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Combining individual-based and meta-modeling: Risk assessment of the European spruce bark beetle (*Ips typographus* L.) at the example of a national park in Germany

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Übereinstimmungserklärung

Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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zu Deutsch: *„Kombination von individuen-basierter Modellierung und Metamodellen: Risikoabschätzung des Großen Achtzähnigen Fichtenborkenkäfers (Ips typographus L.) am Beispiel eines Nationalparks in Deutschland“*

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Abstract

European forests have experienced vitality loss and dieback due to increasing disturbances, temperatures, droughts, and forest management. Around 160 million cubic meters of woody biomass in Germany were damaged from 2018 to 2020. Protected areas can offer insights into the natural resilience of European forests after disturbances. However, they face conflicts such as mass outbreaks and the spread of insect pests that can threaten biodiversity and natural habitats. The European spruce bark beetle (*Ips typographus*) is among Europe's most important and severe forest pest species and can act as an ecological disturbance. Due to ongoing climate change, no weakening is expected in the future. Forest management can directly influence important drivers of disturbance regimes. However, the response times are likely slow, requiring effective and adaptive risk-assessing management. Simulation models can play an important and influential role in such management as decision-making tools or for analysis of important drivers. Such models have been successfully applied in fishery management, disease control, and forest fire management. While there are many models published about *Ips typographus*, there is still no simulation tool that individually describes trees and beetles with their properties and decisions, tests the effectiveness of management measures, and uses spatially explicit data for natural landscapes. This approach would allow for investigating infestation patterns and development in natural landscapes based on individual beetle and tree traits. It could also be used to study the impact of climate change and forest protection management on all spatial scales - from individual beetles to entire landscapes.

The main goal of the thesis is to predict the risk of bark beetle infestations and outbreaks in a national park region in Germany under different climate change and management scenarios as an emergent outcome of individual traits of the European spruce bark beetle and its host tree. To achieve this goal, a combination and improvement of existing models on the life history of *Ips typographus* and its host tree *Picea abies* is done to simulate infestations on an individual level. The results are then scaled to the landscape level using a Markov chain metamodel for 20 years into the future. It is shown how (i) management scenarios consisting of different sanitation felling intensities, and (ii) climate change scenarios representing increasing numbers of yearly beetle generations interact and affect the infestation spread.

Chapter 2 discusses the creation, testing, and implementation of a new simulation model for the dispersal and infestation of Ips typographus in a natural European landscape. The IPS-SPREADS (Infestation Pattern Simulation Supporting PREdisposition Assessment DetailS) model is an innovative combination of existing models on beetle phenology (PHENIPS), spruce tree predisposition (PAS - predisposition assessment systems), and precise mechanistic dispersal flight in an artificial forest (IPS - Infestation Pattern Simulation). The model is used to study the effectiveness of sanitation felling in five different research areas at the border of a national park in Germany under varying annual beetle generation numbers.

Chapter 3 explores the various purposes and types of metamodels used in agent-based modeling and attempts to identify and rank the most suited or efficient model types for each application. This assessment was accomplished through a systematic literature review of 27 scientific publications containing 40 different metamodel applications in an individual-based modeling context. A standardized rating instruction was created and used by the candidate and a group of other Ph.D. students and postdoctoral researchers to objectively rate different metamodel applications, such as upscaling agent-based models or conducting sensitivity analyses.

In Chapter 4 of the dissertation, the IPS-SPREADS simulation model is used to predict the risk of bark beetle infestations in a national park region for 20 years into the future. A metamodel approach based on Markov chains is used to scale the computationally demanding IPS-SPREADS model to larger temporal and spatial scales. The metamodel is calibrated and validated using data on infested trees from 2015 to 2017. The model is then used to assess the effectiveness of sanitation felling in preventing the spread of a bark beetle outbreak from the national park to adjacent forests until 2038.

This work adds to a series of previous studies investigating several aspects of the Norway spruce (*Picea abies*) and European spruce bark beetle (*Ips typographus*) system, such as risk assessment, beetle development, beetle dispersal, and infestation patterns, the effectiveness of forest protection measures against the beetle spread or the impact of bark beetle disturbance on the forest as well as its interaction with other disturbances. The results of the studies presented as thesis chapters 2 to 4 indicate that regardless of the number of yearly beetle generations and the spatial or temporal scale, a sanitation felling intensity of 80 % and above seems to mitigate further mass outbreak propagation. It is also shown that habitat inter-connectivity and individual traits of beetles and host trees substantially affect the infestation patterns. In addition, commonly applied metamodel types and application purposes in an individual-based modeling context are revealed. The most promising model variant varies in regard to the chosen application aim.

Further research directions based on the work presented in this thesis incorporate investigating spatial configurations of mixed forest stands and their effect on the dispersal and infestation risk of the European spruce bark beetle. Furthermore, it is discussed how applying and integrating open-access GIS data, such as the European Unions Copernicus program, could improve model validity and applicability. The effects and implications for implementing and analyzing further management measures, such as buffer zones around protected areas, terrestrial detection based on visual clues, and dispensers with anti-attractants in the proposed model framework, are discussed.

Zusammenfassung

Europas Wälder haben aufgrund von zunehmenden Störungen, Temperaturen, Dürren und vergangener Managemententscheidungen an Vitalität verloren und zeigen großflächige Absterbeerscheinungen. Allein in Deutschland betrug das Schadvolumen von 2018 bis 2020 rund 160 Millionen Kubikmeter. Schutzgebiete können Einblicke in die natürliche Widerstandsfähigkeit der Wälder nach Störungen gewähren, bieten aber auch Potenzial für Konflikte wie Massenvermehrungen und Ausbreitung von Schädlingen, die die biologische Vielfalt und die natürlichen Lebensräume bedrohen können. Der Große Achtzähnige Fichtenborkenkäfer (*Ips typographus*) gehört zu den wichtigsten und schwerwiegendsten Waldschädlingen in Europa. Aufgrund des anhaltenden Klimawandels ist keine Gefährdungsabnahme der Waldbeständen zu erwarten. Während die Forstwirtschaft wichtige Treiber von Störungsregimen direkt oder indirekt beeinflussen kann, sind die Reaktionszeiten sehr langsam und verlangen ein wirksames und adaptives Risikomanagement. Simulationsmodelle können eine wichtige und effektive Rolle für das Management als Entscheidungshilfen oder

zur Analyse wichtiger Treiber spielen. Beispiele für erfolgreiche Anwendungen im Entscheidungsprozess stellen Bereiche wie das Fischereimanagement, die Bekämpfung von Epidemien und das Waldbrandmanagement dar. Obwohl es bereits einige Simulationsmodelle für *Ips typographus* gibt, wurde bisher kein Ansatz untersucht, bei dem sowohl die Bäume als auch die Käfer als Individuen mit Eigenschaften, Wahrnehmung und Interaktionen abgebildet werden. Mit solch einem Modell könnte untersucht werden, wie sich die individuellen Eigenschaften der Käfer und der Bäume auf die Befallsmuster und die Wirksamkeit von Managementmaßnahmen in Abhängigkeit der betrachteten räumlichen oder zeitlichen Skala auswirken.

Das Hauptziel der vorliegenden Dissertation besteht daher darin, das Risiko von Borkenkäferbefall und von Ausbrüchen unter verschiedenen Klimawandel- und Managementszenarien als emergentes Ergebnis individueller Eigenschaften des Großen Achtzähnigen Fichtenborkenkäfers und seines Wirtsbaums zu analysieren. Dies geschieht durch die Kombination, Verbesserung und Anwendung bestehender Modelle zur Lebensgeschichte von *Ips typographus* und dessen Wirtsbaum *Picea abies* am Beispiel einer Nationalparkregion in Deutschland. Die Ergebnisse des Individuen-basierten Modells werden anschließend auf die Landschaftsebene und für 20 Jahre in die Zukunft skaliert, indem ein auf Markov-Ketten basierendes Metamodel kreiert und validiert wird. Es wird gezeigt, wie (i) Managementszenarien bestehend aus verschiedenen Entnahmeintensitäten befallener Bäume sowie (ii) Klimawandelszenarien bestehend aus einer Zunahme der jährlichen Käfergenerationen interagieren und die Befallsausbreitung beeinflussen.

In Kapitel 2 der Dissertation wird die Entwicklung, Überprüfung und Implementierung eines neuen Simulationsmodells für die Ausbreitung und den Befall von *Ips typographus* in einer realen Landschaft Europas diskutiert. Das IPS-SPREADS (Infestation Pattern Simulation Supporting REdisposition Assessment DetailS) Modell ist eine innovative Kombination bestehender Modelle zur Phänologie des Käfers (PHENIPS), der Prädisposition des Wirtsbaumes gegenüber Borkenkäferbefall (PAS - Prädispositionsabschätzsysteme) und der Individuen-basierten Simulation des Ausbreitungsflugs der Käfer in einem künstlichen Wald (IPS - Infestation Pattern Simulation). Das neue Modell IPS-SPREADS wird dann verwendet, um die Wirksamkeit der Entnahme befallener Bäume in fünf verschiedenen Probeflächen des Nationalparks Sächsische Schweiz während zunehmender jährlicher Käfergenerationen zu untersuchen. Darüber hinaus wird der Einfluss individueller Eigenschaften auf das Befallsgeschehen und auf die Wirksamkeit der Entnahme befallener Bäume analysiert.

