Simulating Bark Beetle Outbreak Dynamics and their Influence on Carbon Balance Estimates with ORCHIDEE r7791

Guillaume Marie[1]*, Jina Jeong[2]*, Hervé Jactel[3], Gunnar Petter[4], Maxime Cailleret[5], Matthew J. McGrath[1], Vladislav Bastrikov[6], Josefine Ghattas[7], Bertrand Guenet[8], Anne Sofie Lansø[9], Kim Naudts[11], Aude Valade[10], Chao Yue[12], Sebastiaan Luyssaert[2]

[1] Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ UP Saclay, 91191 Orme des Merisiers, Gif-sur-Yvette, France

[2] Faculty of Science, A-LIFE, Vrije Universiteit Amsterdam, 1081 BT Amsterdam, the Netherlands

[3] INRAE, University of Bordeaux, umr Biogeco, 33612 Cestas, France

[4] ETH Zürich, Department of Environmental Systems Science, Forest Ecology, 8092 Zürich, Switzerland

[5] INRAE, Aix-Marseille Univ, UMR RECOVER, 13182 Aix-en-Provence, France

[6] Science Partner, France

[7] Institut Pierre-Simon Laplace – Sciences du climat (IPSL), 75105 Jussieu, France

[8] Laboratoire de Géologie, Ecole Normale Supérieure, CNRS, PSL Research University, IPSL, 75005 Paris, France

[9] Department of Environmental Science, Aarhus Universitet, Frederiksborgvej 399, 4000 Roskilde, Denmark

[10] Eco & Sols, Univ Montpellier, CIRAD, INRAE, 34060 Institut Agro, IRD, Montpellier, France

[11] Department of Earth Sciences, Vrije Universiteit Amsterdam, 1081 HV Amsterdam, the Netherlands

[12] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A & F University, Yangling, Shaanxi, China

* These authors contributed equally to this study

Corresponding author: Guillaume Marie, guillaume.marie@lsce.ipsl.fr, Jina Jeong, j.jeong@vu.nl, Sebastiaan Luyssaert, s.luyssaert@vu.nl

Abstract : New (a)biotic conditions, resulting from climate change, are expected to change disturbance dynamics, e.g., wind throw, forest fires, droughts, and insect outbreaks, and their interactions. Unprecedented natural disturbance dynamics might alter the capability of forest ecosystems to buffer atmospheric CO_2 increases in the atmosphere, even leading to the risk that forests transform from sinks into sources of CO_2. This study aims to enhance the capability of the ORCHIDEE land surface model to study the impacts of climate change on bark beetle dynamics and subsequent effects on forest functioning. The bark beetle outbreak model is inspired by previous work from Temperli et al. 2013 for the LandClim landscape model. The new implementation of this model in ORCHIDEE r7791 accounts for the following differences between ORCHIDEE and LandClim: (1) the coarser spatial resolution

of ORCHIDEE, (2) the higher temporal resolution of ORCHIDEE, and (3) the pre-existing process representation of windthrow, drought, and forest structure in ORCHIDEE. Simulation experiments demonstrated the model's ability to simulate a wide range of observed post-disturbance forest dynamics. Through an array of simulation experiments across various climatic conditions and disturbance intensities, the enhanced model was rigorously tested for sensitivity. The model accurately mirrored a wide array of observed post-disturbance forest dynamics, including the capacity of forests to resist infestations and variable recovery periods ranging from 7 to 14 years. Notably, the study revealed that incorporating abrupt mortality events into the model, as opposed to a continuous mortality framework, offers profound insights into the short-term carbon sequestration potential of forests under disturbance regimes. This model enhancement underscores the critical need to include disturbance dynamics in land surface models to refine predictions of forest carbon dynamics in a changing climate.

1. Introduction

Future climate will likely bring new abiotic constraints through the co-occurrence of multiple connected hazards, e.g., "hotter droughts", which are droughts combined with heat waves (Allen et al., 2015; Zscheischler et al., 2018), but also new biotic conditions from interacting natural and anthropogenic disturbances, e.g., insect outbreaks following windthrow or forest fires (Seidl et al., 2017). Unprecedented natural disturbance dynamics might alter biogeochemical cycles specifically the capability of forest ecosystems to buffer the CO_2 increase in the atmosphere (Hicke et al., 2012; Seidl et al., 2014) and the risk that forests are transformed from sinks into sources of CO_2 (Kurz et al., 2008a). The magnitude of such alteration, however, remains uncertain principally due to the lack of impact studies that include disturbance regime shifts at global scale (Seidl et al., 2011).

Land surface models are used to study the relationships between climate change and the biogeochemical cycles of carbon, water, and nitrogen (Cox et al., 2000; Ciais et al., 2005; Friedlingstein et al., 2006; Zaehle and Dalmonech, 2011; Luyssaert et al., 2018). Many of these models use background mortality to obtain an equilibrium in their biomass pools. This classic approach towards forest dynamics, which assumes steady-state conditions over long periods of time, may not be suitable for assessing the impacts of disturbances on shorter time scales under a fast changing climate. This could be considered a shortcoming in the land surface models because disturbances can have significant impacts on ecosystem services, such as water regulation, carbon sequestration, and biodiversity (Quillet et al., 2010). Mechanistic approaches that account for a variety of mortality causes, such as age, size, competition, climate, and disturbances, are now being considered and tested to simulate forest dynamics more accurately (Migliavacca et al., 2021). For example, the land surface model ORCHIDEE accounts for mortality from interspecific competition for light in addition to background mortality (Naudts et al., 2015). Implementing a more mechanistic view on mortality is thought to be essential for improving our understanding of the impacts of climate change on forest dynamics and the provision of ecosystem services.

Land surface models also face the challenge of better describing mortality particularly when it comes to ecosystem responses to “cascading disturbances”, where legacy effects from one disturbance affect the next (Zscheischler et al., 2018; Buma, 2015). Biotic disturbances, such as bark beetle outbreaks, strongly depend on previous disturbances as their infestation capabilities are higher when tree vitality is low, for example following drought or storm events (Seidl et al., 2018). This illustrates how interactions between biotic and abiotic disturbances can have substantial effects on ecosystem dynamics and must be accounted for in land surface models to improve our understanding of the impacts of climate change on forest dynamics (Temperli et al., 2013; Seidl et al., 2011). While progress has been made towards including abrupt mortality from individual disturbance types such as wildfire (Yue et al., 2014; Lasslop et al., 2014; Migliavacca et al., 2013), windthrow (Chen et al., 2018) and drought (Yao et al., 2022), the interaction of biotic and abiotic disturbances remains both a knowledge and modeling gap (Kautz et al., 2018).

Bark beetle infestations are increasingly recognized as disturbance events of regional to global importance (Kurz et al., 2008b; Bentz et al., 2010; Seidl et al., 2018). Notably, a bark beetle outbreak ravaged over 90% of Engelmann spruce trees across approximately 325,000 hectares in the Canadian and American Rocky Mountains between 2005 and 2017 (Andrus et al., 2020). In Europe, the spruce bark beetle, *Ips typographus*, has been involved in up to 8% of total tree mortality due to natural disturbances from 1850 to 2000 (Hlásny et al., 2021a). A recent increase in beetle activity, particularly following mild winters (Kurz et al., 2008b; Andrus et al., 2020), windthrow (Mezei et al., 2017), and droughts (Nardi et al., 2023) have been well-documented (Hlásny et al., 2021a; Pasztor et al., 2014), underscoring the need to integrate bark beetle dynamics into land surface modeling.

Past studies used a variety of approaches to model the impacts of bark beetles on forests. While some model treated bark beetle outbreaks as background mortality (Naudts et al., 2016; Luyssaert et al., 2018), others dynamically modeled these outbreaks within ecosystems (Temperli et al., 2013; Seidl and Rammer, 2016; Jönsson et al., 2012). Studies with prescribed beetle outbreaks tend to focus on the direct effects of the outbreak on forest conditions and carbon fluxes, but are likely to overlook more complex feedback processes, such as interactions with other disturbances and longer-term impacts. Conversely, dynamic modeling of beetle outbreaks, provides a more comprehensive view by incorporating the lifecycle of bark beetles, tree defense mechanisms, and ensuing alterations in forest composition and functionality.

Simulation experiments for *Ips typographus* outbreaks using the LPJ-GUESS vegetation model highlighted regional variations in outbreak frequencies, pinpointing climate change as a key exacerbating factor (Jönsson et al., 2012). Simulation experiments with the iLand landscape model suggested that almost 65% of the bark beetle outbreaks are aggravated by other environmental drivers (Seidl and Rammer, 2016). A 4°C temperature increase could result in a 265% increase in disturbed areas and a 1800% growth in average patch size (Siedl and Rammer 2016). Disturbance interactions were ten times more sensitive to temperature changes, boosting the disturbance regime's climate sensitivity. The results of these studies justify the inclusion of interacting disturbances in land surface models, such as ORCHIDEE, which are used in future climate predictions and impact studies (Boucher et al., 2020).

The objectives of this study are: (1) to develop and implement a spatially implicit bark beetle (*Ips Typographus*) outbreak model in the land surface model ORCHIDEE inspired by the work from Temperli et al. (2013), and (2) use simulation experiments to characterize the behavior of this newly added model functionality.

2. Model description

2.1. The land surface model ORCHIDEE

ORCHIDEE is the land surface model of the IPSL (Institut Pierre Simon Laplace) Earth system model (Krinner et al., 2005; Boucher et al., 2020). ORCHIDEE can, however, also be run off-line as a stand-alone land surface model forced by temperature, humidity, pressure, precipitation, and wind conditions. Unlike the coupled setup, which needs to run on the global scale, the stand-alone configuration can cover any area ranging from a single grid point to the global domain.

ORCHIDEE does not enforce any particular spatial resolution. The spatial resolution is an implicit user setting that is determined by the resolution of the climate forcing (or the resolution of the atmospheric model in a coupled configuration). ORCHIDEE can run on any temporal resolution. This apparent flexibility is somewhat restricted as processes are formalized at given time steps: half-hourly (e.g., photosynthesis and energy budget), daily (i.e., net primary production), and annual (i.e. vegetation demographic processes). With the current model architecture meaningful simulations should have a temporal resolution of one minute to one hour for the calculation of energy balance, water balance, and photosynthesis.

ORCHIDEE utilizes meta-classes to describe different types of vegetation. The model includes 13 meta-classes by default, including one class for bare soil, eight classes for various combinations of leaf-type and climate zones of forests, two classes for grasslands, and two classes for croplands. Each meta-class can be further subdivided into an unlimited number of plant functional types (PFTs). The current default setting of ORCHIDEE distinguishes 15 PFTs where the C3 grasslands have now a separate PFT in the boreal, temperate and tropical zone.

At the beginning of a simulation, each forest PFT in ORCHIDEE contains a monospecific forest stand that is defined by a user-defined but fixed number of diameter classes (three by default). Throughout the simulation, the boundaries of the diameter classes are adjusted to accommodate changes in the stand structure, while the number of classes remains constant. Flexible class boundaries provide a computationally efficient approach to simulate different forest structures. For instance, an even-aged forest is simulated by using a small diameter range between the smallest and largest trees, resulting in all trees belonging to the same stratum. Conversely, an uneven-aged forest is simulated by applying a wide range between diameter classes, such that different classes represent different strata.

The model uses allometric relationships to link tree height and crown diameter to stem diameter. Individual tree canopies are not explicitly represented, instead a canopy structure model based on simple geometric forms (Haverd

et al. 2012) has been included in ORCHIDEE (Naudts et al., 2015). Diameter classes represent trees with different mean diameter and height, which informs the user about the social position of trees within the canopy. Intra-stand competition is based on the basal area of individual trees, which accounts for the fact that trees with a higher basal area occupy dominant positions in the canopy and are therefore more likely to intercept light and thus contribute more to stand-level photosynthesis and biomass growth compared to suppressed trees (Deleuze et al., 2004). If recruitment occurs, diameter classes evolve into cohorts. However, in the absence of recruitment, all diameter classes contain trees of the same age.

Individual tree mortality from self-thinning, wind storms, and forest management is explicitly simulated. Other sources of mortality are implicitly accounted for through a so-called constant background mortality rate. Furthermore, age classes (four by default) can be used after land cover change, forest management, and disturbance events to explicitly simulate the regrowth of the forest. Following a land cover change, biomass and soil carbon pools (but not soil water columns) are either merged or split to represent the various outcomes of a land cover change. The ability of ORCHIDEE to simulate dynamic canopy structures (Naudts et al., 2015; Ryder et al., 2016; Chen et al., 2016), a feature essential to simulate both the biogeochemical and biophysical effects of natural and anthropogenic disturbances, is exploited in other parts of the model, i.e., precipitation interception, transpiration, energy budget calculations, the radiation scheme, and the calculation of the absorbed light for photosynthesis.

