disturbance impact as well as spatio-temporal disturbance dynamics are emerging from simulations with BITE.

Biotic disturbances remain incompletely represented in existing dynamic vegetation models. In fact, most vegetation modeling approaches still ignore biotic disturbances completely (Huang et al., 2020). If biotic disturbances are considered in the simulation of vegetation dynamics, models usually focus on a small number of well-known agents, such as *Ips typographus* in Europe (e.g. Fahse and Heurich, 2011; Honkaniemi et al., 2018; Seidl and Rammer, 2017) and *Dendroctonus ponderosae* in North America (e.g. Bone and Altaweel, 2014; Powell and Bentz, 2014). This practice is problematic because it can misrepresent the vulnerability of ecosystems to biotic disturbances, overstating the susceptibility of host species of these prominent disturbance agents relative to other tree species. This issue is particularly relevant when models are used to develop management strategies for reducing disturbance risk (e.g. Dobor et al., 2020; Seidl et al., 2018a). Consequently, an important goal of disturbance modeling has to be a broad and comprehensive representation of (biotic) disturbance agents and their interactions, and the approach presented here is a step stone towards this goal (see Lustig et al., 2017; Sturtevant et al., 2004; Tonini et al., 2018 for other broadly applicable approaches). In particular, design goals of BITE were to provide useful approximations even under data scarcity, and broad applicability for different types of agents, e.g., by using biomass as a common currency for both agents and vegetation.

Simulations with process-based models are afflicted with several sources of uncertainty (O'Neill and Rust, 1979). One important aspect is process uncertainty, i.e. whether all relevant processes have been adequately represented in the model. For example, in the case of Ash dieback and Asian long-horned beetle, we did not have enough data to allow the in-depth simulation of population dynamics. Instead, we made phenomenological assumptions of agent development and impact. Nonetheless we could show that our parsimonious approach was well able to reproduce key patterns of biotic disturbance regimes, even when individual processes had to be bypassed in the simulation due to data gaps (see Table 1). Another important dimension of uncertainty is parameter uncertainty. Parameters in process-based models are frequently derived from the literature, and often hinge on a small number of studies. Furthermore, non-native species might behave different in their invasive range compared to their native range (e.g. Carnegie and Pegg, 2018), and information on their ecology collected in their native range might not necessarily be applicable in their invasive range. Future applications of BITE should thus carefully scrutinize parameters, and test the model against observations relevant for future study systems. While we focused on disturbance impacts and spatio-temporal patterns in our evaluation, future work should also scrutinize the climate sensitivity of the simulated agents (Seidl et al., 2020). More broadly, more empirical and experimental research on biotic disturbance agents is needed to improve simulated forest disturbance regimes.

BITE was deliberately designed to also work in conditions where information on biotic disturbance agents is limited (as is often the case in the context of invasive alien pests and pathogens). As a strong test for agents with limited data availability we included an extinct species, the mastodon, in the set of agents parameterized and evaluated here. To our surprise it was easier to parameterize key processes of disturbance dynamics from the literature for the mastodon compared to species of high current relevance, such as the Asian long-horned beetle. The fact that our quantitative knowledge of charismatic species long extinct seems to be higher than that of species of high current management relevance (e.g. dietary requirements of mastodons vs. suitable host species for Asian



long-horned beetle) underlines the need for basic research on a broad range of biotic disturbance agents. Nonetheless, including species with potentially high impact on forest ecosystems in models even when data is scarce is important to avoid the above-mentioned biases in simulation studies. And while simulating mastodon disturbance in a temperate forest ecosystem may at first sound like a highly hypothetical exercise, the quantitative analysis of interactions between vegetation and past megaherbivores can shed light onto important questions of long-term ecosystem development (Gill et al., 2009; Malhi et al., 2016), and provide insights into how possible reintroductions of megaherbivores could shape forest ecosystems. Simulation models have, for instance, been used to show how abiotic disturbances have influenced critical transitions of ecosystems in the Holocene (e.g. Henne et al., 2015), which is something that could also be investigated for biotic disturbance agents in the future.

Here, we have demonstrated the utility of our new modeling framework for six widely different biotic disturbance agents. And while we here have focused on agents individually a key strength of a general modeling framework like BITE is that interactions between agents can be simulated. Interactions between disturbance agents are a key element of forest disturbance regimes (Buma, 2015; Honkaniemi et al., 2018; Seidl and Rammer, 2017). An attack by *Hymenoscyphus fraxineus*, for instance, frequently results in infestations by *Armillaria* sp., which decreases the stability of a tree and greatly increases its mortality risk (Chandelier et al., 2016; Enderle et al., 2013). Similarly, Heterobasidion root rot decreases the rooting strength of trees and makes them considerably more susceptible to windthrow (Honkaniemi et al., 2017a). Because such disturbance interactions are often amplifying, they are a key element in the high sensitivity of disturbance regimes to climate change (Seidl et al., 2017; Seidl and Rammer, 2017). Disturbance interactions should thus be explored in depth in the future, in order to more comprehensively simulate past and future forest disturbance regimes.

To simulate forest disturbance regimes dynamically models of disturbance agents need to be coupled with models of vegetation dynamics (Huang et al., 2020; Seidl et al., 2011). Here, BITE was coupled with the individual-based forest landscape and disturbance model iLand to demonstrate the patterns emerging from an integrated simulation of disturbance agents and forest development. However, BITE was designed with clear interfaces and a modular structure, and thus could also be easily adopted to other vegetation modeling frameworks. This is particularly relevant as the simulation of disturbances has been identified as an important weakness of current dynamic global vegetation models (Fisher et al., 2018; Huang et al., 2020; McDowell et al., 2020). The approach presented here could provide important building blocks for an improved consideration of biotic disturbances in models used to inform policy makers around the globe. Changes in disturbance regimes and novel emerging biotic disturbance agents will have unprecedented impacts on forests, and challenge our knowledge of how to address disturbances in management (Ayres and Lombardero, 2018; Hobbs et al., 2006). Improved simulation approaches hold great potential to help address the challenge of changing forest disturbance regimes.

## 5. Software and data availability section

Software name BITE – Biotic disTurbance Engine.  
 Developer Werner Rammer.  
 Year first official release 2021.  
 Hardware requirements PC.  
 System requirements Windows, Linux.  
 Program language C++, JavaScript.  
 Program size 2.8 MB.  
 Availability <http://iland.boku.ac.at/startpage>.  
 License GPL-3.0.  
 Form of repository JavaScript files.  
 Size of archive 43.6 KB.

Access form Figshare ([figshare.com/articles/software/Agent\\_JavaScript\\_files\\_for\\_BITE\\_model/13603439](https://figshare.com/articles/software/Agent_JavaScript_files_for_BITE_model/13603439))

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envsoft.2021.104977>.

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