Kapitel 3 widmet sich der Anwendungsgebiete und Typen von Metamodellen, die für Agenten-basierten Modelle verwendet werden, und versucht, die vielversprechendsten Modelltypen je Anwendung zu identifizieren. Dies geschieht mittels einer systematischen Literaturanalyse, die 27 wissenschaftliche Veröffentlichungen mit insgesamt 40 verschiedenen Metamodellanwendungen für Individuen-basierte Modelle untersucht. Ein standardisiertes Bewertungsverfahen wird erstellt und vom Kandidaten zusammen mit einer Gruppe von Doktoranden und Postdoktoranden angewendet, um die Metamodelle im Bezug auf ihr Anwendungsziel objektiv zu bewerten.

In Kapitel 4 der Dissertation wird das entwickelte IPS-SPREADS Modell verwendet, um das Risiko von Borkenkäferbefall in einer Nationalparkregion für 20 Jahre in die Zukunft vorherzusagen. Dafür wird ein Metamodell basierend auf Markov-Ketten entwickelt, welches das rechenintensive IPS-SPREADS Modell auf größere zeitliche und räumliche Skalen hebt. Dieses Metamodell wird mittels Befallsdaten aus der

Nationalparkregion für die Jahre 2015 bis 2017 validiert. Im Anschluss wird das Metamodell dann verwendet, um die Wirksamkeit der Entnahme befallener Bäume für die Ausbreitungsbekämpfung eines Borkenkäfermassenbefalls vom Nationalpark in die angrenzenden Wälder während eines 20-jährigen Zeitraums zu untersuchen.

Die vorliegende Arbeit baut auf einer Reihe von Studien auf, die verschiedene Aspekte des Systems von Großem Achtzähnigen Fichtenborkenkäfer (*Ips typographus*) und Gemeiner Fichte (*Picea abies*) untersuchen: Prädispositionsbewertung, Käferentwicklung, Ausbreitungs- und Befallsmuster sowie die Wirksamkeit von Waldschutzmaßnahmen gegen die Befallsausbreitung. Die Ergebnisse der als Kapitel zwei bis vier vorgestellten Studien zeigen, dass unabhängig von der Anzahl der jährlichen Käfergenerationen und der räumlichen oder zeitlichen Skala eine Entnahmeintensität befallener Bäume von 80 % und mehr die Ausbreitung eines Massenbefalls zu mindern scheint. Es wird auch gezeigt, dass die Habitatvernetzung und die individuellen Eigenschaften der Käfer und Wirtsbäume die Befallsmuster beeinflussen. Darüber hinaus werden häufig angewandte Metamodelltypen und Anwendungszwecke in einem Individuen-basierten Modellierungskontext zusammengetragen und die vielversprechendste Modellvariante je Anwendungsgebiet extrahiert.

Zum Schluss werden weitere Forschungsrichtungen basierend auf den vorgestellten Studien diskutiert, wie zum Beispiel die Untersuchung der räumlichen Konfiguration von Mischwäldern und deren Auswirkungen auf das Befallsgeschehen des Großen Achtzähnigen Fichtenborkenkäfers. Des Weiteren wird diskutiert, wie die Anwendung und Integration von frei verfügbaren GIS-Daten, wie beispielsweise des Copernicus Programms der Europäischen Union, die Validität und Anwendbarkeit der entwickelten Modelle verbessern können. Am Ende werden potenzielle Implikationen für die Implementierung und Analyse weiterer Managementmaßnahmen wie Pufferzonen um Schutzgebiete, terrestrische Erkennung von Borkenkäferbefall sowie Dispenser mit Anti-Aggregationspheromonen im Rahmen der vorgestellten Modellstudien diskutiert.

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1 Introduction

1.1 Current knowledge and methodological approaches

The following sections will depict the current knowledge and methodological approaches concerning climate change, bark beetle disturbances, and simulation tools for analysis and decision-making (Figure 1.1). First, climate change and its effects on disturbances and pest calamities in managed and unmanaged forests of Europe will be highlighted. After that, a condensed literature review will be given on the ecology and management of the European spruce bark beetle *Ips typographus*. In the end, insights into models as tools for analysis and decision-making will be presented, emphasizing the importance of modeling and different examples in decision-making in general and, for *Ips typographus* in particular.

1.1.1 Climate change, disturbances and pest calamities in forests of Europe

Climate change and forests of Europe

Historical situation As one of the most abundant ecosystems in Central Europe, forests underlie varying biotic and abiotic drivers such as storms, insects, or human intervention. As a result, different aspects of the forest ecosystem are impacted, such as species distribution, stand structure, or forest extent, which can affect the drivers mentioned above and their impact on the ecosystem. In contrast to other biomes, the climate change sensitivity of forests stems from the long life span of trees and the resulting disability to adapt to rapid environmental changes (Profft and Frischbier, 2009; Lindner et al., 2010). In recent years, climate change could be observed to alter and impact drivers of forest dynamics (Seidl et al., 2011), leading to more likely and more intense disturbances in European forests (Seidl et al., 2014). This intensification is further impacted by past management decisions, as species and stand structure richness was reduced to increase standing timber volume (Seidl et al., 2011). After large-scale deforestation in medieval times, today's Central European forests are often restricted to sites with sub-optimal conditions such as shallow soil, nutrient deficiency, or water deficiency or surplus, respectively (Frischbier et al., 2014). Between 1600 and

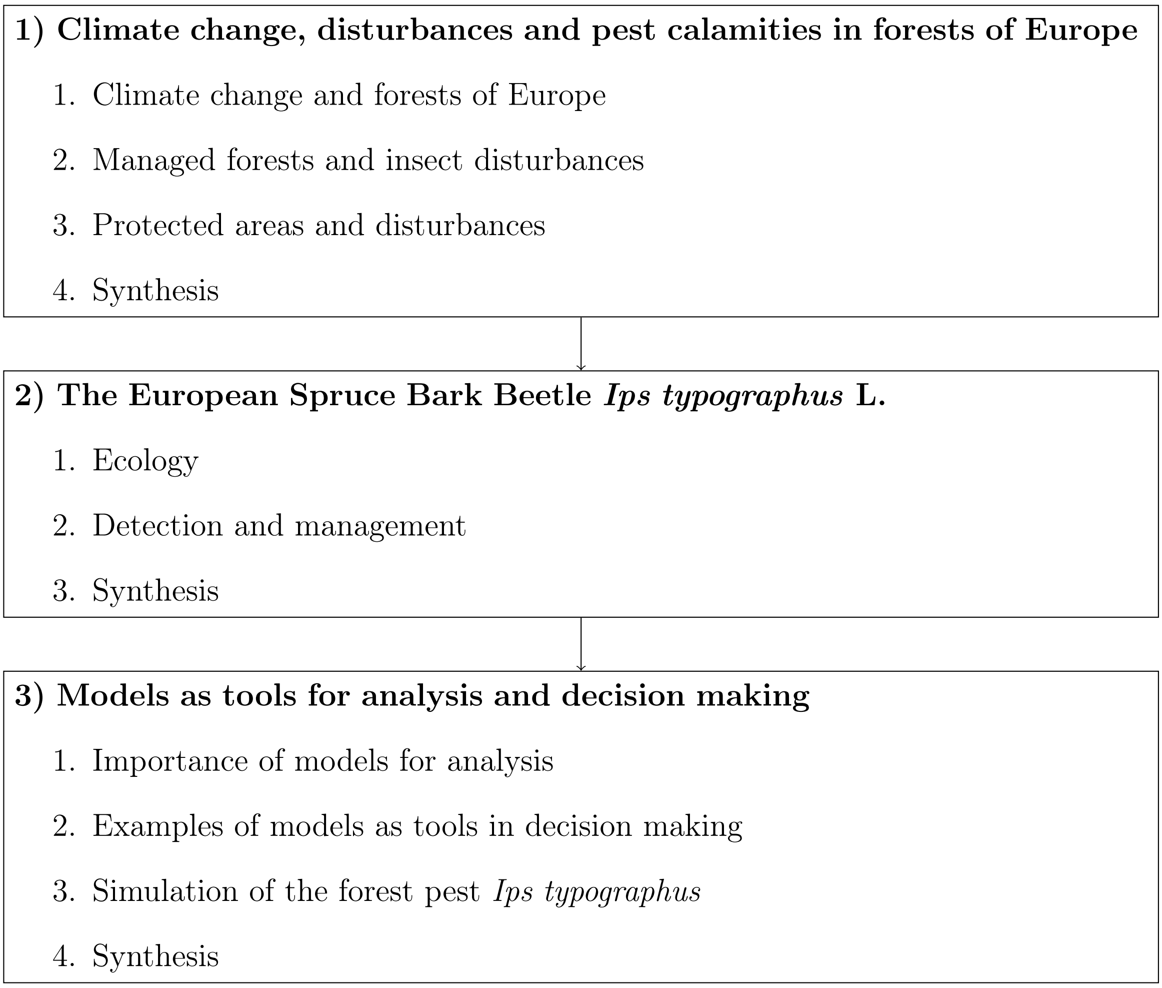

Figure 1.1: Outline of current knowledge and methodological approaches section of the dissertation

2010, the area of deciduous forests converted into conifers amounted to 538,000 km^2, and the area with high-stand management increased by 818,000 km^2 (McGrath et al., 2015). In addition, the area of unmanaged forests decreased by 612,000 km^2 (McGrath et al., 2015) and the share of forests with a mean age of above 100 years decreased from 26 % in 1950 to 17 % in 2010 (Vilén et al., 2012). Compared to other biogeographical regions, the adaptation potential of European forests is considered to be pretty low, as the genetic and structural diversity is limited (Frischbier et al., 2014). Reasons for this assessment are seen in the low biodiversity and the low connectivity of populations and biotopes in the cultural landscape and the loss, genetic depletion, and specialization of species partly because of refugees during and re-migration after glaciation of Europe (Frischbier et al., 2014). With a baseline like this, profound vulnerability analysis is needed to adequately respond to climate change and develop adaptation strategies (Frischbier et al., 2014).