Since revision 7791, mortality from bark beetle outbreaks is now explicitly accounted for and thus conceptually excluded from the so-called environmental background mortality. Subsequently, changes in canopy structure resulting from growth, forest management, land cover changes, wind storms, and bark beetle outbreaks are accounted for in the calculations of the carbon, water, and energy exchanges between the land surface. ORCHIDEE's functionality that is not of direct relevance for this study, e.g., energy budget calculations, soil hydrology, snow phenology, albedo, roughness, photosynthesis, respiration, phenology, carbon and nitrogen allocation, land cover changes, product use, and the nitrogen cycle are detailed in (Krinner et al., 2005; Zaehle and Friend, 2010; Naudts et al., 2015; Vuichard et al., 2019).

2.2. Origin of the bark beetle module: the LANDCLIM legacy

Although mortality from windthrow (Yi-Ying et al., 2018) and forest management (Naudts et al., 2016; Luyssaert et al., 2018) were already accounted for in ORCHIDEE prior to r7791, insect outbreaks and their interaction with other disturbances were not. The LandClim model (Schumacher, 2004) and more specifically the bark beetle module developed by Temperli et al. (2013) has been used as basis to develop the bark beetle module in ORCHIDEE r7791.

LandClim is a spatially explicit stochastic landscape model in which forest dynamics are simulated at a yearly time step for 10–100 km^2 landscapes consisting of 25 m× 25 m patches. Within a patch recruitment, growth, mortality and competition among age cohorts of different tree species are simulated with a gap model (Bugmann, 1996) in response to monthly mean temperature, climatic drought, and light availability. LandClim, for which a detailed

description can be found in (Schumacher, 2004; Temperli et al., 2013), includes the functionality to simulate the decadal dynamics and consequences of bark beetle outbreaks at the landscape-scale (Temperli et al., 2013). In the LandClim approach, the extent, occurrence and severity of beetle-induced tree mortality are driven by the landscape susceptibility, beetle pressure, and infested tree biomass. While the LandClim beetle module was designed and structured to be generally applicable for northern hemisphere climate-sensitive bark beetle-host systems, it was originally parameterized to represent disturbances by the European spruce bark beetle (*Ips typographus* Linnaeus) in Norway spruce (*Picea abies* Karst.; Temperli et al. 2013).

As LandClim and ORCHIDEE are developed for different purposes, their temporal and spatial scales differ. These differences in model resolution justify developing a new model while still following the principles embedded in the LandClim approach. LandClim assesses bark beetle damage at 25 m x 25 m patches and to do so it uses information from other nearby patches as well as landscape characteristics such as slope, aspect and altitude. The susceptibility of a landscape to bark beetle infestations is calculated using multiple factors such as drought-induced tree resistance, age of the oldest spruce cohort, proportion of spruce in the patch's basal area, and spruce biomass damaged by windthrow. These factors, presented as sigmoidal relationships, ranging from 0 to 1 (denoting none to maximum susceptibility respectively) are combined in a susceptibility index for each Norway spruce cohort in a patch. Bark beetle pressure is quantified as the potential number of beetles that can infest a patch, and its calculation considers, among others, previous beetle activity, maximum possible spruce biomass that beetles could kill, and temperature-dependent bark beetle phenology. Finally, the susceptibility index and beetle pressure are used to estimate the total infested tree biomass and total biomass killed by bark beetles for each cohort within a patch.

In ORCHIDEE, however, the simulation unit is about six orders of magnitude larger, i.e. 25 km x 25 km. Hence, a single pixel in ORCHIDEE exceeds the size of an entire landscape in LandClim. Where landscape characteristics in LandClim can be represented by a statistical distribution, the same characteristics in ORCHIDEE are summarized in a single value. These differences between LandClim and ORCHIDEE imply that the original bark beetle module cannot be implemented in ORCHIDEE without deep adjustments. We develop a pixel-level model that does not require spatial information and statistical distributions of landscape characteristics.

In the newly developed module of ORCHIDEE, the foundational concept is retained from LANDCLIM, yet the variables influencing susceptibility calculations have largely been modified, with the exception of the phenology model, which continues to follow the framework established by Temperli et al. in 2013. Given the extensive and significant alterations, a direct comparison between ORCHIDEE and LANDCLIM may no longer be pertinent. However, we have developed a flowchart (Fig. 2) to provide an overarching perspective of our advancements, facilitating an understanding of how it diverges from the initial methodology.

2.3. Bark beetle outbreak development stages

Bark beetle outbreak development stages are useful to understand the dynamics of an outbreak (Fig. 1) and have been described in numerous studies (Wermelinger, 2004; Edburg et al., 2012; Hlásny et al., 2021a). Nonetheless, in ORCHIDEE r7791, we design a model framework which simulates the dynamic of bark beetle outbreak as a continuous process. Hence, endemic, epidemic, build-up and post-epidemic stages are not explicitly simulated and these stages were only introduced to structure the model description. If needed, these stages could be distinguished while post-processing the simulation results if (arbitrary) thresholds are set for specific variables such as $i_{beetles\ pressure}$, $i_{beetles\ mass\ attack}$, or $B_{beetles\ kill}$ (these variables are defined further below).

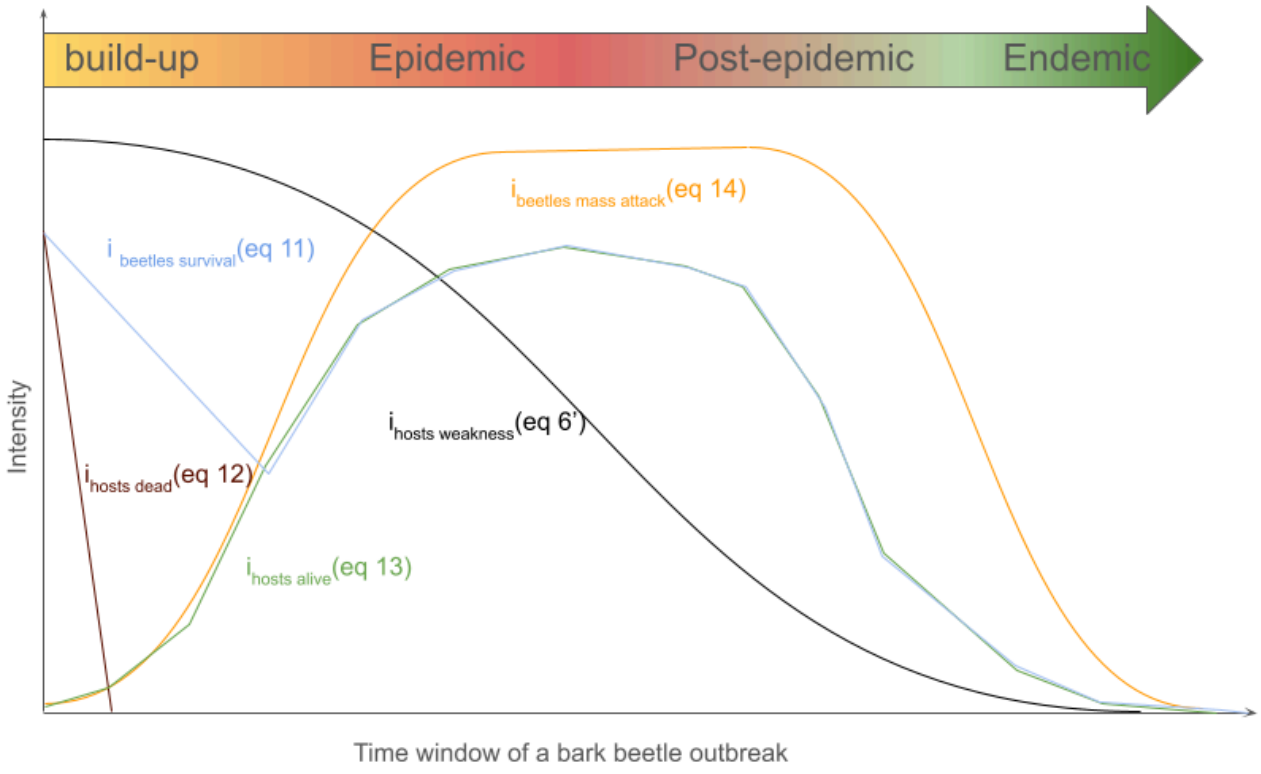


Figure 1 : This figure illustrates the dynamic interplay of factors during a bark beetle outbreak. It depicts the intensity and timeline of key variables such as beetle survival, beetles mass attack, and host weakness (section 2.4). The time window spans four outbreak development stages: build-up, epidemic, post-epidemic, and endemic. The curves represent key variables, showing the escalation of beetle attacks and subsequent decline in host population, which eventually leads to a stabilization of the system in the endemic phase.

2.4. Bark beetle damage in ORCHIDEE

Table 1: List of symbols

Symbol	Description	Units
α	Alpha parameter from the self thinning relationship	unitless
β	Beta parameter from the self thinning relationship	unitless
act_{limit}	B_{kill}/B_{total} at which $i_{beetles\ activity} = 0.5$	$gC.m^{-2}$
$B_{beetles\ kill}$	Biomass of spruce killed by bark beetle annually	$gC.m^{-2}$
$B_{windthrow\ kill}$	Biomass of spruce killed by windthrow event	$gC.m^{-2}$
$B_{beetles\ attacked}$	Biomass of spruce attacked by bark beetle annually	$gC.m^{-2}$
B_{total}	Total living spruce stand biomass	$gC.m^{-2}$
B_{wood}	Spruce woody biomass	$gC.m^{-2}$
BP_{limit}	$i_{beetle\ pressure}$ at which $i_{beetles\ mass\ attack} = 0.5$	unitless
D_{max}	Maximum Tree stand density	$tree.ha^{-1}$
$D_{age\ class}$	Spuce age classes stand density	$tree.ha^{-1}$
DD_{eff}	Cumulative effective Degrees Day	$°C.Day^{-1}$
DD_{ref}	Reference Degrees Day to fulfill one beetle generation	$°C.Day^{-1}$
$Dia_{quadratic}$	Mean quadratic diameter	meters
$DR_{beetles}$	$B_{beetles\ kill}/B_{total} * 100$	%
$DR_{windthrow}$	$B_{windtrow\ kill}/B_{total} * 100$	%
F_{spruce}	Spruce stand area fraction	unitless
$F_{age\ class}$	Spruce age classes area fraction	unitless
$F_{non\text{-}spruce}$	Non-spruce area fraction	unitless
G_{limit}	Beetles generation number at which $i_{beetle\ generation} = 0.5$	Generation
$i_{hosts\_competition}$	Spruce trees under competition pressure	unitless
$i_{hosts\_weakness}$	Weak to bark beetle attack spruce trees	unitless
$i_{hosts\_attractivity}$	Spruce attractiveness for bark beetles	unitless
i_{hosts_dead}	defenseless spruce trees uprooted or cutted	unitless
i_{hosts_alive}	Potential living spruce hosts for bark beetle	unitless
$i_{hosts\_defence}$	Spruce trees capacity to resist to a bark beetle attack	unitless
i_{hosts_share}	Spruces hidden by other species to bark beetle detection	unitless
$i_{hosts\_competition,\ age\_class}$	Weak to bark beetle attack spruce trees	unitless
$i_{hosts\_defence,\ age\ class}$	Spruce trees capacity to resist to a bark beetle attack	unitless
$i_{hosts\_health,\ age\_class}$	Spruce trees health condition	unitless
$i_{beetles\_pressure}$	Proxy of bark beetle population level	unitless
$i_{beetles\_survival}$	Bark beetle winter survival index	unitless
$i_{beetles\_generation}$	Bark beetle generation index	unitless
$i_{beetles\_activity}$	Previous bark beetles activity index	unitless

$i_{beetles\_mass\_attack}$	Bark beetles mass attack capability	unitless
max_{Nwood}	Value of N_{wood} at which $i_{hosts\ dead}$ = 1.0	unitless
N_{wood}	Spruce wood necromass	$gC.m^{-2}$
$P_{success,\ age\ class}$	Probability of successful attack	unitless
P_{attack}	Probability of beetles attack	unitless
PWS_{max}	Maximum long term Spruce water stress	unitless
PWS_{spruce}	Spruce water stress	unitless
$PWS_{age\ class}$	Spruce age classes water stress	unitless
PWS_{limit}	Spruce water stress at which $i_{hosts\ defense}$ = 0.5	unitless
RDi_{limit}	Relative density index at which $i_{hosts\ competition}$ = 0.5	unitless
$RDi_{weakness}$	Relative density index at which $i_{host\ weakness}$ = 0.5	unitless
RDi_{spruce}	Spruce stand relative density index [0,1]	unitless
$RDi_{age\ class}$	Spruce age classes relative density index [0,1]	unitless
$S_{competition}$	Shape parameter in the calculation of $i_{hosts\ competition}$	unitless
$S_{weakness}$	Shape parameter in the calculation of $i_{hosts\ weakness}$	unitless
$S_{drought}$	Shape parameter in the calculation of $i_{hosts\ defense}$	unitless
S_{share}	Shape parameter in the calculation of $i_{hosts\ share}$	unitless
$S_{activity}$	Shape parameter in the calculation of $i_{beetle\ activity,\ y-1}$	unitless
$S_{generation}$	Shape parameter in the calculation of $i_{beetle\ generation}$	unitless
Sh_{spruce}	Share fraction of Spruce	unitless
Sh_{limit}	Share fraction at which $i_{hosts\ share}$ = 0.5	unitless
T_{air}	Air Temperature	°C

The biomass of trees killed by bark beetles in one year and one pixel ($B_{beetles\ kill}$) is calculated as the product of the biomass of trees attacked by bark beetle ($B_{beetles\ attacked}$) and the probability of a successful attacks ($P_{success,\ age\ class}$) averaged over the number of age classes and weighted by their actual fraction ($F_{age\ class}$) for a given tree species (F_{spruce}). The approach assumes that a successful beetle colonization always results in the death of the attacked tree which is a simplification from reality (A. Leufvén et al. 1986).

$$B_{beetles\ kill} = \sum_{nb\ age\ classes}^{age\ class=1} P_{success,\ age\ class} \times B_{beetles\ attacked} \times \frac{F_{age\ class}}{F_{spruce}} \qquad (1)$$

During the endemic stage, $B_{beetles\ attacked}$ and $B_{beetles\ kill}$ are at their lowest values and the damage from bark beetles has little impact on the structure and function of the forest. Losses from $B_{beetles\ kill}$ can be considered background mortality.