Climate change Global warming is leading to more visible changes in the Earth's climate, including increased temperatures and a higher frequency of extreme weather events such as heat waves and droughts (Seidl and Kautz, 2022). Higher latitudes and land areas are experiencing more substantial warming than equatorial regions or oceans, resulting in an increased likelihood of heatwaves (Seidl and Kautz, 2022) and fewer annual frost days (Jacob et al., 2014). Rising temperatures also increase the variability of summer temperatures within and between years (Schär et al., 2004; Fischer et al., 2012), leading to increased disturbance activity from insects, pathogens, and fire (Seidl and Kautz, 2022). The warmer climate also reduces the frequency of disturbance-inhibiting effects such as a decrease in snow-related disturbances (Gobiet et al., 2014; Seidl et al., 2017). The impact of climate on disturbances is consistent between temperate and boreal ecosystems (Seidl et al., 2020), with an expected increase in disturbances in boreal forests as northern latitudes warm faster than the global average (Stocker et al., 2013; Seidl and Kautz, 2022). Precipitation changes are less consistent than temperature changes. There has been a slight increase in global summer precipitation per decade between 1901 and 2008 (Stocker et al., 2013). Projections with stabilization of radiative forcing of 4.5 W per m^2 (RCP4.5) show up to a 25 % increase in mean annual precipitation in some parts of Europe and up to a 15 % decrease in others (Jacob et al., 2014). These differences are mainly due to changes in spring, summer, and autumn precipitation (Seidl and Kautz, 2022), with winter precipitation expected to remain stable. In winter, precipitation is expected to increase across Europe except for Andalusia, Sicily, and southern Greece (Jacob et al., 2014). More frequent heavy rainfall events and more extended summer dry periods will likely occur, particularly in Southern Europe (Jacob et al., 2014). Decreased precipitation and longer dry periods increase the likelihood of bark beetle outbreaks or fires and reduce floods, pathogens, and avalanches (Seidl and Kautz, 2022). These effects are amplified by warmer temperatures (Seidl et al., 2020), and the role of precipitation in disturbance regimes decreases with increasing latitude (Seidl et al., 2017). Predictions of future wind changes are more uncertain than temperature and precipitation changes (Nikulin et al., 2011; Shaw et al., 2016; Seidl and Kautz, 2022). There may be a slight decrease in average wind speed and the probability of strong wind events (Ulbrich et al., 2009; Kjellström et al., 2011), but an increase in maximum wind speeds could lead to more frequent disturbances (Seidl et al., 2017). Climate scenarios for the next century predict a 23 % increase in storm damage in Europe

(Ranson et al., 2014).

Direct effects of climate change on forest disturbances The direct effects of climate on disturbance activities are more pronounced for abiotic than for biotic disturbances (Seidl et al., 2020). For example, increased wind speeds can lead to larger areas of wind throw and could advance the spread of fire (Gardiner et al., 2010; Billmire et al., 2014). Elongated dry seasons can reduce dead organic material's humidity and increase the vulnerability to fires (Williams and Abatzoglou, 2016). Biotic disturbance agents are primarily driven by climate's influence on temperature and metabolism's dependency on temperature thresholds (Seidl and Kautz, 2022). For example, increased temperatures can increase the number of generations per year for bark beetles (Jönsson et al., 2011), reduce winter mortality (Koštál et al., 2011), and increase the range of suitable regions that were previously too cold (Battisti et al., 2005). The responses of disturbances to direct climate effects are typically prompt and often non-linear (Seidl and Kautz, 2022). Minimum wind speeds are often needed for wind disturbances to occur (Blennow et al., 2010), and snow avalanches only happen within an exact temperature range (Germain et al., 2009). Upper-temperature thresholds for insect populations exist, beyond which reproduction and metabolism will be reduced and subsequently stop (Lange et al., 2006; Baier et al., 2007). Besides its impact on large-scale disturbances such as storms or forest fires, climate change also influences selective small-scale failure of individual tree species, forest structures, or forest development phases due to drought, frost, or species-specific pests (Frischbier et al., 2014). In addition, climate change gradually modifies site and environmental conditions such as climatic water balance or vegetation period length (Frischbier et al., 2014), which play an essential role in the vitality of trees and their abilities to fend off pathogens or diseases (Netherer and Nopp-Mayr, 2005).

Indirect effects of climate change on forest disturbances Climate-induced vegetation structure and composition changes are indirect climate effects (Seidl and Kautz, 2022). These changes can significantly impact forest health and function but often occur with a delay (Seidl and Kautz, 2022). For example, reduced net primary production due to dry conditions can result in less flammable material and a reduced forest fire risk (Pausas and Ribeiro, 2017). Conversely, with adequate precipitation, warming, and increased CO2 density, productivity can increase (Cao and Woodward, 1998; Reyer et al., 2014), leading to more giant trees and higher susceptibility to wind throw (Blennow et al., 2010). Changing tree species composition due to rising temperatures can also impact the forest's predisposition to host-specific biotic disturbances such as bark beetles (Temperli et al., 2013), potentially neutralizing the direct effects of increased bark beetle populations (Seidl and Kautz, 2022). Many indirect effects have the potential to weaken disturbance effects after a considerable time delay (Seidl and Kautz, 2022). For example, climate change-induced extension of the vegetation period increased atmospheric CO2 concentration, and regional precipitation may positively affect forests (Araujo et al., 2011; Milad et al., 2011), with the most significant positive effects expected in northern and western Europe for a short to medium period (Lindner et al., 2010). In the longer term, increasing drought and disturbance risks will likely cause adverse effects, which will most likely outweigh positive trends in southern and eastern Europe (Lindner et al., 2010).

Climate change also affects interactions between disturbances (Seidl and Kautz, 2022), an essential part of the disturbance system (Canelles et al., 2021). These interactions can reinforce or dampen, with positive influences being more dominant than negative ones on a global scale (Seidl and Kautz, 2022). For example, abiotic disturbances can reinforce biotic agents (Seidl et al., 2017): Increased root pathogen activity due to climate change can reduce tree stability and increase susceptibility to windthrow (Whitney et al., 2002), which is an essential factor for bark beetle outbreaks (Wermelinger and Jakoby, 2022) and can reinforce bark beetle disturbances under warmer climatic conditions (Seidl, 2017). On the other hand, negative interactions between disturbances reduce resources for subsequent disturbance events (Seidl and Kautz, 2022). For example, severely burned forests usually have a low probability of being burned again or infested by bark beetles soon (Hart et al., 2015; Seidl et al., 2016a).

Climate change is a significant driver of forest disturbances, along with drought, fire, landslides, pollution, pathogens, snowstorms, wind, and floods (Canelles et al., 2021). However, past and current management interventions also strongly influence forest dynamics in Europe (Seidl et al., 2011). For example, while increased temperatures and droughts mainly drive the area of forests burned due to climate change, wind, and bark beetle damage are mainly driven by changes in forest extent, species composition, and stand structure (Seidl et al., 2011), which are directly influenced by forest management. Therefore, an overview of forest pest disturbances and management is provided as an example of risk management in the forests of Europe.

Managed forests and insect disturbances

Insect pests Insect pests significantly impact forest landscapes, affecting almost 35 M ha annually, mainly in boreal and temperate biomes (van Lierop et al., 2015). Changes in temperature, precipitation, and drought can affect insect development and reproduction (Ayres and Lombardero, 2000; Kingsolver et al., 2011), resulting in changes in population dynamics and outbreaks. Insect outbreaks can be affected by various disturbances, such as drought (Sangüesa-Barreda et al., 2015; Temperli et al., 2015), forest management (Bauce and Fuentealba, 2013; Rosenberger et al., 2018), fire (Parker et al., 2006; Chou et al., 2010; Hicke et al., 2012; Jenkins et al., 2014), windstorms (Reyes and Kneeshaw, 2008; Potterf and Bone, 2017), pollution (Roth et al., 1998; Agrell et al., 2005), and other pests or diseases (Jones et al., 2015; Borkowski and Skrzecz, 2016). Forest management can positively and negatively affect insect outbreaks at different scales, from individual trees to landscapes (Hindmarch and Reid, 2001; Ager et al., 2007; Johansson et al., 2007; Temperli et al., 2014). Higher temperatures and changes in moisture availability may increase insect development and survival rates (van Lierop et al., 2015; Malesky et al., 2018). As a result of climate change, atmospheric pollution, species introductions, and land-use change, pest outbreaks in forest ecosystems have increased (Allen et al., 2015; Anderegg et al., 2015; Battipaglia et al., 2014; Creeden et al., 2014; Kollberg et al., 2015; Meddens et al., 2015; Gunst et al., 2016). In particular, a changing climate is expected to increase insect outbreaks' frequency, severity, and duration (Dale et al., 2001; Gray, 2008; Volney and Fleming, 2007; Dukes et al., 2009; Bentz et al., 2010).