The biomass of trees attacked by bark beetles ($B_{beetles\ attacked}$) is defined as an attempt from the bark beetles to overcome the tree defenses and thus succeeding in boring holes in the bark in order to reach the sapwood. $B_{beetles\ attacked}$ is calculated at the pixel level by multiplying the actual stand biomass of spruce (B_{total}) and the probability that bark beetles attack spruce trees in the pixel ($P_{attacked}$).

$$B_{beetles\ attacked} = B_{total} \times P_{attacked} \quad (2)$$

$P_{attacked}$ represent the ability of the bark beetles to spread and to locate new suitable spruce trees as hosts for breeding. $P_{attacked}$ is calculated by the product of two indexes (all indexes in this study are denoted i and are analogue the the susceptibility indexes from Temperli et al. 2013): (1) the beetle pressure index ($i_{beetles\ pressure}$) which a proxy of the bark beetle population and (2) the stand attractiveness index ($i_{hosts\ attractivity}$) which is a proxy of the overall stand health. Health was here defined as the ability of the forest to resist an external stressor such as bark beetle attacks.

$$P_{attacked} = i_{hosts\ attractivity} \times i_{beetles\ pressure} \quad (3)$$

2.5. Stand attractiveness

The stand attractiveness index ($i_{hosts\ attractivity}$) varies between 0.5 and 1. When $i_{hosts\ attractivity}$ tends to 0.5, the stand is constituted mainly by healthy trees which are less attractive for beetles whereas an $i_{hosts\ attractivity}$ approaching 1 represents a highly stressed forest suitable for colonization by bark beetles. Factors that contribute to the stress of a forest in ORCHIDEE are: nitrogen limitation, limited carbohydrate reserves, and monospecific spruce forest. Trees experiencing extended periods of environmental stress are expected to have less carbon and nitrogen reserves available for defense compounds, making them vulnerable for bark beetle attacks even at relatively low beetle population densities (Raffa et al., 2008). Nonetheless, reserves pools in ORCHIDEE r7791 have not yet been evaluated so, instead proxies were used such as long term drought (PWS_{max}) and relative density index (RDi) which were already simulated in ORCHIDEE r7791.

$$i_{hosts\ attractivity} = max(i_{hosts\ competition}, i_{hosts\ defense}) \times i_{hosts\ share} \quad (4)$$

Where $i_{hosts\ competition}$ and $i_{hosts\ defense}$ both represent proxies for the reduction of the nitrogen and carbohydrate reserve due to strong competition for light and soil resources, and repetitive years that are drier than average. For this study, the average drought intensity during the last three years is considered, as a proxy of spruce stand healthiness:

$$i_{hosts\ defense} = 1 / (1 + e^{S_{drought} \cdot (1 - PWS_{max} - PWS_{limit})}) \quad (5a)$$

Where,

$$PWS_{max} = \sum_{nb\ age\ class}^{age\ class=1} max(PWS_{spruce}, \ldots, PWS_{spruce,n-3}) \times \frac{F_{age\ class}}{F_{spruce}} \quad (5b)$$

Where PWS_{max} is the maximum plant water stress index during the last 3 years, PWS_{limit} is the plant water stress below which the healthiness of the stand will strongly be affected. In addition to drought, overstocked forest may also decrease the overall healthiness of a spruce stand ($i_{hosts\ competition}$).

$$i_{hosts\ competition} = 1 / (1 + e^{S_{competition} \cdot (RDi_{spruce} - RDi_{limit})}) \quad (6a)$$

In ORCHIDEE, the relative density index (RDi) is used to quantify the competition between trees at the stand level. At an RDi of 1, the forest is expected to be at its maximum density given the carrying capacity of the site, implying the highest level of competition between trees. RDi_{limit} represents the limit at which the bark beetle outbreak starts to decline because of lack of suitable host trees. At the spatial scale of the ORCHIDEE model, RDi_{limit} could be considered as a parameter for spatial upscaling since it describes how many trees survive after an outbreak which is very dependent on the size of the pixel. When a pixel represents a single stand (~1 ha) all trees may be killed during an outbreak so RDi_{limit} will be setup close to 0. When an ORCHIDEE pixel is used to represent an area of 2500 km², not all trees will be killed which is reflected in setting RDi_{limit} = 0.4.

RDi_{spruce} is computed as follows:

$$RDi_{spruce} = \sum_{nb\ age\ class}^{age\ class=1} \frac{D_{age\ class}}{D_{max}} \times \frac{F_{age\ class}}{F_{spruce}} \quad (6b)$$

Where $D_{age\ class}$ is the current tree density of an age class and $F_{age\ class}$ is the fraction of spruce in the pixel that resides in this age class. D_{max} represents the maximum stand density of a stand given its diameter. In ORCHIDEE D_{max} is calculated based on the mean quadratic diameter (cm) of the age class and two species specific parameters, α and β:

$$D_{max} = (Dia_{quadratic,\ age\ class}/\alpha)^{(1/\beta)} \quad (6c)$$

The index $i_{hosts\ share}$ (used in eq. 4) takes into account that in a mixed tree species landscape, even a few non-host trees may chemically hinder bark beetles in finding their host trees (Zhang and Schlyter, 2004) explaining why insect pests, including *Ips typographus* outbreaks, often cause more damage in pure compared to mixed stands (Nardi et al., 2023). ORCHIDEE r7791 does not simulate multi-species stands but does account for landscape-level heterogeneity of forests with different plant functional types. The bark beetle module in ORCHIDEE assumes that within a pixel, the fraction of spruce over other tree species is a proxy for the degree of mixture:

$$i_{hosts\ share} = 1 / (1 + e^{S_{share} \cdot (sh_{spruce} - sh_{limit})}) \quad (7a)$$

Where,

$$Sh_{spruce} = F_{none-spruce} / F_{spruce} \quad (7b)$$

2.6. Implicit representation of bark beetle populations

The bark beetle pressure Index ($i_{beetles\ pressure}$) is formulated based on two components: (1) the bark beetle breeding index of the current year ($i_{beetles\ generation}$), and (2) an index of the loss of tree biomass in the previous year due to bark beetle infestation ($i_{beetles\ activity}$). $i_{beetles\ activity}$ is thus a proxy of the previous year's bark beetle activity. The expression accounts for the legacy effect of bark beetle activities by averaging activities over the current and previous years. In this approach, the susceptibility index ($i_{beetles\ survival}$) serves as an indicator for increased bark beetle survival which could result from favorable conditions for beetle demography (see next section).

$$i_{beetles\ pressure} = i_{beetles\ survival} \times \frac{(i_{beetles\ generation} + i_{beetles\ activity})}{2} \quad (8)$$

The model calculates $i_{beetles\ generation}$ from a logistic function, which depends on the number of generations a bark beetle population can sustain within a single year:

$$i_{beetles\ generation} = 1 / (1 + e^{-S_{generation} \cdot (\frac{DD_{eff}}{DD_{ref}} - G_{limit})}) \quad (9)$$

Where $S_{generation}$ and G_{limit} are tuning parameters for the logistic function, DD_{eff} represents the sum of effective temperatures for bark beetle reproduction in $°C \cdot day^{-1}$, while DD_{ref} denotes the thermal sum of degree days for one bark beetle generation in $°C \cdot day^{-1}$. Saturation of $i_{beetles\ generation}$ represents the lack of available breeding substrate when many generations develop over a short period.

DD_{eff} is calculated from January 1st until the diapause of the first generation. In ORCHIDEE, diapause is triggered when daylength exceeds 14.5 hours (e.g., April 27th for France). Each day before the diapause with a daily average temperature above 8°C is accounted for in sumTeff. This approach simulates the phenology of bark beetles, which tend to breed earlier when winter and spring were warmer, thus allowing for multiple generations in the same year (Hlásny et al., 2021a). More details on the phenology model are available in Temperli et al. 2013.

The bark beetle activity of the previous year ($i_{beetles\ activity}$) is calculated as:

$$i_{beetles\ activity} = 1/(1 + e^{-S_{activity}(\frac{B_{kill,y-1}}{B_{total}} - act_{limit})}) \quad (10)$$

Where $i_{beetles\ activity}$ denotes the biomass of the stand damaged by bark beetles in the previous year, B_{total} is the total biomass of the stand, and $S_{activity}$ and act_{limit} are parameters that drive the intensity of this negative feedback.

During the build-up stage (Fig. 1) the population of bark beetles can either return to its endemic stage (Fig. 1) if tree defense mechanisms are preventing bark beetles from successfully attacking healthy trees, or evolve into an epidemic stage (Fig. 1) if the tree defense mechanisms fail. During this stage, tree canopies remain green, therefore, this stage is also known as the green stage (Fig. 1). During the post-epidemic stage, the forest is still subject to higher mortality than usual but signs of recovery appear (Hlásny et al., 2021a). Recovery may help the forest ecosystem to return to its original state or switch to a new state (different species, change in the forest structure) depending on the intensity and the frequency of the disturbance (Van Meerbeek et al., 2021).

2.7. Bark beetle survival

The capacity of the bark beetles to survive the winter in between two breeding seasons is a crucial mechanism explaining massive tree mortality due to an outbreak. During regular winters, winter mortality for bark beetles is around 40% for the adults and 100% for the juveniles (Jönsson et al. 2012). In our scheme, this mortality rate is implicitly accounted for in the calculation of the bark beetle survival index ($i_{beetles\ survival}$). A lack of data linking bark beetle survival to anomalous winter temperatures prevented us from including this information as a modulator of $i_{beetles\ survival}$. Instead the model simulates the excess of survival due to the abundance of suitable tree hosts which decreases the competition for shelter and food:

$$i_{beetles\ survival} = max(i_{hosts\ dead}, i_{hosts\ alive}) \quad (11)$$

The availability of wood necromass from trees that died recently, particularly following windstorms, plays a critical role in bark beetle survival and proliferation. In the year following a windstorm, uprooted and broken trees may offer an ideal breeding substrate for bark beetles, facilitating their population growth.

In Temperli et al. (2013) an empirical correlation between windthrow events and bark beetle susceptibility was established. ORCHIDEE enhances realism by considering the actual suitable hosts (living or recently dead trees) as the primary driver of bark beetle survival. To avoid overestimating bark beetle population growth, max_{Nwood} has been introduced. This ensures that an excess of breeding substrate does not artificially inflate beetle numbers, acknowledging that recent dead trees lose their freshness and thus suitability for breeding after a year. Any addition of dead trees beyond max_{Nwood} is considered ineffective in affecting the bark beetle population.

This relationship is quantitatively represented in ORCHIDEE through the dead host index, $i_{hosts\ dead}$, which is driven by the availability of recent dead trees. The formulation of $i_{hosts\ dead}$ is as follows:

$$i_{hosts\ dead} = min(\frac{N_{wood}}{B_{wood}} / max_{Nwood}, 1) \quad (12)$$

Here, N_{wood} represents the quantity of woody necromass from the current year, B_{wood} is the total woody biomass in the stand, and max_{Nwood} is the threshold of the ratio N_{wood}/B_{wood} signifying the maximum level. This index captures the immediate increase in dead trees post-windthrow, which may drive bark beetle breeding. However, after a year, this substrate becomes unsuitable for breeding and is excluded from the $i_{hosts\ dead}$ calculation.

Finally, max_{Nwood} can also be considered as a parameter that depends on the spatial scale of the simulation. The mortality rate of trees ($DR_{windtrow}$) that will trigger an outbreak is very different across spatial scales. Where a relatively high share of dead wood is needed to trigger an outbreak at the patch-scale, a much lower share of dead wood suffices at the landscape-scale to trigger a widespread bark beetle outbreak. So these parameters must be set up according to the spatial resolution of the simulation experiment.

$i_{hosts\ alive}$ denotes the survival of bark beetles which is facilitated by the abundance of suitable trees which reduces the competition among bark beetles for breeding substrates and therefore increases their survival.

$$i_{hosts\ alive} = i_{beetles\ mass\ attack} \times i_{hosts\ weakness} \quad (13)$$

The amount of suitable tree hosts. $i_{hosts\ weakness}$ is driven by two factors: (1) the abundance of weak trees which can be more easily infected by bark beetles. ORCHIDEE does not explicitly represent weak trees, but tree health is thought to decrease with an increasing density given the stand diameter. The index for host suitability is thus calculated by making use of the relative density index (RDi_{spruce}).

$$i_{hosts\ weakness} = 1 / (1 + e^{S_{weakness} \cdot (RDi_{spruce} - RDi_{weakness})}) \quad (6a')$$

Equation 6a' is close to equation 6a but the parameter $S_{weakness}$ has been reduced by a factor of two in order to reflect that $i_{hosts\ weakness}$ are more sensitive to RDi than $i_{hosts\ competition}$. (2) $i_{hosts\ mass\ attack}$ which represent the ability of bark beetles to attack healthy trees when the number of bark beetles is large enough. This index only depends on the size of the bark beetle population ($i_{beetles\ pressure}$ see eq. 8)

$$i_{hosts\ mass\ attack} = 1 / (1 + e^{S_{mass\ attack} \cdot (i_{beetles\ pressure} - BP_{limit})}) \quad (14)$$

Where $S_{hosts\ mass\ attack}$ and BP_{limit} are parameters. $S_{mass\ attack}$ controls the steepness of the relationship while BP_{limit} is the bark beetle pressure index at which the population is moving from endemic to epidemic stage where mass attacks are possible.

The epidemic stage corresponds to the capability of bark beetles to mass attack healthy trees and overrule tree defenses (Biedermann et al., 2019). At this point in the outbreak, all trees are potential targets irrespective of their health. Owing to the widespread mortality of individual trees, the forest dies resulting in a stage also known as the red stage (Fig. S2, stage 3). Three causes may explain the end of an epidemic: (1) the most likely cause is a high interspecific competition among beetles for tree host when the density is decreasing (decreasing $i_{hosts\ alive}$) (Pineau et al., 2017; Komonen et al., 2011), (2) a series of very cold years will decrease their ability to reproduce (decreasing $i_{beetles\ \ generation}$), and (3) a rarely demonstrated increasing population of beetle predators (Berryman, 2002). In ORCHIDEE r7791, the first two causes are represented but the last, i.e., the predators are not represented.

2.8. Tree mortality from bark beetle infestation

When bark beetles attack a tree, the success of their attack will likely depend on the capacity of the tree to defend itself from the attack. Trees defend themselves against beetle attacks by producing secondary metabolites (Huang et al., 2020). The high carbon and nitrogen costs of these compounds limit their production to periods with environmental conditions favorable for growth (Lieutier, 2002). The probability of a successful bark beetle attack is driven by the size of the bark beetle population ($i_{beetle\ pressure}$) and the weakness of each tree. ORCHIDEE, however, is not simulating individual trees but rather diameter classes within an age class. An index of tree weakness for each age class ($i_{hosts\ health,\ age\ class}$) was calculated as:

$$P_{success,\ age\ class} = i_{hosts\ health,\ age\ class} \times i_{beetles\ pressure} \quad (15)$$

A tree rarely dies solely from bark beetle damage (except during mass attacks) as female beetles often carry blue-stain fungi, which colonizes the phloem and sapwood, blocking the water-conducting vessels of the tree. This results in tree death from carbon starvation or desiccation. As ORCHIDEE r7791 does not simulate the effects of changes in sapwood conductivity on photosynthesis and the resultant probability of tree mortality, the index of weakened trees index ($i_{hosts\ health,\ age\ class}$) makes use of two proxies similarly to equation 5 and 6 but simplified to be calculated only for one age class at the time:

$$i_{hosts\ health,\ age\ class} = \frac{(i_{hosts\ competition,\ age\ class} + i_{hosts\ defense,\ age\ class})}{2} \quad (16)$$

$$i_{hosts\ defense,\ age\ class} = 1 / (1 + e^{S_{drought} \cdot (1 - PWS_{age\ class} - PWS_{limit})}) \quad (5a')$$

Contrary to equation 5a, $PWS_{age\ class}$ is the plant water stress from the current year.

$$i_{hosts\ competition,\ age\ class} = 1 / (1 + e^{S_{competition} \cdot (RDi_{age\ class} - RDi_{limit})}) \quad (6a'')$$

$$RDi_{age\ class} = \frac{D_{age\ class}}{D_{max}} \quad (6b'')$$

To access the Bark beetle damage rate ($DR_{bettles}$), we simply divide $B_{beetles\ kill}$ by B_{total}.

2.9. Flow of the calculations

As the equations presented above contain feedback loops the flow of the calculation is shown in Fig. 2.

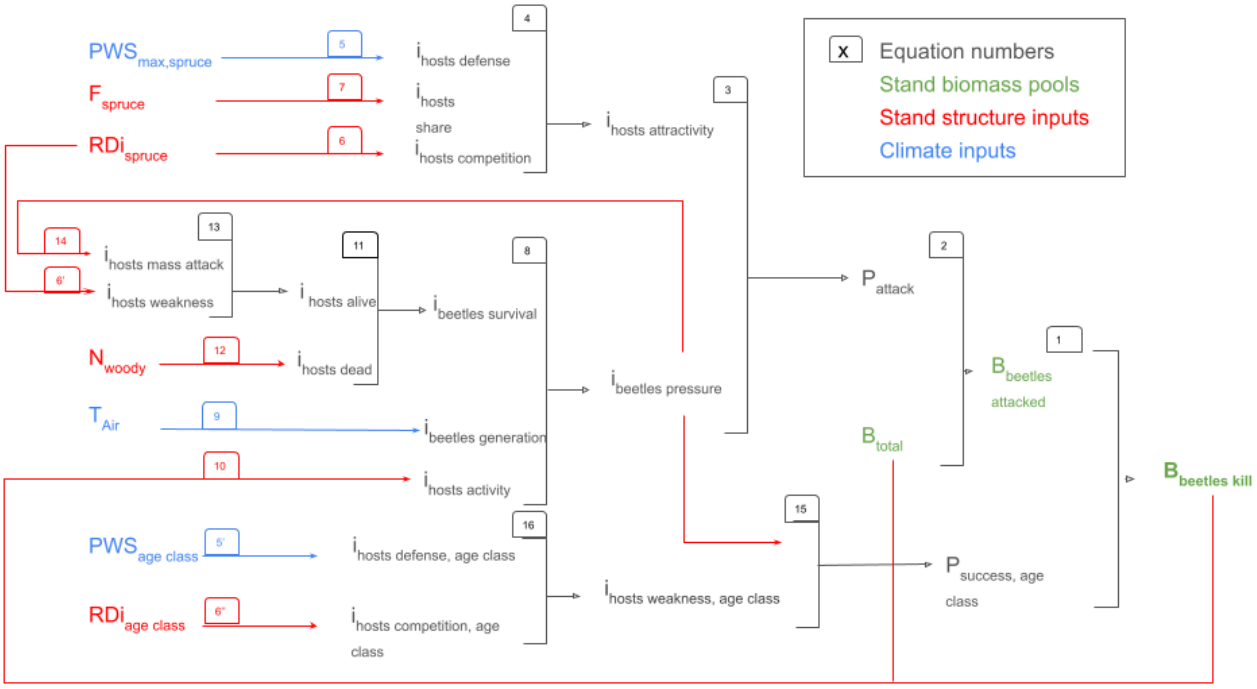


Figure 2: Flow of the calculations in the bark beetle outbreak module developed in this study. The numbers correspond to the equation numbers provided in this study.

3. Methods and material

3.1. Model configuration

Given the large-scale nature of the ORCHIDEE we carried out a sensitivity experiment of the bark beetle outbreak functionality rather than focusing the evaluation on matching observed damage volumes at specific case studies. Such an approach is thought to reduce the risk of overfitting the model to specific site conditions (Abramowitz et al., 2008).

ORCHIDEE r7791 including the bark beetle module was run for 8 FLUXNET sites, selected to simulate a credible temperature and precipitation gradient for spruce (see further below). For each location, the half-hourly meteorological data from the flux tower were gap filled and reformatted so that they could be used as climate forcing by the ORCHIDEE. Boundary conditions for ORCHIDEE, such as soil texture, pH and soil color were retrieved from the USDA map, for the corresponding pixel. The observed land cover and land use for the pixel were ignored and set to pure spruce because this study did not investigate the effect of species mixture in the simulation experiments. The resolution of the pixel chosen for this analysis is 2500 km². It corresponds to a fine resolution for ORCHIDEE large-scale simulations but a coarse resolution for studying bark beetle outbreaks.

The climate forcings were looped over as much as needed to bring the carbon, nitrogen, and water pools to equilibrium during a 340 years long spinup followed by a windthrow event and a 100-years simulation. The results presented in this study come from the 100-years long site simulations. Given the focus on even-aged monospecific spruce forests in regions where spruce growth is not constrained by precipitation, variables such as $i_{hosts\ share}$ and $i_{hosts\ defense}$ were omitted from this study. Note that ORCHIDEE do not account for possible acclimation of the bark beetle population to each location.

3.2. Site selection

Bark beetle populations are known to be sensitive to temperature as they are more likely to survive a mild winter (Lombardero et al., 2000) and tend to breed earlier when winter and spring are warmer than usual, allowing for multiple generations in the same year (Hlásny et al., 2021a). In order to assess the temperature effect of the bark beetle outbreak module in ORCHIDEE, eight locations in Europe were selected (Table 2) which represent the range of climatic conditions within the distribution area of Norway spruce (*Picea Abies* Karst L.) which is the main host plant for *Ips typographus*, the bark beetle species under investigation.

Table 2: Climate characteristics of the eight sites used in the simulation experiments gradient underlying our experimental setup. The site acronyms refer to the site names used in the FLUXNET database (Pastorello et al. 2020).

Site (FLUXNET)	**HYY**	**SOR**	**THA**	**WET**	**HES**	**FON**	**REN**	**COL**
Full name	Hyytiala	Soroe	Tharandt	Wetstein	Hesse	Fontainebleau	Renon	Collelongo
Country	Finland	Danmark	Germany	Germany	France	France	Italy	Italy
Latitude (°N)	61.8	55.5	50.9	49.0	48.4	48.7	46.5	41.8
Longitude (°E)	24.3	11.6	13.6	14.8	7.1	2.8	11.4	13.6
MAT (°C)	3.8	8.2	8.2	7.7	9.5	10.2	4.7	6.3
MinAT (°C)	-10.8	2.7	-3.9	-5.2	0.1	-1.1	-6.3	-3.8
MAP ($mm.y^{-1}$)	522	811	734	587	653	989	752	1050
Mean annual net radiation ($w.m^{-2}$)	42.1	49.4	52.5	68.0	53.7	50.3	67.7	68.3

For these eight locations, half-hourly weather data from the FLUXNET database (Pastorello et al., 2020) were used to drive ORCHIDEE. Some of these locations (FON, SOR, HES, COL, WET) are in reality not covered by spruce but all sites are, however, located within the distribution of Norway spruce. In this study, site locations were selected to use observed weather data to simulate a credible temperature and rainfall gradient for spruce.

3.3. Sensitivity to model parameters

The sensitivity assessment evaluates the responsiveness of four key variables ($i_{hosts\ weakness}$, $i_{beetles\ mass\ attack}$, $i_{beetles\ generation}$, $i_{beetles\ activity}$) of the bark beetle model of ORCHIDEE. The assessment aims to demonstrate the ability of ORCHIDEE to simulate diverse dynamics of bark beetle infestations. The selection of $i_{hosts\ weakness}$, $i_{beetles\ activity}$, $i_{beetles\ mass\ attack}$, and $i_{beetles\ generation}$ was based on two criteria: (1) their substantial influence on the dynamics of the bark beetle epidemic, and (2) their independence from direct measurable data, rendering them less suitable for evaluation through literature review.

For each variable, three distinct values were assigned to two parameters labeled “S” and “limit”. The S parameter determines the shape of the logistic relationship, with three values tested for each variable: (a) S=-1, yielding a linear relationship, (b) -1<S<-100, resulting in a logistic curve, and (c) S>-100, turning the logistic relationship into a step function.