Mixed forest stands The quantitative review of more than 600 study cases by Jactel et al. (2020) found that insect herbivory was, on average, lower in mixed forest stands than in pure stands. However, the extent to which tree species diversity reduced damage depended on herbivore diet breadth and tree species composition (Jactel et al., 2020). In particular, tree species diversity effectively reduced damage from specialist herbivores in mixed stands with phylogenetically distant tree species (Jactel et al., 2020). Pest management has traditionally relied on agrochemicals, which are effective for short-term control of pests (Jactel et al., 2020). However, the negative environmental consequences of their widespread use, including persistence in the environment and the development of pest resistance, have become a significant concern (Holmes and MacQuarrie, 2016). Pest diversity increases with tree diversity at low levels but is reduced at higher levels of tree diversity (Guo et al., 2019). This increase suggests that tree diversity can regulate pest invasion through facilitation and dilution, with their relative strengths varying depending on overall diversity (Guo et al., 2019). In the last decades, an increasing amount of literature supports the associational resistance hypothesis (Barbosa et al., 2009), which states that more diverse plant communities are less susceptible to insect damage (Iverson et al., 2014), which includes forests (Jactel and Brockerhoff, 2007; Vehviläinen et al., 2007; Castagneyrol and Jactel, 2012). One reason for the increased resistance of diverse plant communities to insect damage may be that herbivores have a more challenging time locating and reaching host plants when diluted among non-host plants (Castagneyrol et al., 2014; Tahvanainen and Root, 1972; Jactel et al., 2005). In addition, species richness and abundance of natural enemies of pest species usually increase with plant diversity (Scherber et al., 2010; Castagneyrol and Jactel, 2012).

Integrated pest management In forest management, control and measures against pests are defined as integrated pest management: '[...] a decision-based process involving coordinated use of multiple tactics for optimizing the control of all classes of pests [...] in an ecologically and economically sound manner' (Prokopy, 2003). This definition implies four main aspects for the forest management practice (Ehler, 2006): simultaneous management of multiple forest pests, monitoring of pests as well as their natural enemies or antagonists, usage of treatment or economic thresholds for the application of pesticides, and, integrated usage of multiple and suppressive tactics. Management measures for reducing the emergence and severity of pest damages include promoting mixed-species and age-heterogeneous forests that are well adapted to the site they are growing (Kausrud et al., 2012). In order to keep the damage of pest disturbances low and to reduce the spread to further forest parts, significant accumulations of damaged logs should be debarked or removed before the next pest swarming (Kausrud et al., 2012). On the other side, removing all the dead wood on damaged sites is not advised as this may reduce the diversity and abundance of predator and natural enemies of the given forest pest (Kausrud et al., 2012). Measures to reduce the vulnerability of forests to climate change should reduce forest sensitivity to adverse climate change effects or increase their adaptive capacity to cope with changing environmental conditions (Kolström et al., 2011). Examples of such measures are selecting more drought-resistant species and genotypes (Kolström et al., 2011) or diversifying forest structure by applying continuous cover forestry as uneven-aged stands to decrease the volume of damaged trees or woody biomass due to wind disturbances (Pukkala et al., 2016; Potterf et al., 2022).

As peaks of disturbances seem to be driven mainly by natural events and affect managed and unmanaged areas simultaneously (Senf et al., 2017), protected areas of different spatial scales can provide insights into the development and possible resilience of forests after various disturbances without management intervention providing valuable information on the direction and severity of disturbance agents (Senf et al., 2017). On the other side, protected areas can endanger surrounding forests, for example, with the spread of forest pests (Potterf et al., 2019) or be endangered by invading alien species (Tunison et al., 2001; Coleman et al., 2011; Krzyżanowska et al., 2018).

Protected areas and disturbances

Definition Protected areas are described as 'clearly defined geographical space[s], recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values' (Dudley, 2008). While this definition focuses on protected areas' geographical, legal, and temporal dimensions, their purpose, spatial extent, or management intensity can vary greatly. As such, the International Union for Conservation of Nature and Natural Resources (IUCN) lists seven categories of protected areas (Dudley, 2008): strict nature reserve, wilderness area, national park, natural monument, species management area, protected landscape/seascape, a protected area with sustainable use of natural resources. For example, the strict nature reserve (Ia) is the most strictly protected category, with no or very dedicated management, and does not define a particular spatial extent (Dudley, 2008). As another example, a national park (category II) is defined as a large area where natural development is the primary goal of a large proportion of the park (Dudley, 2008).

Opportunities Protected areas provide a unique opportunity for comparing and examining disturbances at various scales and types. Senf et al. (2017) found that protected areas can be used to compare the effects of disturbances on managed and unmanaged landscapes. A study focusing on disturbances in nature reserves and surrounding forests with timber yield management in Slovakia found that forests in the reserves seemed to be less affected by disturbances than the managed forest areas despite management efforts to reduce disturbance risks (Potterf et al., 2022). Furthermore, protected areas can be used to study the effectiveness of standard control efforts, such as conservation practices and restoration efforts, in a non-managed environment (Clarke and Billings, 2003). One specific example of using protected areas for restoration is the re-introduction of wolves into the Yellowstone environment (Ripple and Beschta, 2003). This management action has helped to restore the balance of the ecosystem and promote the preservation of biodiversity, including the restoration of riparian species.

Risks and conflicts Protected areas can face various risks and conflicts. One such risk is the invasion of exotic plants. According to a study by Balaguru et al. (2016), exotic plants can threaten the biodiversity and integrity of protected areas by changing the species composition and disrupting the nutrient cycling and hydrology of the habitat. In some cases, wildlife in protected areas can also pose a risk to humans. For example, bison in Yellowstone National Park have been found to carry *Brucella abortus*, the causative agent of brucellosis, which can be transmitted to cattle in the surrounding areas (Kilpatrick et al., 2009). In addition to direct risks and conflicts, protected areas can also face indirect challenges, such as losing local support for conservation efforts. For instance, a study by (Naughton-Treves, 1998) found that crop loss to wildlife in Uganda's Kibale National Park led to local resistance to conservation efforts. The study found that fields within 500 meters of the forest boundary lost 4 to 7 % of their crops on average per season, with some fields being destroyed. In national parks such as the Bavarian Forest (Germany) or the Tatra Mountains (Polen and Slovenia) with extensive and spruce-dominated forests, large-scale infestations and mass outbreaks of the European spruce bark beetle could be observed during the last decades (Grodzki et al., 2006; Müller et al., 2008). These mass outbreaks can risk surrounding forest areas, as insect infestations from windthrown and beetle-killed trees inside the protected area can spread outward (Potterf et al., 2019).

Synthesis

Increasing disturbances, temperatures, droughts, and forest management have led to European forests' vitality loss and dieback. From 2018 to 2020, around 160 million cubic meters of woody biomass were damaged alone in Germany (BMEL, 2020). Protected areas can provide insights into the natural resilience of European forests after disturbances but face conflicts such as mass outbreaks and the spread of insect pests that can threaten their biodiversity, natural habitats, and surrounding landscapes. The European spruce bark beetle (*Ips typographus*) is among the most critical and severe forest pest species in Europe and can act as an ecological disturbance Wermelinger and Jakoby (2022). Because of this and that there is no weakening to be expected in the future due to the ongoing climate change (Wermelinger and Jakoby, 2022), a condensed review on the ecology and management of this bark beetle species will be given in the following section.

1.1.2 The European Spruce Bark Beetle *Ips typographus* L.

There are a variety of publications on the ecology and management of *Ips typographus* ranging from scientific articles, such as Morris et al. (2017); Havašová et al. (2017); Mezei et al. (2017); Thorn et al. (2018); Dobor et al. (2020), and reviews, like Christiansen and Bakke (1988); Stenseth and Kirkendall (1989); Wermelinger (2004)), over books (Hoch et al., 2020) and theses, such as Dworschak (2013); Kautz (2013), to practical guidance (NW-FVA, 2015) and newspaper articles, such as Sonnemann et al. (2020); Peter et al. (2020). This strong representation in all kinds of literature types and contents of knowledge highlights the importance of this insect for the European forestry section. In the following paragraphs, a condensed review on the ecology, detection, and management of *I. typographus* is presented based on the first comprehensive literature review from Wermelinger (2004), which was enhanced by literature from 2004 to 2022.

Ecology

Remigration after ice age It is suggested that during the ice age, the refugial areas of the European Spruce Bark beetle (*Ips typographus*) and of its host tree (*Picea abies* (L.) Karst.) were located in the south (Apennine, Dinaric, and Carpathian Alps) and north of Moscow (Stauffer et al., 1992, 1999; Wermelinger, 2004). From there, the insect remigrated to Central, Northern, and Western Europe with its host tree.