The second parameter called “Limit” determines the threshold, derived from expert insights, at which the logistic relationship will reach its midpoint value of 0.5 ($RDi_{weakness}$, BP_{limit}, Act_{limit}, or G_{limit}). For instance, $RDi_{weakness}$ is set at 0.55, indicating $i_{hosts\ weakness}$ midpoint sensitivity (Eq. 6’). Setting BP_{limit} at 0.12 results in an $i_{beetles\ mass\ attack}$ midpoint when $i_{beetles\ pressure}$ is 0.12, selected for its proximity to scenarios where $i_{hosts\ dead}$ equals 1.0 (Eq. 14). Act_{limit}, was positioned at 0.06, signifies $i_{beetles\ activity}$ midpoint at a $DR_{beetles}$ = 6% from the preceding year, exceeding endemic levels yet not reaching epidemic outbreaks (Eq. 10). Lastly, G_{limit} is fixed at 1.0, denoting $i_{beetles\ generation}$'s midpoint upon completing one generation annually, underpinning the rarity of bark beetle outbreaks with fewer than one generation per year (Eq. 9). Starting from these reference values, a “restrictive” simulation was run in which the “Limit” parameter values were reduced by 50%. Likewise a “permissive” simulation was run to test 50% higher “Limit” parameter values.

This assessment explores 36 parameters value combinations (3 x 3 parameter values x 4 parameters). The simulations were run for the THA site, where they were repeated for a $DR_{windthrow}$ of 0.1 and 10%. The effect of the parameters with a negligible windthrow event, i.e., killing only 0.1% of the trees, was tested to confirm that the selected parameters did not simulates false positives, i.e. ORCHIDEE simulating a bark beetle outbreak in the absence of windthrow. Note that this sensitivity analysis aims to document model behavior, rather than seeking precise parameter values (see section 3.4).

3.4. Parameter tuning

The simulation experiment presented in this section was repeated for all eight sites and those results were used to tune key model parameters. In order to select parameters values for $i_{hosts\ weakness}$, $i_{beetles\ mass\ attack}$, $i_{beetles\ generation}$, $i_{beetles\ activity}$ that resulted in simulations reproducing observed dynamics of bark beetle outbreaks, the literature was searched for peer-reviewed papers that reported quantitative characteristics of bark beetle outbreaks (Table 3). Four characteristics could be documented:

- The delay between the windthrow event and the start of the bark beetle outbreak.
- The length of the bark beetle outbreak is defined by the number of years required for a bark beetle population to go back to its endemic level.
- The cumulative number of trees per unit area, killed by the bark beetles at the end of an outbreak.
- The tree mortality rate ($DR_{beetles}$) during an endemic stage.

As already mentioned in the section 2.4, at landscapes scale we do not expect that the all spruces in the landscape will be killed by an outbreak, so we choose to set RDI_{limit} to 0.4 which mean that an outbreak will not kill more than 60 % of the trees in one pixel irrespective of the outbreak intensity.

Table 3 : Literature-based summary of characteristics of large-scale bark beetle outbreaks.

Outbreak characteristics	Observations/model outputs from literatures	How to check in ORCHIDEE ?
Delay before the start of an outbreak	A notable surge in the population of *I. typographus*, a species of bark beetle, was observed in windthrow areas during the second to third summer following the storm (Wichmann and Ravn, 2001; Wermelinger, 2004; Kärvemo and Schroeder, 2010; Havašová et al., 2017).	Using the tree mortality rate by bark beetles ($DR_{beetles}$), one can measure the number of years since the storm before reaching the maximum mortality rate (epidemic stage).
Length of an outbreak	Studies suggest that bark beetle outbreaks in Europe can last anywhere from 11 to 17 years (Hlásny et al., 2021b; Mezei et al., 2014; Bakke, 1989).	Using the tree mortality rate by bark beetles ($DR_{beetles}$), one can measure the number of years since the storm before reaching the minimum mortality rate (endemic stage).
Severity rate of an outbreak	A severe bark beetle outbreak resulted in a 52%-60% reduction in tree numbers at large landscape scale (>2000km²) (Pfeifer et al., 2011; Morehouse et al., 2008)	Count the number of trees killed by bark beetles until the end of the outbreak, then divide by the number of trees just after the storm event.
Endemic mortality rate	Total background mortality is around 1.2%/year. Bark beetles are estimated to account for 40% of the total mortality (≈0.5%/year) (Das et al., 2016; Berner et al., 2017; Hlásny et al., 2021b).	After the end of the outbreak, count the number of trees that die every year. Then average it.

3.5. Impact of climate and windthrow : simulation experiment

In this simulation experiment, the amount of fresh dead tree hosts (N_{wood}) used by the bark beetles to breed was controlled by modifying the maximum damage rate of a windthrow event ($DR_{windthrow}$) in ORCHIDEE. Seven $DR_{windthrow}$ were simulated (i.e, 0.1%, 5%, 7.5%, 10%, 15%, 20%, 35%). Given the monotonic nature of the relationships between $DR_{windthrow}$ and $i_{hosts\ dead}$ (Eq. 12), each event triggers a proportional increase in the dead host availability ($i_{hosts\ dead}$) scaling between 0 and 1 (Fig. 3). Through its equations, ORCHIDEE assumes that for damage rates above 20% $i_{hosts\ dead}$ will always be equal to 1.0. RDi_{spruce}, however, may further decrease with increasing windthrow damage, which makes the 35% damage rate still interesting to investigate. Although the simulations were run for all $DR_{windthrow}$, only four windthrow damage rates were presented to enhance the readability of the result section including a windstorm resulting in a 35% damage rate (Fig. 3).

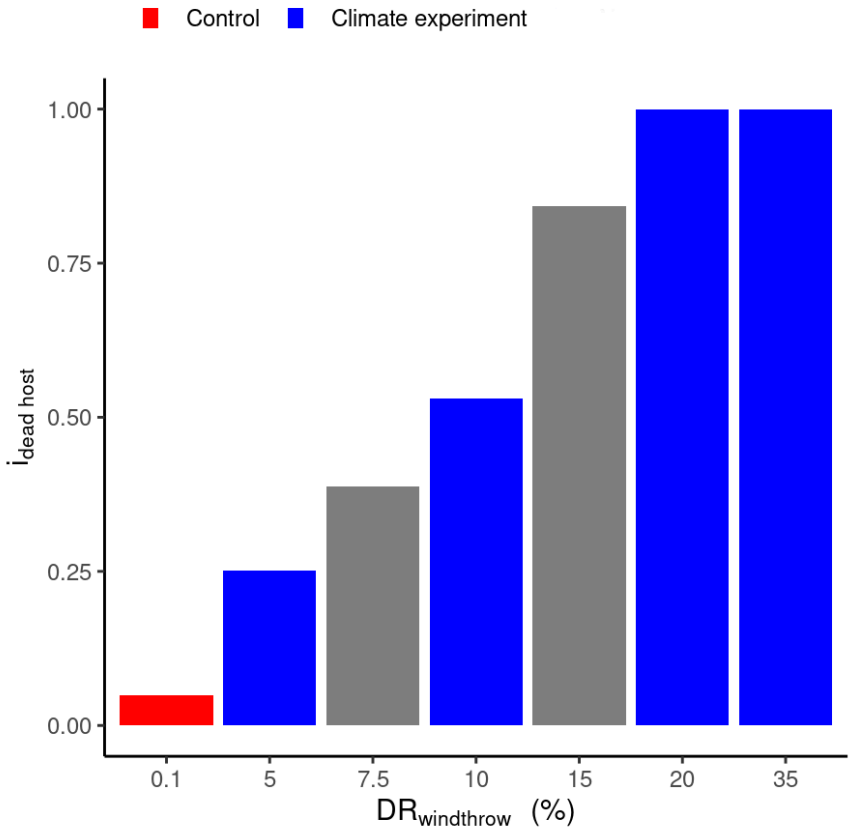


Figure 3: Relationship between windthrow damage rate ($DR_{windthrow}$) and dead host index ($i_{hosts\ dead}$). For each site a $DR_{windthrow}$=0.1% was used as the control simulation because an endemic bark beetle population is expected following such a low intensity event. Four $DR_{windthrow}$ were selected for subsequent presentation of the results because they cover the entire range for the $i_{hosts\ dead}$.

565

566 Site selection was based on the average numbers of generation a bark beetle population can achieve in one year. As
567 described in Temperli 2013, the main driver of numbers of generation a bark beetle population can achieve in one
568 year is the number of days higher than 7.5°C during winter time which is the reason why temperature is so important
569 for bark beetle reproduction. By taking REN, THA, WET and HES, we can investigate a range in bark beetle
570 generations between 0.8 and 3.5 (Fig. 3) which is a relevant range already observed in Europe. Restraining our
571 analysis to only four sites will simplify the presentation in the results section.

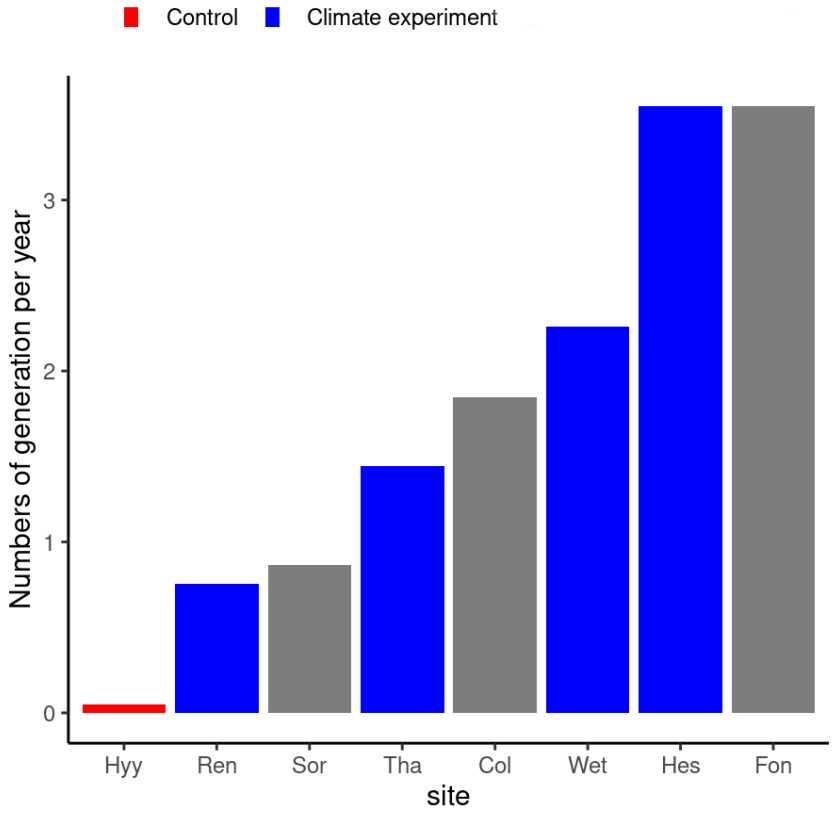


Figure 4: Average number of bark beetle generations during the 5 years following the wind storm for the 8 sites. The HYY site in Finland was selected as the control site for the REN, THA, WET and HES sites. Only results from the control and selected sites are shown in the results to enhance readability of the figures. Although all simulations were also run for SOR, COL and FON their results were found to be too similar to the results of selected sites to present them as well.

572

573 For the climate gradient, the HYY site was chosen to serve as a control since the numbers of generation is lower
574 than 1 for which no outbreak should happen under any circumstances. Under present climate conditions, an outbreak
575 in HYY should be considered as a false positive. Likewise, a $DR_{windthrow}$=0.1% is considered too low to trigger an
576 outbreak and was therefore used as the control for the wind damage rate tests.

577

578 The experiment consisted of 25 simulations, i.e., 5 selected sites (including a control) x 5 wind damage rates
579 (including a control). Three output variables were assessed: bark beetle damage rate ($DR_{beetles}$), total biomass (B_{total}),
580 and net primary production (NPP). Total was investigated over 100 years whereas $DR_{beetles}$ and NPP were assessed
581 for the first 20 years following a windthrow.

582

583 ### 3.6. Continuous vs abrupt mortality

Where most land surface models use a turnover time to simulate continuous mortality (Thurner et al., 2017; Pugh et al., 2017), ecological reality is better described by abrupt mortality events. An idealized simulation experiment was used to qualify the impact of abrupt mortality on net biome productivity by changing from a framework in which mortality is approximated by a constant background mortality to a framework in which mortality occurs in abrupt, discrete events. To test the impact of a change in mortality framework two versions of ORCHIDEE were compared to create an idealized simulation experiment: (1) a version simulating mortality as a continuous process, labeled ”the smooth version”, and (2) the version capable of simulating abrupt mortality from windthrow and subsequent bark beetle outbreaks, labeled ”the abrupt version” and (3) a version in which windthrow is activated but bark beetles outbreak is include in the mortality background. The effect of simulating abrupt mortality was evaluated over 20, 50, and 100 year time horizons.

The effect of changing the framework of simulating mortality from continuous to abrupt was qualified on the basis of 120 simulations (8 sites x 7 windthrow damage rates x 2 model versions + 8 x 1 smooth version) of 100 years each. The simulations with abrupt mortality were run first. Subsequently, the number of trees killed was quantified and used as a reference value for the continuous mortality set-up. This approach resulted in the same quantities of dead trees at the end of the simulation for both frameworks, which then differed only in the timing of the simulated mortality. This precaution is necessary to avoid comparing two different mortality regimes where the result would mainly be explained by the intensity of the mortality rather than by its underlying mechanisms.

Changes in forest functioning were evaluated through the temporal evolution of accumulated net biome productivity (NBP) over a 100-years time frame. NBP is defined as the regional net carbon accumulation after considering losses of carbon from fire, harvest, and other episodic disturbances. NBP is a key variable in the carbon cycle of forest ecosystems) as it integrates photosynthesis, autotrophic, and heterotrophic respiration. In ORCHIDEE, NBP is calculated as proposed in Chapin et al., 2006). Changes in net biome productivity are thus the result of changes in photosynthesis, which in turn is driven by changes in leaf area, autotrophic respiration, and heterotrophic respiration. The latter is influenced by the availability of litter inputs, including litter from trees that died from the bark beetle outbreak.

4. Results

4.1. Sensitivity to model parameters

The impact of spruce stand competition ($i_{hosts\ weakness}$) on outbreak dynamics was examined by adjusting the parameters $S_{weakness}$ and $RDi_{weakness}$ in equation 6a'. When $S_{weakness}$ resulted in a linear relationship ($S_{weakness} = -1$), no peak in bark beetle damage occurred for the three tested values of $RDi_{weakness}$ (permissive, reference, restrictive) at a 10% windthrow damage rate (Fig. 5, 4th row, 2nd column). However, employing a step function ($S_{weakness} > -100$) led to either sporadic peaks of bark beetle damage with a permissive $RDi_{weakness}$ or a two-year outbreak with a maximum damage rate of 60% with a restrictive $RDi_{weakness}$ (Fig. 5, 4th row, 2nd column), neither of which aligns with the observations summarized in Table 3.

The most favorable outcome was obtained with a logistic relationship ($-1 < S_{weakness} << -100$), where $RDi_{weakness}$ dictated the duration of the outbreak: 11, 16, and 25 years for restrictive, reference, and permissive parameter values, respectively (Fig. 5, 4th row, 2nd column). Either the restrictive or reference parameter value could be utilized since a range of 11-16 years aligns with the observations (Table 3). To examine false positives, sensitivity tests were repeated for a 0.1% windthrow damage rate. None of the nine parameter combinations triggered an outbreak (Fig. 5, 4th row, 1st column), suggesting that false positives due to the calculation of $i_{hosts\ weakness}$ are improbable.

The feedback effect of bark beetle mass attack capability ($i_{beetles\ mass\ attack}$) when the bark beetle population reaches a certain threshold was evaluated by varying $S_{mass\ attack}$ and BP_{limit} (Eq. 14). Linear relationships ($S_{mass\ attack} = -1$) resulted in similar outbreak dynamics for all BP_{limit} values, with the model settling on a constant endemic damage post-outbreak, though higher than observed (Table 3). Introducing a logistic or step function minimally altered outbreak dynamics except when assuming a step function for the restrictive value, which prevented an outbreak.Repeating sensitivity tests for a 0.1% windthrow damage rate showed that assuming linear or logistic relationships could trigger an outbreak (Fig. 5, 3th row, 1st column), indicating that false positives may arise from the calculation of $i_{hosts\ mass\ attack}$.

The impact of bark beetle activities from the previous year ($i_{beetles\ activity}$) on outbreak dynamics was investigated by varying $S_{activity}$ and act_{limit} (Eq. 10). Linear or logistic relationships resulted in overly prolonged outbreaks (>30 years) compared to observations (Table 3, 1st row, 2nd column), whereas assuming a step-function relationship simulated a decline in the outbreak after 14 years. Sensitivity tests repeated for a 0.1% windthrow damage rate showed that assuming a linear relationship could trigger an outbreak (Fig. 5, 1st row, 1st column), suggesting potential false positives from the calculation of $i_{beetles\ activity}$.

To explore the effect of bark beetle activities from the previous year on outbreak dynamics ($i_{hosts\ generation}$), $S_{generation}$ and G_{limit} from equation 9 were varied. Bark beetle damage rate was more sensitive to G_{limit} than $S_{generation}$, but only a linear relationship with the reference $G_{limit} = 1.0$ yielded an intermediate outbreak intensity consistent with the location (continental climate). Other combinations resulted in either too strong or no peak during the outbreak. Repeating sensitivity tests for a 0.1% windthrow damage rate showed that none of the nine parameter combinations triggered an outbreak (Fig. 5 2nd row, 1st column), indicating that false positives from the calculation of $i_{beetles\ generation}$ are unlikely.

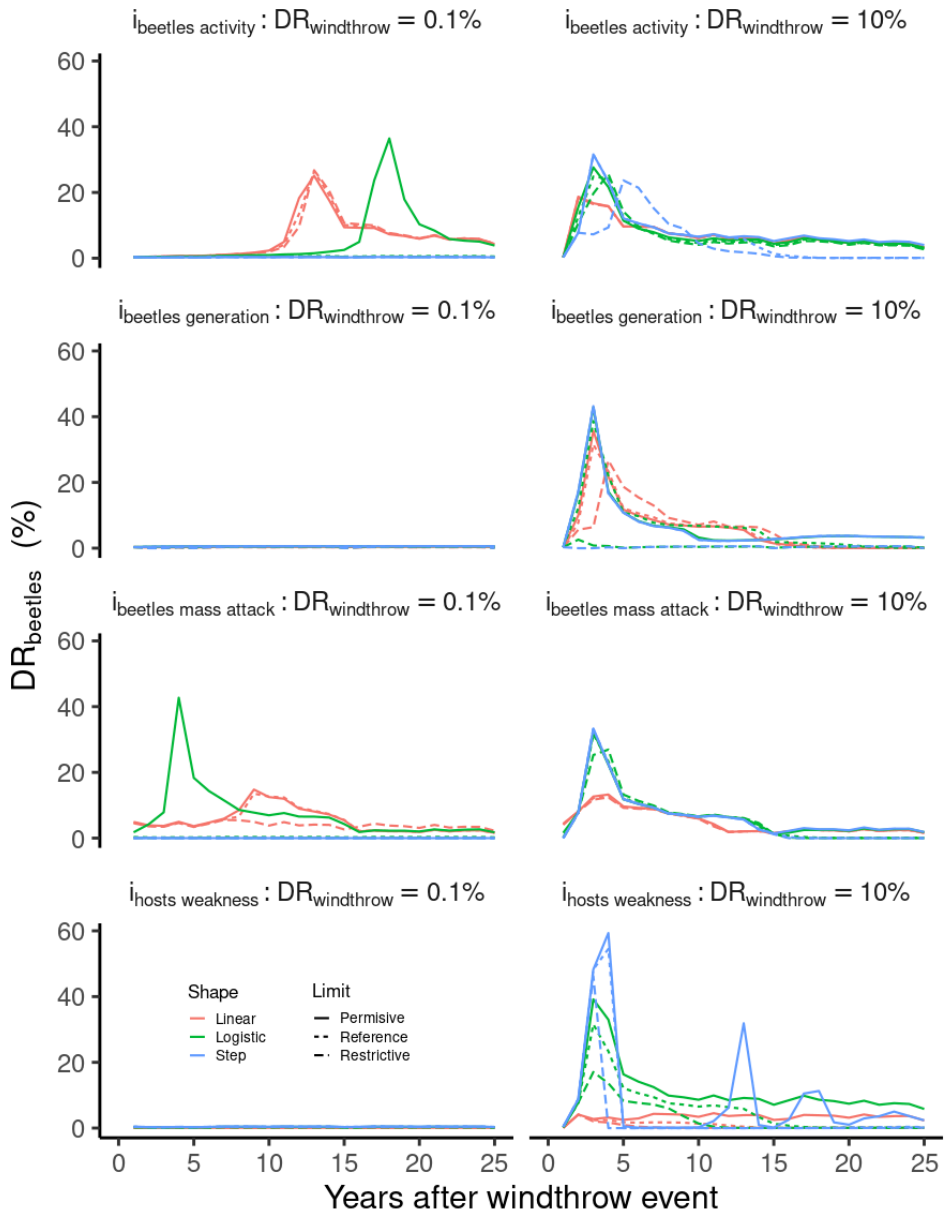


Figure 5: Simulation results from the sensitivity experiment at the THA site. Eight parameters from four equations were evaluated. Each equation represents an index from the bark beetle outbreak module ($i_{hosts\ weakness}$, $i_{hosts\ mass\ attack}$, $i_{beetles\ activity}$, $i_{beetles\ generation}$). Each index is represented by a logistic function defined by a shape parameter (S) and a limit parameter (L). Three values were chosen for each parameter resulting in 9 pairs of parameters for each index. Colored lines represent the shape parameter varying from linear : S = -1, logistic -1< S < -100, to step function where S < -100. Line type represents three different values for L parameters where references are values of $RDi_{weakness}$, BP_{limt}, act_{limit} and G_{limit} (given in Table 4), whereas permissive and restrictive représent a 50% decrease or increase respectively.

4.2. Model tuning

By comparing the outcomes of the sensitivity tests (section 4.1) to a summary of observations (Table 3), a first estimate of the values of several parameters was proposed (Table 4).

Table 4: Parameters values from the bark beetle module tested in the sensitivity analysis. Values labeled with (*) correspond to the parameters adjusted following the sensitivity analysis results.

Parameter	Source	Value
$S_{generation}$	This study: from SA (see 3.1.4)	-1.0 (*)
G_{limit}	Adapted from Temperli et al. 2013	1.0 (*)
DD_{ref}	Adapted from Temperli et al. 2013	547.0
$S_{drought}$	Adapted from Temperli et al. 2013	-9.5
PWS_{limit}	Adapted from Temperli et al. 2013	0.4
max_{Nwood}	This study: scale dependent (see 2.4.2)	0.2
$S_{activity}$	This study: from SA (see 3.1.3)	-500 (*)
act_{limit}	This study: from SA (see 3.1.3)	0.06 (*)
$S_{weakness}$	This study: from SA (see 3.1.1)	-5.0 (*)
$RDi_{weakness}$	This study: from SA (see 3.1.1)	0.55 (*)
RDi_{limit}	This study: scale dependent (see 2.4.1)	0.4
$S_{mass\ attack}$	This study: From SA (see 3.1.2)	-30.0 (*)
BP_{limit}	This study: scale dependent (see 3.1.2)	0.12 (*)
S_{share}	This study: not used (see 2.5)	15.5
SH_{limit}	This study: not used (see 2.5)	0.6

4.3. Impact of climate and windthrow on bark beetle damage

In ORCHIDEE, the hottest sites, HES and WET, experienced significant bark beetle outbreaks across a wide spectrum of windthrow mortality rates, whereas colder sites like REN and THA saw outbreaks only in response to the most severe windthrow events (Fig. 6). A greater average number of bark beetle generations in the years following windthrow events led to higher bark beetle damage rates at the peak of outbreaks. For instance, at a 35% windthrow mortality rate, HES reached a maximum bark beetle damage rate of 50%, whereas REN's maximum was 22% (Fig. 6).

Interestingly, high windthrow mortality rates could also lead to delays and lower maximum $DR_{beetles}$ (Fig. 6). For instance, at the HES site, 10%, 20%, and 35% windthrow damage rates triggered maximum $DR_{beetles}$ of 50%, 43%, and 37%, respectively (Fig. 6). Conversely, low $DR_{windthrow}$, like 5% at WET, delayed the peak of bark beetle

outbreaks by 9 years (Fig. 6). Additionally, the model simulated a post-epidemic stage during which the outbreak damage rate remained relatively low (<10%) and lasted between 3 to 10 years (Fig. 6). Overall, the simulated outbreaks lasted between 11 to 20 years, consistent with field observations (Table 3).