Closely related bark beetle species are *Ips amitinus*, *Ips cembrae*, and *Ips acuminatus* (Stauffer et al., 1997).

Host tree colonization The Norway spruce (*Picea abies*) is the preferred host for colonization by so-called pioneer males of *Ips typographus* (Wermelinger and Jakoby, 2022). According to Byers (2004) and (Saint-Germain et al., 2007), these males are primarily guided by visual cues and the presence of specific volatile chemicals in the host tree (kairomones) to locate suitable trees for colonization. Once they have found a suitable tree, they bore into the bark and release chemicals called aggregation pheromones, which consist of monoterpenoids (Blomquist et al., 2010). These pheromones attract other members of their species to the tree (Wermelinger and Jakoby, 2022). The beetles mate under the bark, and the females then lay their eggs in the galleries created by the males (Wermelinger and Jakoby, 2022). The hatched larvae develop in the nutrient-rich phloem of the tree and pupate at the end of their larval galleries (Wermelinger and Jakoby, 2022).

Temperature dependency The development and reproduction of *I. typographus* is temperature-dependent (Netherer et al., 2019; Wermelinger and Seifert, 1998, 1999). The minimum temperature for the development of *I. typographus* is 8.3 °C (Coeln et al., 1996; Wermelinger and Seifert, 1998). For the beetle to complete its entire life cycle, a heat sum of 334 (Wermelinger and Seifert, 1998) or 365 (Wermelinger, 2004) is required. Temperature also affects the reproduction of *I. typographus* (Wermelinger and Seifert, 1998, 1999): The minimum temperature for egg production is 11.4 °C, while the optimum temperature for juvenile development is 30.4 °C and for reproduction is 28.9 °C (Wermelinger and Seifert, 1998, 1999). Intra-specific competition due to high breeding density can affect the behavior and reproduction of *I. typographus* (Wermelinger, 2004). This impact can result in shorter maternal galleries and reduced oviposition (Anderbrant, 1990). The sex ratio of the progeny also depends on the gradation phase, with much more than 50 % females at the beginning and nearly 50 % towards the end of an outbreak (Lobinger and Skatulla, 1996). The winter mortality rate for *I. typographus* is roughly 50 % for adults (Faccoli, 2002) and can be up to 100 % for eggs and larvae (Netherer, 2003; Koštál et al., 2011; Dworschak et al., 2014).

Flight activity The flight activity of the European Spruce bark beetle is influenced by several factors, including temperature (Funke and Petershagen, 1994; Lobinger, 1994; Wermelinger et al., 2012), hours of sunshine (Baier et al., 2007; Doležal and Sehnal, 2007), and rain (Marini et al., 2012; Stadelmann et al., 2013). Temperature is one of the main factors affecting bark beetle flight activity (Funke and Petershagen, 1994; Lobinger, 1994; Wermelinger et al., 2012): At a minimum temperature of 16.5 °C, bark beetles will begin to fly. Optimum flight conditions are between 22 and 26 °C, while flight activity will be reduced at temperatures above 30 °C (Funke and Petershagen, 1994; Lobinger, 1994; Wermelinger et al., 2012). In addition to temperature, the number of hours of sunshine can also impact bark beetle flight activity (Baier et al., 2007; Doležal and Sehnal, 2007): Reduced flight activity has been observed when there are fewer than 17 hours of sunshine, and the onset of diapause (a period of reduced activity) has been observed at 14.5 hours of sunshine or less. Rain can also inhibit bark beetle flight activity (Marini et al., 2012; Stadelmann et al., 2013). Pioneering males tend to emerge and begin flying earlier than females (Zuber and Benz, 1992). Other flight parameters for bark beetles include a speed of 5 meters per second, a height of mostly below 20 meters, and a distance of one to five kilometers (Forsse and Solbreck, 2009). Most individuals will remain within 500 meters of the source if enough breeding material is present (Wichmann and Ravn, 2001; Kautz et al., 2011; Stadelmann et al., 2013; Kautz et al., 2016).

Host tree selection and chemical communication *Ips typographus* individuals use pheromones to communicate with each other and select suitable breeding sites. The selection of host trees for breeding is influenced by several factors, including tree vitality and habitus (Byers, 2004). However, the main driver of host selection is the presence of kairomones (Faccoli and Stergulc, 2004; Pureswaran and Borden, 2005), which are chemical compounds (volatiles) emitted by the host tree that attract bark beetles (Byers, 2004). Once an *Ips typographus* individual successfully infests a host tree, it will begin to emit aggregation pheromones (Faccoli and Stergulc, 2006) attracting both sexes alike (Schroeder, 2010). The aggregation pheromones produced by infesting *I. typographus* are much more attractive than the kairomones of the host tree (Wermelinger, 2004; Schroeder, 2010). If the substrate is unsuitable for breeding or already fully occupied (Schlyter et al., 1989; Byers, 2004), the bark beetle will produce repellent pheromones (Francke et al., 1995). These anti-aggregation pheromones are so potent that they can reduce the attractiveness of traps baited with aggregation pheromones (Niemeyer et al., 1995b; Reddemann and Schopf, 1996; Zhang et al., 1999). Only after their energy reserves have been depleted will bark beetles begin to react to pheromones (Gries, 1985; Nêmec et al., 1993).

Dispersal and infestation distances When marked and released individuals of *Ips typographus* are recaptured, it is found that only about 8 % are recovered at a distance of 100 meters, and only about 2 % are recovered at distances of 1200 - 1600 meters (Weslien and Åke Lindelöw, 1990). These rates are similar to those found by other researchers (Zumr, 1992; Duelli et al., 1997). During epidemic conditions, new infestations of *Ips typographus* often appear within 100 meters of the original infestation site (Havašová et al., 2017; Netherer et al., 2019). However, during endemic conditions, new infestations can appear several kilometers from the source (Forsse and Solbreck, 2009; Zumr, 1992; Schroeder, 2010). Reemerging parent beetles, which are those that produce sister broods, seem to facilitate reduced dispersal distances (Zolubas and Byers, 1995). At most, only about one-third of a bark beetle population will directly respond to pheromones after emergence (Wermelinger, 2004). In bivoltine populations with two generations per year, the first generation tends to disperse more extensively than the second generation (Furuta et al., 1996).

Natural enemies Natural enemies of *I. typographus* include several predatory and parasitic insects, as well as pathogens. The most predominant antagonistic insects of *I. typographus* include Cleridae (predatory beetles), Dolichopodidae (flies), Lonchaeidae (flies), Pteromalidae (parasitic wasps), as well as Braconidae (both predatory and parasitic wasps) (Weslien and Schroeder, 1999; Wermelinger, 2002; Wermelinger et al., 2012). The species assemblage of these natural enemies depends on the host tree species, the bark texture (Lawson et al., 1996), and the section of the tree infested (Wermelinger, 2002). Host-finding by natural enemies of *I. typographus* mostly occurs through the detection of volatiles (Mills et al., 1991) produced either by the host tree, by microorganisms introduced by the bark beetle (Pettersson, 2000, 2001; Sullivan et al., 2000) or by *Ips typographus* itself (Bakke and Kvamme, 1981; Aukema et al., 2000; Zhou et al., 2001). Natural enemies of *I. typographus* typically reach and leave the trees later than their prey (Weslien and Regnander, 1992; Wermelinger, 2002), which can make it difficult for them to control the population of bark beetles effectively. However, the number of natural enemies increases during outbreaks of *I. typographus* (Weslien, 1994; Aukema and Raffa, 2004b,a; Latty and Reid, 2009), which can help to reduce the damage caused by the beetles. Silvicultural practices can influence the occurrence and efficiency of natural enemies of *I. typographus* (Schlyter and Lundgren, 1993; Weslien and Schroeder, 1999). Pathogens are more frequently found in late-emerging beetles (Wegensteiner and Weiser, 1996), and mortality in the offspring production due to parasitism and predation can range from 30 % to 82 % (Wermelinger, 2002). Cold winter temperatures can kill both bark beetles and their natural enemies (Faccoli, 2002), while damp conditions can promote infections with fungi (Wegensteiner et al., 2015).

Host tree defense The susceptibility of trees to infestations by *Ips typographus* is influenced by several factors, which include the bark anatomy and physiological condition of the tree (Wermelinger, 2004). The first level of tree defense against bark beetles is the release of stored resin upon penetration attempts (Baier, 1996b,a; Rohde et al., 1996; Lieutier et al., 1997; Paczkowski et al., 2021). This release is known as primary, preformed, or constitutional resistance (Paine et al., 1997). Trees with thick bark and dense resin ducts are more resistant to bark beetle infestation (Nihoul and Nef, 1992; Baier, 1996b), and higher resin flow has been observed in mixed stands of trees (Baier et al., 2002). The second level of tree defense involves changes in the local metabolism around the entrance holes made by the bark beetles (Wermelinger, 2004). This metabolism change includes the production of defensive chemicals, such as procyanidins, which can impair the food quality and hinder the establishment of bark beetle broods (Rohde et al., 1996; Kautz et al., 2014; Krokene, 2015). The third level of tree defense involves systemic changes in the whole tree metabolism (Wermelinger, 2004). Trees will produce fewer carbohydrates but more proteins needed for defense against bark beetles (Wermelinger, 2004). If the attack density of bark beetles is high, the fourth level of tree defense involves the formation of new periderm tissue and resin ducts as a wound reaction (Wermelinger, 2004). It is assumed that 30 to 200 simultaneously attacking beetles are needed for a successful infestation of a Norway spruce (Jönsson et al., 2007).

Predisposition of forest stands Forest stands with a higher proportion of spruce trees are more likely to be affected by infestations of *Ips typographus* (Netherer and Nopp-Mayr, 2005; Faccoli and Bernardinelli, 2014; Bryk et al., 2021). Older trees are also more susceptible to bark beetle infestation (Becker and Schröter, 2000; Wermelinger, 2004; Netherer and Nopp-Mayr, 2005; Kärvemo et al., 2014; Thiele et al., 2017; Mezei et al., 2017), as they are less able to defend themselves against the beetles. Exposure to the sun and wind can also increase the susceptibility of a forest stand to bark beetle infestation (Lobinger and Skatulla, 1996; Jakuš, 1998b; Netherer and Nopp-Mayr, 2005; Hais and Kučera, 2008; Faccoli and Stergulc, 2004, 2006, 2008; Stadelmann et al., 2014; Sproull et al., 2016; Paczkowski et al., 2021). Stands that are exposed to more sunlight and wind are more likely to be affected, as these conditions can help the bark beetles to disperse and establish new infestations. Soil productivity (Dutilleul et al., 2000; Netherer and Nopp-Mayr, 2005) and water supply (Lexer, 1995; Netherer and Nopp-Mayr, 2005) can also affect the susceptibility of a forest stand to bark beetle infestation. Stands on productive soils with adequate water supply are more likely to support large populations of bark beetles. Similarly, stands at higher elevations (Netherer and Nopp-Mayr, 2005; Faccoli and Bernardinelli, 2014; Chinellato et al., 2014; Sproull et al., 2016) are more susceptible to bark beetle infestation, as the beetles can survive and reproduce at higher temperatures. Finally, the presence of heart rot can increase the susceptibility of a forest stand to bark beetle infestation (Lexer, 1995).

Infestation patterns The dynamics of infestations by *Ips typographus* are influenced by a range of factors, including the abundance of natural enemies, the health of the host trees, and environmental conditions. During endemic conditions, when the population of *I. typographus* is low, the beetles only infest weakened or sick trees, as they cannot overcome the defense of healthy trees (Faccoli and Stergulc, 2008; Faccoli, 2009). However, when favorable conditions such as a low abundance of natural enemies, weakened host trees, drought, or storms arise (Wermelinger, 2004), the population of *I. typographus* can increase rapidly and transition from endemic to epidemic conditions (Raffa et al., 2008). Starting points for gradations, or large-scale infestations, can combine wind throws, water stress, and increased mean temperatures (Wermelinger, 2004). Snow breaks, other wind throws, and heavy cone production can amplify and prolong the outbreak (Heurich, 2001). After storms with broken trees or at low elevations, the abundance of bark beetles tends to peak in the second summer after the incident (Wermelinger, 2004). In contrast, after storms with uprooted trees or in mountain ranges, the abundance tends to peak within the third summer (Forster, 1993; Wermelinger and Seifert, 1999; Becker and Schröter, 2000; Göthlin et al., 2000). *I. typographus* prefers broken or wind-thrown trees over remaining stumps (Feiger et al., 1996; Göthlin et al., 2000) and large trunks over thin ones (Wermelinger, 2004). As the density of maternal galleries increases, the number of larvae decreases (Anderbrant, 1990). Over the period from 1958 to 2001, forest loss due to mass outbreaks of *I. typographus* is estimated to be approximately 2.88 million cubic meters, and an increase in the following decades is expected (Schelhaas et al., 2003; Seidl et al., 2011). Climatic changes drive the frequency and intensity of the population dynamics of *I. typographus* (Allen et al., 2010; Marini et al., 2012; Faccoli and Bernardinelli, 2014; White, 2015), with increasing temperatures and changes in precipitation patterns likely to lead to more frequent and severe outbreaks in the future.

Detection and management

Salvage logging Salvage logging is removing wind thrown timber and felling infested trees to reduce the infestation risk of nearby trees. This logging is especially effective if done on time, as noted by (Göthlin et al., 2000; Grodzki et al., 2003, 2006; Stadelmann et al., 2013; Havašová et al., 2017). When performing salvage logging, it is crucial to prioritize larger areas to minimize subsequent damage, as suggested by (Schroeder, 2013). One effective method of salvage logging is known as sanitation felling, which involves cutting trees before the emergence of adult beetles (Wermelinger, 2004) and within a radius of approximately 100 m around infested trees (Kautz et al., 2011). The disposal of the brood should also be considered, as burning or chipping are both appropriate methods (Wermelinger, 2004). It is crucial to avoid cutting or debarking during the winter months, as this can also kill antagonists (Wermelinger et al., 2012). Infested logs can also be used as traps if the removal occurs after the spring generation's infestation and before the emergence of the new generation (Wichmann and Ravn, 2001). Debarking is a potentially less elaborate measure for this time-sensitive situation (Wermelinger, 2004; Schroeder, 2010). In order to achieve a lasting reduction of the population and reproduction rate, a persistent application of sanitation felling or debarking is necessary (Jönsson et al., 2012), which should reduce the population by 80 to 95 % to be effective (Fahse and Heurich, 2011). However, it should be noted that persistent and broadly applied sanitation felling can reduce deadwood biomass and negatively affect the biodiversity of saprobiontic insects (Lindenmayer et al., 2008; Waldron et al., 2013; Thorn et al., 2018). For this reason, it is not recommended in protected areas such as national parks (Thorn et al., 2018).

Beetle trapping Bark beetle trapping is a method of catching bark beetles using pheromones and traps. The amount of beetles caught varies greatly depending on conditions such as exposition, sun exposure, temperature, and the presence of potential breeding material such as woody debris, log stacks, and wind throw of living trees (Lobinger, 1995). However, it should be noted that at most, only up to 10 % of the population can be caught with pheromone traps (Weslien and Åke Lindelöw, 1990; Lobinger and Skatulla, 1996; Baier et al., 2007), making them insignificant as a protection measure (Dimitri et al., 1992; Lobinger and Skatulla, 1996; Wichmann and Ravn, 2001). While low trap catches can correlate with low infestations, the opposite does not necessarily have to be the case (Weslien, 1992; Lindelöw and Schroeder, 2001). Traps can be facilitated to prevent attacks on living trees (Niemeyer et al., 1990; Dubbel et al., 1995; Jakus, 2001), but this requires significant effort (Dimitri et al., 1992; Jakuš, 1998a). Trap trees (trees or logs deployed with a pheromone dispenser and optional insecticide application) are considered to be up to 14 (Drumont et al., 1992) or up to 30 times (Raty et al., 1995) more efficient than artificial traps. Extensive use of such trap trees has been reported to protect windfalls (Gregoire et al., 1997).

Chemical control One option for the chemical control of *Ips typographus* is using pyrethroids, a type of synthetic insecticide that can be highly toxic to insects (Drumont et al., 1992). Another option is using azadirachtin, a natural insecticide derived from the seed of the *Azadirachta indica* plant (Hoch et al., 2020). When applying these insecticides, it is crucial to adhere to the principle of minimal risk for human health and the environment (Fettig and Hilszczański, 2015; Hoch et al., 2020). This means protecting oneself from toxic reactions, such as wearing protective gear and maintaining a safe distance from water areas (Hoch et al., 2020). It is also essential to avoid exposing non-target organisms to insecticides (Hoch et al., 2020).

Forest stand management Forest stand management is the process of managing the composition and structure of a forest in order to achieve specific goals, such as improving the health and productivity of the forest, providing habitat for wildlife, or mitigating the effects of climate change. A critical aspect of forest stand management is the reduction of spruce proportion and promoting mixed stands (Neuner et al., 2015; Kärvemo et al., 2016) to reduce the risk and severity of bark beetle infestation. Another critical aspect of forest stand management is carefully selecting sites for spruce plantations. These should only be planted on sites within the ecological optimum of the tree, such as moist, cool sites or sites at higher elevations (Overbeck and Schmidt, 2012; Marini et al., 2012). This can help ensure the spruce trees' health and long-term viability. Bark beetle risk management in forests is a set of strategies and techniques used to reduce the risk of bark beetle infestations and the resulting damage to forests. Following (Kärvemo et al., 2014), these strategies can help use resources efficiently, reduce the additional wood devaluation caused by bark beetles, minimize the infestation risk for forests adjacent to damaged areas, and hinder bark beetle dispersal into other areas. One effective strategy for reducing the risk of bark beetle infestations is to shorten the rotation period, which can reduce the risk over time (Neuner et al., 2015; Thiele et al., 2017). Additionally, it is crucial to focus measures on valuable stands (Schmidt et al., 2010) and on large areas of damaged or infested trees (Schroeder, 2010; de Groot et al., 2021). Timely removal of damaged and weakened trees can also be effective (de Groot et al., 2021), but it is crucial to avoid additional exposure of the forest stand during tree removal (Kautz, 2013).