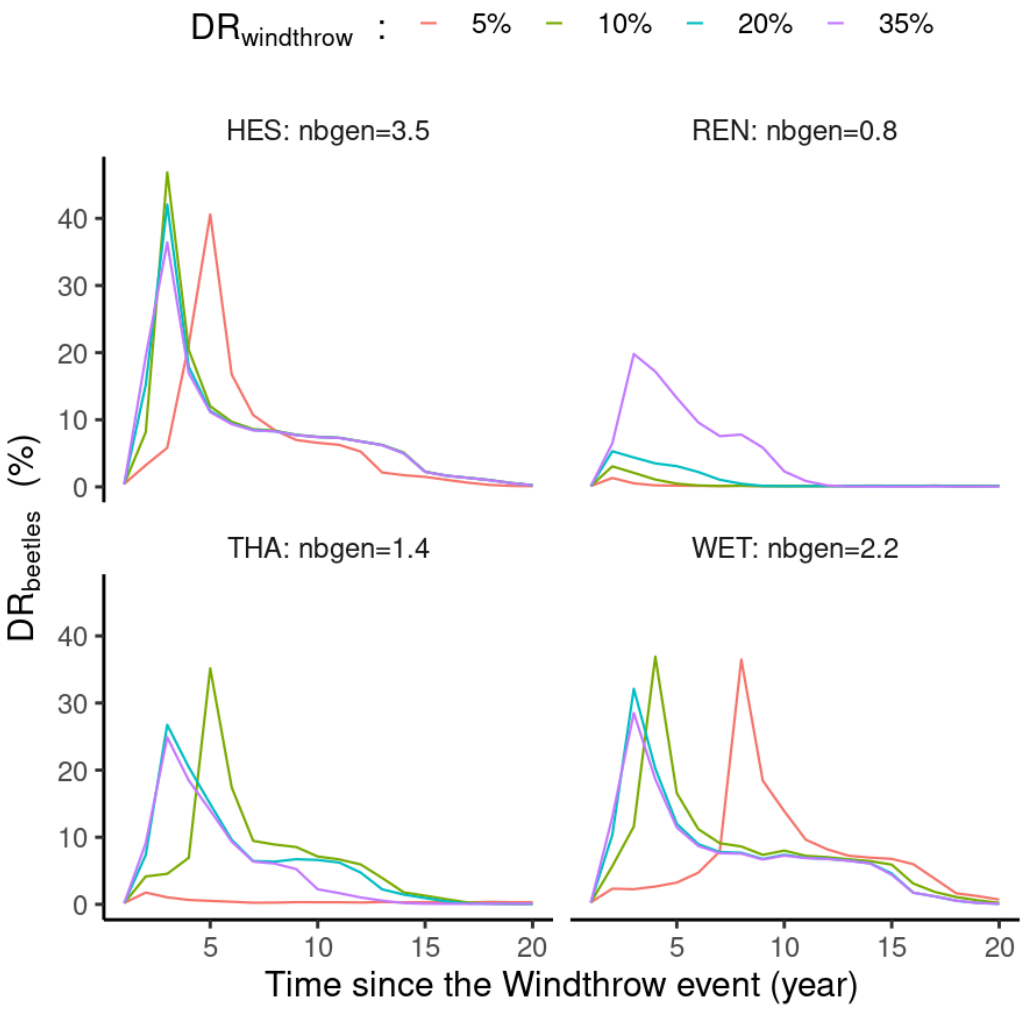


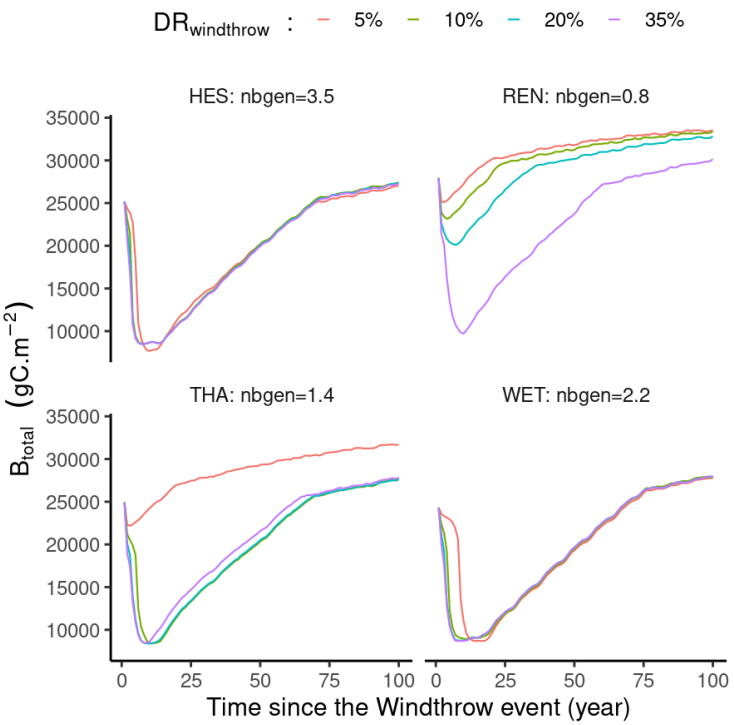
Figure 6: Simulation results of 24 simulations (4 sites x 4 windthrow damage rate $DR_{windthrow}$). Lines represent the annual bark beetle damage rate as a fraction of the total biomass ($DR_{beetles}$). Nbgen is the average number of bark beetle generations during five years after the windthrow event. $DR_{windthrow}$ represents the percentage of biomass loss by a windthrow event at the start of the simulation.

At the coldest site, HYY, ORCHIDEE predicted only a small number of bark beetle generations, preventing outbreaks from occurring. This observation validates the initial parameter tuning (Table 4), indicating that it is robust enough to prevent false positives, such as the model triggering outbreaks in sites where bark beetles cannot reproduce.

4.4. Impact of climate and windthrow on stand biomass and Net Primary Production

With the exception of REN, all sites experience a decrease in total biomass until around 9.000 $gC.m^{-2}$ by the end of the outbreak, which typically lasted 10 to 20 years (Fig. 7). It is noteworthy that regardless of the severity of maximum damage inflicted by bark beetles, the overall cumulative damage consistently results in the same amount of biomass loss (Fig. 7). This characteristic is a key objective of the bark beetle module. Essentially, the model can simulate significant epidemic events even if the initial trigger, such as the windthrow event in our study, is not particularly intense. Once a tipping point is reached, at a biomass level of 9.000 $gC.m^{-2}$ or RDi_{limit} = 0.4, there's no turning back until that threshold is passed. Interestingly, at the REN site where the number of generations is approximately one, the outbreak only reaches the tipping point with a high windthrow damage rate (35%) (Fig. 7).

Throughout the outbreak period, there was a notable decrease in Net Primary Productivity (NPP), as illustrated in the second panel in Fig. 7, primarily attributed to a sharp decline in leaf area index, although not explicitly depicted. Subsequent to the epidemic phase, the forest undergoes recovery by regenerating its leaf area index. Consequently, individual leaf area indices tend to escalate to attain the overall stand leaf area index, concurrently boosting individual growth rates. Following the outbreak, the reduction in stand tree density due to bark beetle damage mitigates autotrophic respiration, albeit not displayed, and fosters recruitment, also not depicted, thereby augmenting NPP or forest growth (Fig. 7). Consequently, carbon use efficiency tends to be higher in sparsely populated stands compared to densely populated ones.



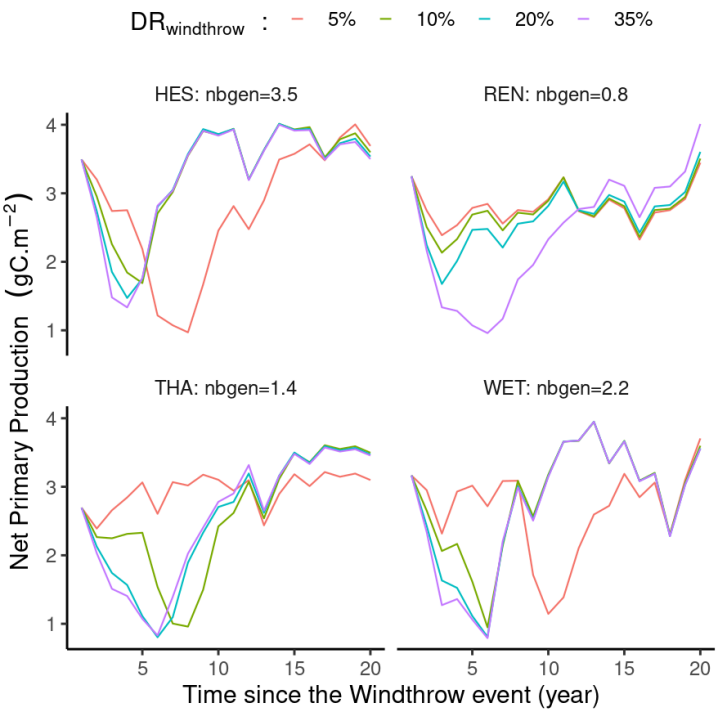


Figure 7: Simulation results of 24 simulations (4 sites x 4 windthrow mortality rate). Lines represent the annual average net primary production (NPP) in gC.m^{-2} or Total stand biomass (B_{total}) in gC.m^{-2}. Nbgen is the average number of achieved bark beetle generations during five years after the windthrow event. $DR_{windthrow}$ represents the percentage of biomass loss by a windthrow event at the start of the simulation.

4.5. Continuous vs abrupt mortality

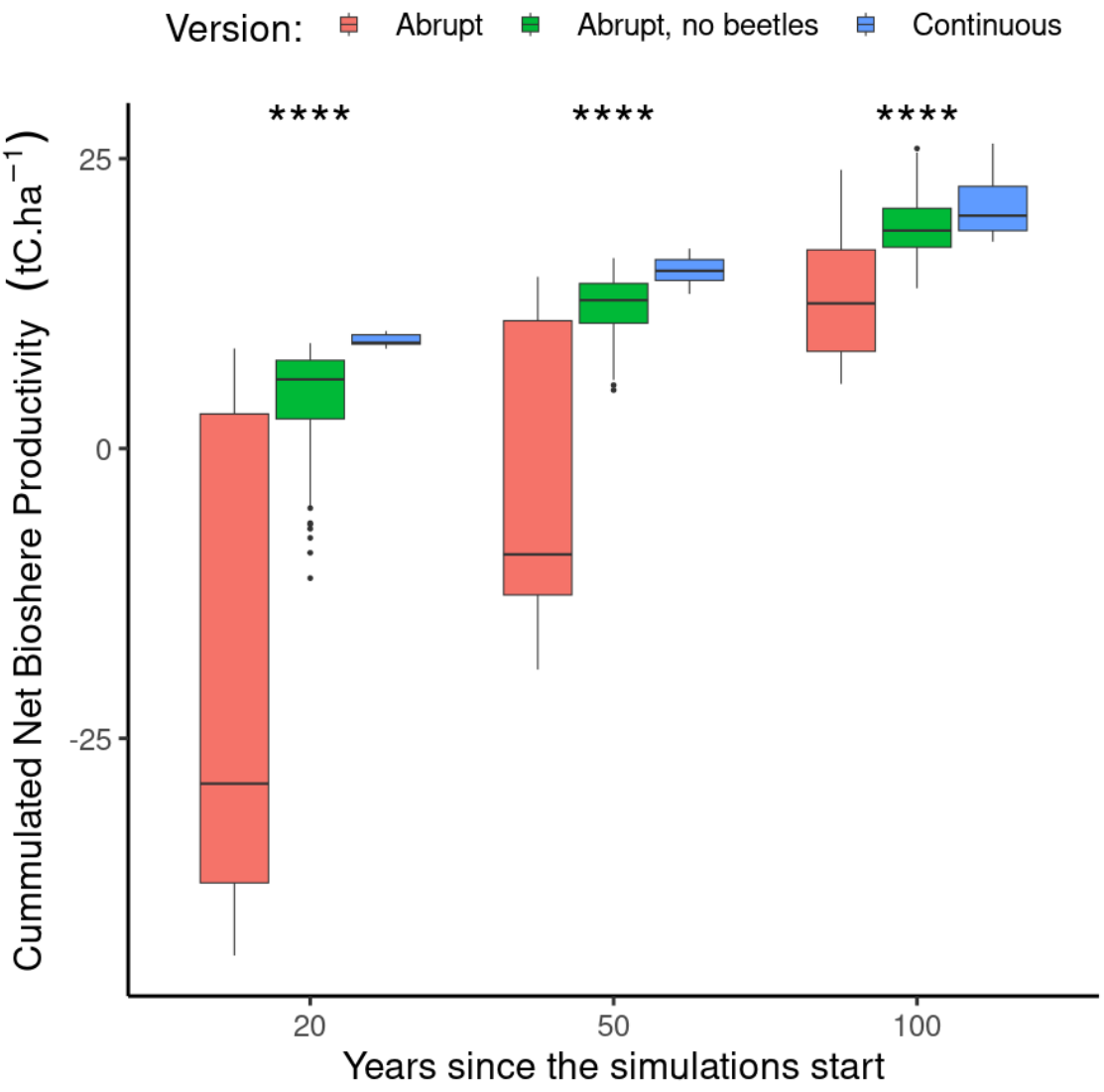


Figure 8: Difference in cumulative net biome production at three discrete time horizons (i.e. 20, 50 and 100 years) between a continuous (blue, n=8), abrupt (red, n=56), abrupt with no bark beetles outbreak (green, n=56) mortality framework. Note that in the continuous mortality framework the mortality rate was adjusted to obtain a similar number of trees killed after 100 years as in the abrupt mortality framework. The variation of each boxplot arises due to different locations and prescribed storm intensities. Each boxplot displays the median value (thick horizontal line), the quartile range (box border), and the 95% confidence interval (vertical line).