Synthesis

Large-scale outbreaks of forest insect pests such as *Ips typographus* can be triggered by climate change via increasing temperatures, drought, and storms (Jactel et al., 2019), which emphasizes the importance of improving risk assessment and management systems in forestry (Thom et al., 2013). While it is indicated that forest management can influence important drivers of disturbance regimes directly, it is also emphasized that the corresponding response times are likely to be slow (Thom et al., 2013), requiring, in turn, effective and adaptive risk-assessing management. As simulation models can play an essential and influential role in such a management (Seidl et al., 2022) as decision-making tools or for analysis of essential drivers (Seidl, 2017; Niu et al., 2014), the following section will give an overview of models as tools for analysis and decision making in general and for forest disturbance and pests such as *Ips typographus* in particular.

1.1.3 Models as tools for analysis and decision making

Importance of models in ecology

In the 21st century, every ecologist should in some aspect be involved in modeling due to its increasing importance in all aspects of scientific studies (Seidl, 2017): One reason for the importance of models in ecology lies within their capability to study complex interactions within social-ecological systems as well as to identify variables that drive patterns of interest (Sofaer et al., 2019; Schlüter et al., 2019). Another reason for the models' importance in current years is the broad and ever-increasing range of data on ecosystem characteristics that improve modeling capacities and accuracy (Erb et al., 2017; Sofaer et al., 2019). A third reason for the importance of modeling in ecology can be taken from the current trend of upscaling models, which makes them an essential tool for integrating data from multiple sources and scales alike (Seidl, 2017).

For best results, it is advised to balance empirical and model-based research (Seidl, 2017) and facilitate transparent and open communication to ensure model precision and integration into decision-making processes (Addison et al., 2013). It is highly beneficial to collaborate with experts of other domains (Sofaer et al., 2019) to allow for cross-pollination between methods and to utilize a wide range of tools and approaches (Seidl, 2017). Over time, such collaborations can positively influence scientific productivity (Petersen, 2015). As environmental conditions, information availability, statistical methods, and computational capacity constantly change, iterative modeling approaches, such as updating models based on new data and information, are to be desired (Sofaer et al., 2019). Methods such as surveys or sensitivity analysis help to identify areas of uncertainty in model assumptions or highlight disagreement in the model (Crall et al., 2013). These insights are essential to improve the ongoing modeling process and guide future field studies (Sofaer et al., 2019).

Examples of models as tools in decision making

Infectious disease Infectious diseases are typically described by Susceptible-Infected-Removed (SIR) models, which predict threshold responses to population size and R0, the ratio of contagion to recovery rate (Kermack and Mckendrick, 1927). Despite their usefulness, these models can be challenging to apply, especially for complex diseases like influenza, because crucial parameters must be estimated each year from limited information (Hooten et al., 2010), and the onset of an outbreak is often stochastic, nonlinear, and sensitive to initial conditions (Niu et al., 2014). Despite this, real-time modeling has been used successfully in forecasting outbreaks: During the 2001 foot-and-mouth epidemic in the United Kingdom, real-time modeling helped inform decisions to restrict animal movement and cull livestock populations (Keeling et al., 2003; Tildesley et al., 2008). These actions were credited with controlling the outbreak, and more generally, successes like these have contributed to developing disease modeling as a more predictive science (Tildesley et al., 2008). Outside the context of real-time forecasting, Bayesian state-space models have been used for combined parameter and state estimation in a variety of infectious disease systems (Niu et al., 2014), including measles in sub-Saharan Africa (Ferrari et al., 2008), white pine blister rust in the greater Yellowstone ecosystem (Hatala et al., 2011), and a chronic wasting disease of North American mule deer (Farnsworth et al., 2006).

Fish stock Fish stock assessment models can be used to infer current and target fish stock abundance and the maximum sustainable yield from time series of fish catch data or to reconstruct the virtual abundance of each annual cohort fished from time series of detailed fishery catch-at-age data (Methot and Wetzel, 2013). In addition to stock assessment, species distribution modeling is commonly used to estimate the presence and absence of fish species based on each fishing location's geographical and environmental characteristics (Niu et al., 2014). Examples of commonly used methods include hierarchical Bayesian spatial models (Muñoz et al., 2013) and generalized linear and additive models (GLM and GAM) (Guisan et al., 2002). Bayesian kriging was used to generate maps of horse mackerel occurrence probabilities that incorporate spatial and parameter uncertainties, characteristic geographical data, and chlorophyll a concentration (Muñoz et al., 2013).

Wildfire Fire management often relies on fire frequency, severity, and spread predictions to assist decision-making (McKenzie et al., 2000; Xue et al., 2012). In addition, fire plays a crucial role in the global carbon cycle (Bowman et al., 2009). For example, Linn (2005) modeled the forward spread of grassland fires under different atmospheric conditions and initial fire line lengths. Accurate fire prediction requires not only physical models but also data sets of fuel and weather, which can vary significantly in time and space (Keane et al., 2001). Furthermore, fire behavior is highly nonlinear and complex, with interactions between combustion processes, landscape, atmosphere, vegetation, and human factors (Lavorel et al., 2007). The performance of fire models is also sensitive to boundary conditions, which are often unknown (Sullivan, 2009).

Terrestrial carbon cycle Biogeochemical models on the terrestrial carbon cycle, which range from simple models with dozens of parameters to complex models with thousands of parameters, have been widely used to study ecosystem responses and feedback to climate changes over long time scales (McGuire et al., 2001; Friedlingstein et al., 2006), or to investigate the interactions of multiple global-change factors on land management and ecosystem services on shorter time scales (Schroter et al., 2005; Schmid et al., 2006; Pretzsch et al., 2008).

Species distribution Species distribution modeling can support various decision-making processes, including designing surveys to find new populations, identifying priority areas for conservation and management, and developing regulatory decisions and compliance strategies (Sofaer et al., 2019). This type of modeling can provide valuable information for guiding these decisions and improving the effectiveness of conservation and management efforts (Sofaer et al., 2019).

Simulation of the forest pest *Ips typographus*

General aspects In general, simulation models can be designed to include the effects of uncertain, multiple interacting disturbances characterized by cumulative effects, nonlinear dynamics, cross-scale interactions, and, most importantly, with the potential to capture unobserved dynamics (Clark and Gelfand, 2006; Ager et al., 2007; Taylor et al., 2009; Baker and Robinson, 2010; James et al., 2011; Keane et al., 2015; Maroschek et al., 2015; Leite et al., 2018). Such simulation models are appropriate for assessing changes in insect species ranges, predicting novel insect outbreaks, and anticipating host-insect relationships under novel environmental conditions (Taylor et al., 2009; Maino et al., 2016; Barbet-Massin et al., 2018). Most modeling studies use spatially explicit models at the landscape or stand level and explore more extended time frames than empirical studies (up to 300 years) (James et al., 2011; Hoffman et al., 2012, 2013; Sturtevant et al., 2012; Loehman et al., 2017). The ability to explore long-term dynamics is essential in the case of insect pest disturbances because of the long-term spatial legacies they can create and, in some cases, the cyclical population dynamics they generate (Robert et al., 2020). Future environmental change is uncertain, as are the dynamics of stochastic disturbances. Simulation models allow for the direct integration of this uncertainty through scenario testing. Model-mediated exploration of such uncertain parameter space is essential to understand how different sources of uncertainty might impact the target system (Canelles et al., 2021). Other challenges to developing applicable models of forest disturbance include integrating multiple relevant processes and their interactions at different spatiotemporal scales and modeling them mechanistically (Baker and Robinson, 2010). Addressing these challenges requires explicit assumptions and simplifications, compromising realism while maintaining coherence, internal consistency, and plausible descriptions of modeled dynamics (Baker and Robinson, 2010; Morán-Ordóñez et al., 2019). However, interest in using simulation modeling to explore disturbance interactions seems to be increasing: 83 % of the model-based studies were published after 2010 (Canelles et al., 2021).

Overview on existing models As seen in the section about forest disturbances, one of the primary forest pests benefiting from several climate-induced changes, such as increasing temperatures or decreasing precipitation, as well as other disturbances like wind throw or snow breakage, is the European spruce bark beetle *Ips typographus*. As such, a variety of model applications are present, aiming for different purposes within the pest regime, ranging from predisposition assessment of forest stands for beetle infestations (Netherer and Nopp-Mayr, 2005), over the simulation of seasonal development and assessment of begin of beetle flight (Baier et al., 2007) to the mechanistic description of the beetles' dispersal flight through an artificial forest (Kautz et al., 2014, 2016). In the following paragraphs, a summary of models published within the last two decades on *Ips typographus* will be given, with particular attention to model type, spatial and temporal resolution as well as the purpose of these models (Table 1.1).

PAS The predisposition assessment systems from Netherer and Nopp-Mayr (2005) aim to provide tools for understanding the complex relationships between natural disturbances and predisposing site and stand-related characteristics in forest management. The systems were developed using knowledge-based expert models for hazard assessment and identified critical factors for the predisposition of forests to various biotic and abiotic agents. The specific model for the European spruce bark beetle was applied and verified in the High Tatra Mountains and found to correspond significantly to the pattern of bark beetle attacks in the research area. The assessment system offers flexibility and can be used for various applications, such as a checklist or spatial analysis. Forest stand parameters include tree age, spruce proportion, or tree density. Parameters of the forest site encompass, among others, the slope position, soil water supply, or solar irradiation. The spatial resolution of the PAS model is bound to the individual forest stand size. As the model is calculated once, no temporal resolution is available.