699 The total accumulated net biome production (NBP) was evaluated using the ORCHIDEE model across three
700 different timeframes: 20, 50, and 100 years. At the 20-years mark, the average accumulated NBP notably differed
701 between the continuous, abrupt and the abrupt without bark beetles outbreak (abrupt, no beetles) mortality
702 frameworks: -19.5±2.7 tC.ha^{-1}, -3.7±0.7 tC.ha^{-1} and 9.3±0.2 tC.ha^{-1} for the abrupt , abrupt, no beetles and continuous

mortality frameworks, respectively. These differences were statistically significant (Wilcoxon, p-value<0001), indicating a substantial initial reduction in NBP with the 'Abrupt' models, as ecosystems behaved as carbon sources, whereas under the 'Continuous' model, they acted as carbon sinks (Fig. 8). The variability in NBP demonstrated the broad temperature gradient in Europe and indicated that despite many locations potentially acting as sources under the 'Abrupt' framework, some may transition to carbon sinks within the first 20 years following a disturbance.

Moving to the 50-years horizon, the difference between the three frameworks decreased, with net biome productions of -3.8±1.6, 11.7±0.4 and 14.9±0.5 $tC.ha^{-1}$ for the abrupt, abrupt, no beetles and continuous mortality frameworks, respectively. The sink strength difference remained statistically significant (Wilcoxon, p-value<0.001), with the NBP in the 'Abrupt' framework approaching carbon neutrality while without bark beetles outbreak ecosystems already become a sink of carbon. The variability of responses depending on climatic conditions persisted, with the 'Abrupt' framework showing a greater range compared to the 'Continuous' one. Some locations transitioned from carbon sources to carbon sinks under the 'Continuous' framework, indicating a more resilient and gradual recovery in ecosystem productivity (Fig. 8).

At the 100-years mark, the average accumulated NBP for the 'Abrupts' and 'Continuous' frameworks became much closer (Wilcoxon, p-value<0.001), with values of 12.6±0.7, 18.9±0.5 and 19.9±1.2 $tC.ha^{-1}$, respectively (Fig. 8). The data showed a return to positive Cumulative NBP values, suggesting a long-term recovery and potential return to pre-disturbance productivity levels within the century following the windthrow events. The 'continuous' model version displayed a consistently higher median value, suggesting a more resilient recovery over the long term.

5. Discussion

5.1. Simulating the dynamics of bark beetle outbreaks and their interaction with windthrow

Our Bark beetle outbreak model formulation has demonstrated its capability to simulate a broad range of disturbance dynamics. The variation in the outbreak dynamics and the response of the outbreak to its main drivers (Fig. 5 & 6) give confidence in the ability of ORCHIDEE to simulate various outbreak scenarios observed across the temperate and boreal zones under changing climate conditions.

Windthrow events have significant ecological maining because such disturbances offer fresh breeding substrates, which in turn increase bark beetle populations (Lausch et al., 2011). Our modeling results align with these findings, indicating that windthrows causing damage of 5% or more may trigger beetle outbreaks (Fig. 6). Additionally, Wermelinger (2004) reported a strong increase in bark beetle populations post-windthrow, a pattern that our ORCHIDEE simulations also reflect. The model pinpoints a buildup stage—spanning 1 to 9 years, where bark beetle numbers increase prior to peaking, with the duration influenced by the severity of the windthrow and the prevailing climate (Fig. 6).

Temperature is another critical factor affecting bark beetle life cycles. Studies by Benz et al. (2005) have highlighted how intra- and interannual variation in temperature impact bark beetles, with warmer conditions fostering multiple generations per year, whereas cooler, damp climates slow breeding and survival rates. In line with these findings, ORCHIDEE's temperature-dependent simulations show variations in bark beetle impacts across different sites; cold winters at locations such as SOR and REN reduced bark beetle activity compared to warmer sites like THA and WET (Fig. 6). Lieutier et al. (2004) documented that significant bark beetle numbers can trigger mass attacks on healthy trees. Our model incorporates this dynamic, illustrated by epidemic stages where living trees become viable hosts, which then exacerbates the growth of the beetle population.

The aftermath of windthrow and subsequent bark beetle infestations also affects the forest carbon and nitrogen cycles. This impact is observed in the form of snags—standing dead trees that undergo decomposition. As Rhoades, (2019) observed, this can disrupt the link between soil and ecosystem carbon and nitrogen dynamics, a point echoed by (Custer et al., 2020). While ORCHIDEE models the decay of fallen logs, it does not account for snags. Nevertheless, the model suggests a recovery period ranging from 5 to 15 years, contingent upon the intensity of the bark beetle outbreak (Fig. 7). As snags create gaps in the canopy, conditions favorable to natural forest regeneration emerge, corroborating the affirmation of Jonášová and Prach, 2004. The ORCHIDEE model forecasts an increase in tree recruitment due to the sharp reduction in stand density, allowing more sunlight to penetrate to the forest floor, thereby stimulating growth (Fig. 7).

5.2. Emerging property from interacting disturbances

While this study hasn't provided a precise quantification of the impact of incorporating abrupt mortality versus a fixed continuous background mortality, it demonstrated that the impact of abrupt mortality can vary across locations and over time, i.e., ecosystem functions, such as carbon storage, are affected by natural disasters like pest outbreaks, having significant impacts on short-to-mid-term carbon balance estimates. The simulation experiments also highlighted that the legacy effects of disturbances can endure for decades, even for a simplified representation of forest ecosystems such as ORCHIDEE, where the recovery might be too fast due to the absence of snags (Senf et al., 2017).

The ability to simulate resistance as an emerging property is evident from Fig. 6 and 7 for locations REN, where no bark beetle outbreaks were observed following a medium windthrow event (5%-20%). However, in all simulated locations that couldn't resist a bark beetle outbreak, the forest was resilient and ecosystem functions were restored to the level from before the windthrow. The elasticity of, e.g., the carbon sink capacity ranged from 7 to 14 years. This elasticity is in line with current observational evidence from Millar and Stephenson, 2015 who found very little evidence of ecosystem shifts due to natural disturbances in forests, Finally, after the disturbance and the recovery of vegetation structure, the ecosystems simulated by ORCHIDEE showed persistence, i.e. the ability to continue along their initial developmental path. In this study we follow the definitions of Grimm and Wissel, 1997 for resistance, resilience, elasticity, and persistence.

5.3. Are cascading disturbances important for carbon balance estimates ?

The enhanced complexity introduced into the ORCHIDEE model by incorporating abrupt mortality events, as opposed to a fixed-rate continuous mortality, prompts the question: does this model refinement yield significant new insights into carbon balance estimates? Our century-long timeframe analysis demonstrates that the net biome production (NBP; as defined in Chapin et al., 2006)—the metric for carbon balance—ultimately aligns between the continuous and abrupt mortality frameworks, thereby affirming the model's capacity for convergence (Fig. 8). This suggests that irrespective of the nature of the mortality events, the forest ecosystem exhibits a recovery phase, marked by a growth boost that compensates for the growth deficits incurred during the disturbance.

Yet, our experiment has not taken into account the frequency of disturbances. Given the profound influence of disturbance legacies on carbon dynamics, a recurrence interval shorter than the forest's recovery time might result in a tipping point. Such a scenario could diminish the forest's carbon sequestration potential in the post-100-year period, and in extreme cases, may even lead to ecosystem collapse—outcomes not explored in the current simulations nor reflected in recent literature, such as the review by Millar and Stephenson (2015).

In the mid-term, spanning 20 to 50 years, the widely used continuous mortality model appears to inflate the carbon sink capabilities of forests when juxtaposed with abrupt mortality scenarios. Since policy frameworks, including the Green Deal for Europe (2023) and the Paris Agreement | CCNUCC (2023), often hinged upon these medium-term predictions, they would benefit from adopting model simulations that integrate abrupt mortality events to avoid an overestimation of forests' carbon sink capacities. Furthermore, the accuracy of carbon balance estimates strongly depends upon the initial state of the forest in the model. Forest conditions markedly affect carbon uptake rates. Thus, incorporating an abrupt mortality framework into the ORCHIDEE model could substantially refine and fortify the predictive power of our carbon balance assessments across short, medium, and long-term scales.

5.4. Shortcomings of the bark beetle outbreak model

The bark beetle outbreak module developed in this study builds upon the strengths of the previously established LandClim model, though it also inherited some of its limitations. One notable shortcoming is the module for beetle phenology, which is an empirical model making use of accumulated degrees-days. Since the module's conception a decade ago, Europe's climate has undergone substantial changes, primarily manifested in warmer winters and springs (Copernicus, 2024). Because of these changes, chances have increased for two or even more bark beetle generations within a calendar year (Hlásny et al., 2021a). These changes call for an update of the beetle's phenology model to align with these more recent observations (Ogris et al., 2019).

A second limitation is that our study, ORCHIDEE, has been parameterized to simulate only Ips Typographus in Europe. In order to change the Beetles/trees hosts ecosystem e.g. pine bark beetle in North America (Dendroctonus monticolae Hopkins), the sensitivity of indexes must be revised, for example pine beetle is not breeding on the dead

wood falling from withrow but very sensitive to drought event(Preisler et al., 2012). $i_{hosts\ defense}$, and $i_{hosts\ dead}$ as well as the phenology model will need to be revised.

Another issue is the model's consideration of drought. As outlined in the method section, drought is treated as an exacerbating factor, rather than a primary trigger as is the case for windthrow. This understanding was accurate a decade ago (Temperli et al., 2013); however, emerging evidence increasingly suggests that drought events may indeed trigger bark beetle outbreaks across Europe (Netherer et al., 2015; Nardi et al., 2023). Consequently, this extreme drought as a trigger should be incorporated in a future revision of ORCHIDEE's bark beetle outbreak module.

6. Outlook

This study simulated how windthrow interacts with bark beetle infestations in unmanaged forests. Future research will incorporate additional interactions, such as: the interplay between droughts, storms, and bark beetles; storms, bark beetles, and fires; as well as forest management, storms, and bark beetles.

The bark beetle outbreak module could also be enhanced by simulating: (a) standing dead trees (or snags), which would help account for differences in wood decomposition between snags and logs (Angers et al., 2012; Storaunet et al., 2005), (b) the migration of bark beetles to neighboring locations, which becomes significant to account for in a model that operates at spatial resolutions below approximately 10 kilometers, and (c) an up-to-date beetle phenology module which accounts for the recent change in their behavior induced by climate change.

This research provides an initial qualitative assessment of a new model feature. However, the application of the model necessitates an evaluation of the simulations against observations of cascading disturbances at the regional scale, which is the topic of an ongoing study.

7. Conclusion

Our approach enables improving the realism of the bark beetle model in ORCHIDEE without reducing its generality (Levins, 1966). The integration of a bark beetle outbreak module in interaction with other natural disturbance such as windthrow into the ORCHIDEE land surface model has resulted in a broader range of disturbance dynamics and has demonstrated ORCHIDEE's capacity to simulate various disturbance interaction scenarios under different climatic conditions. Incorporating abrupt mortality events instead of a fixed continuous mortality calculation provided new insights into carbon balance estimates. The study showed that the continuous mortality framework, which is commonly used in the land-surface modeling community, tends to overestimate the carbon sink capacity of forests in the 20 to 50 year range in ecosystems under high disturbance pressure, compared to scenarios with abrupt mortality events.

Apart from these advances, the study revealed possible shortcomings in the bark beetle outbreak model including

the need to update the beetle's phenology model to reflect recent climate changes, and the need to consider extreme drought as a trigger for bark beetle outbreaks in line with emerging evidence. Looking ahead, future work will further develop the capability of ORCHIDEE to simulate interacting disturbances such as the interplay between extreme droughts, storms, and bark beetles, and between storms, bark beetles, and fires.

The final step would be to realize a complete quantitative evaluation based on observation data such as produced by (Marini et al., 2017) in order to assess the capability of ORCHIDEE to simulate complex interaction between multiple sources of tree mortality affecting the carbon balance at large scale.

8. Code availability

- R script and data are available at : https://doi.org/10.5281/zenodo.8004954 or DOI https://doi.org/10.5281/zenodo.8004954
- ORCHIDEE rev 7791 code is also available from: https://forge.ipsl.jussieu.fr/orchidee/browser/branches/publications/ORCHIDEE_gmd-2023-05

9. Data availability

- The Fluxnet climate forcing data are available at https://fluxnet.org/
- The simulation results use in this study are available at https://doi.org/10.5281/zenodo.8004954

10. Author contribution

G. Marie, S. Luyssaert designed the experiments and G. Marie conducted them. Following discussions with H. Jactel, G. Petter and M. Cailleret, G. Marie developed the bark beetles model code and performed the simulations. J. Jeong integrated the wind damage and bark beetle modules with each other. G. Marie, J. Jeong, V. Bastrikov, J. Ghattas, B. Guenet, A.S. Lansø, M.J. McGrath, K. Naudts, A. Valade, C. Yue, and S. Luyssaert, contributed to the development, parameterization and evaluation of the ORCHIDEE revision used in this study. G. Marie, J. Jeong, and S. Luyssaert prepared the manuscript with contributions from all co-authors.

11. Competing interests

No competing interest

12. Acknowledgements

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