PHENIPS The phenology model PHENIPS was developed to simulate the seasonal development of *Ips typographus* at the Kalkalpen national park in Austria (Baier et al., 2007). The multiple regression model is based on a digital elevation model and uses temperature and solar radiation data to calculate micro climatic conditions for the beetles. The model was validated by comparing observed and predicted phenological events in the field and found a mean absolute error of 1.3 days for the onset of infestation and a mean error of 39 degree days for the emergence of filial beetles. The model can precisely monitor bark beetle development at the stand or tree level and assess the potential impact of bark beetle outbreaks at a regional scale. The spatial

Table 1.1: Overview on simulation models on *Ips typographus* peer reviewed and published within the last two decades. PAS - Predisposition Assessment Systems (Netherer and Nopp-Mayr, 2005); PHENIPS - Phenology model (Baier et al., 2007); PICUS - Hybrid forest patch model (Seidl et al., 2008); SAMBIA - Spatial Simulation of Interactions of Bark Beetles and Antagonists under Management at the Stand Scale (Fahse and Heurich, 2011); iLand - individual-based forest LANDscape and Disturbance model (Seidl et al., 2012); IPS - Infestation Pattern Simulation (Kautz et al., 2014, 2016); IPS-wind (Potterf and Bone, 2017).

Name	Type	Resolution	Purpose
PAS	knowledge-based expert model	S: forest stand; T: once	risk assessment of forest stands
PHENIPS	phenology model	S: 10 x 10 m grid cells; T: day	calculate begin an duration of life stages of *I. typographus* as well as flight and infestation activity
PICUS	stochastic hybrid patch model	S: 10 x 10 x 5 m cells; T: year / month	impact of climate change, management and disturbances on long term dynamic forest succession
SAMBIA	individual-based model	S: 4.5 x 4.5 m grid cells; T: annual time steps	analyzing, understanding and predicting the spatial and temporal development of bark beetle outbreaks as well as the impact of management measures or natural enemies
iLand	individual-based process model	S: 2 x 2 x 2 m; T: years	simulate forest ecosystem dynamics under changing climate and disturbance regimes, with a particular focus on modeling the interactions and feedback between climate, management, and disturbance regimes
IPS	individual-based model	S: 5 x 5 m grid cells; T: few days (one beetle generation)	understand dispersal and infestation patterns emerging from individual traits of bark beetles and host trees
IPS-wind	individual-based model	S: 5 x 5 m grid cells; T: 10 years	interactions between wind disturbance and beetle population dynamics

scale represented by the model is expressed as squared grid cells with a width of ten meters, whereas the temporal resolution is given in days.

PICUS The model PICUS v1.41 (Seidl et al., 2008) is a hybrid forest patch model that combines patch models and process-based production models. It is based on a 10-meter by 10-meter patch array and simulates detailed three-dimensional light regimes and spatially explicit seed dispersal. Inter- and intra-species competition are modeled using the patch model approach presented by Lexer and Hönninger (2001). At the same time, stand-level net primary production is derived using the radiation use efficiency of the 3-PG model (Physiological Principles in Predicting Growth) (Landsberg and Waring, 1997). The model requires monthly temperature input, precipitation, radiation, and vapor pressure deficit (Seidl et al., 2008). Bark beetles are not simulated as individual agents in this model: Based on site, stand, and weather data, infestation risks of individual trees or forest stands are calculated.

SAMBIA SAMBIA is a spatially explicit agent-based simulation model that primarily provides a tool for analyzing and understanding the spatial and temporal aspects of bark beetle outbreaks at the stand scale (Fahse and Heurich, 2011). It also allows for estimating the effectiveness of concurrent impacts of both antagonists and management to confine outbreak dynamics in practice. The simulation results indicated a distinct threshold behavior of the system in response to pressure by antagonists or management of the bark beetle population. A simple rule of thumb for successful control of an outbreak was extracted from the simulations: if roughly 80 % of individual beetles are killed, outbreaks will rarely occur. Despite simulating trees as individuals, beetles are only depicted as numbers on a grid cell without individual properties or environmental interactions. The spatial resolution of the model is defined by its 128 grid cells depicting each a square with a width of 4.5 meters. Time is measured in annual steps, and up to five years are usually simulated.

iLand The individual-based forest landscape and disturbance model (iLand) uses a hierarchical multi-scale approach to coupling individual-based vegetation dynamics and eco-physiological processes to simulate the adaptive agents in forest ecosystems, such as individual trees, at large scales (Seidl et al., 2012). It achieves this scalability by using a pattern-based rendering of ecological field theory to model resource availability at the landscape scale and by integrating local resource competition and physiological resource use via a hierarchical multi-scale framework. iLand combines approaches from community ecology, ecosystem ecology, and landscape ecology to address ecosystem stewardship and resilience questions. In this model, bark beetles are simulated as one of the different disturbance agents. They are not described as individuals but as packages, kernels, or so-called super agents respectively (Régnière et al., 2015), which contain just enough beetles to have at least a slight chance to successfully infest a potential host tree (Seidl et al., 2012). These packages are deployed in a random direction and at a randomly drawn distance from a predefined distribution but do not consider beetle fitness or a decision for infestation attempts on the way or at the destination in this process. Space in iLand is modeled as a three-dimensional and cubic grid with a width of two meters. As it is designed to simulate landscapes, it provides the opportunity to simulate, for example, 10,000 ha. Time is modeled in days, and a simulation covers up to several years.

IPS The Infestation Pattern Simulation (IPS) model is an individual-based, spatially explicit model that simulates how individual traits affect system-level dispersal and infestation patterns (Kautz et al., 2014, 2016). The model's processes include dispersal, host selection, aggregation, and colonization or rejection by host defense on a local scale. Host-bark beetle interactions are highly dynamic, with individual adaptive behavior taking into account space- and time-dependent variations in traits. The model provides a conceptual framework linking individual behavior to system-level patterns and is a valuable tool for understanding the complex spatiotemporal processes that govern host-bark beetle dynamics. It was the first model to describe beetles as real individuals with individual properties such as energy, age, or dispersal distance. The IPS model depicts 251,001 grid cells, each depicting a square of five-meter width. Time is modeled as steps of several seconds (the time a beetle needs to fly from one cell to another), and a simulation amounts to one whole beetle generation (several days).

IPS-wind In 2017, Potterf and Bone enhanced the IPS model by incorporating wind throw and examined how wind throw events impact bark beetle population transitions from endemic to epidemic levels. The results showed that the transition slows with an increasing spatial extent of a wind throw event and larger clusters of wind thrown trees. In contrast, scattered patterns of wind thrown trees accelerate the timing of this transition. This study contributes to our understanding of the role of large-scale wind disturbance in European bark beetle outbreaks. It provides a basis for further research on the impact of potential forest management strategies to mitigate the risk of bark beetle outbreaks. As they met computational limitations by applying the IPS-wind model for several years and large beetle populations, they fell back on using a super-agent approach (Régnière et al., 2015) in order to reduce the simulation cost of individual beetles (Potterf and Bone, 2017). Space is modeled as 10,201 grid cells in the horizontal plane, each depicting a square with a five-meter width. Time is modeled in time steps depicting several seconds, and simulation experiments are done for up to ten years.

Synthesis

Simulation models are valuable tools for analyzing complex ecological systems in a changing world and for decision-making. There are several successful applications of such models in fishery management, disease control, or wildfire management. There are also many different models published about *Ips typographus*, one of the primary forest pests in Europe. Even though these models cover a wide variety of purposes, no simulation tool is available that combines beetles as real individuals with individual properties and decisions, the applicability of management measures to test their effectiveness, and uses spatially explicit data to be applied in a natural landscape. For the first time, this approach would allow investigation of the infestation patterns and development in a natural landscape emerging from the individual traits of beetles and trees. It could be used to investigate the impact of climate change and forest protection management on all spatial scales - from each beetle to the whole landscape.

1.2 Objectives and content of this thesis

1.2.1 Objectives

The main objective of the thesis is to spatially explicitly predict the risk of bark beetle infestation and outbreaks under climate change and management scenarios across different spatial and temporal scales and for an example region consisting of a national park in Germany. For this, a novel combination of published models on different aspects of the life history of *Ips typographus* and its host tree *Picea abies* is produced and enhanced to simulate bark beetle infestations on the individual level every year. With the so-called metamodel framework, where a model is applied to mimic another more complex model, the newly developed and mechanistic precise individual-based model results are scaled to the landscape level by applying a Markov chain metamodel for twenty years into the future. In detail, the following research questions are addressed:

1. How effective is sanitation felling on a local scale, and what parameters influence its effectiveness?
    a) The individual-based model IPS-SPREADS can reproduce the severity and direction of infestation development observed within the Saxony Switzerland national park from 2015 to 2017.
    b) Sanitation felling at the border of a national park can effectively reduce the damage in adjacent and managed forest areas.
    c) Parameters such as the number of beetle sources, number of beetles, the distance of beetle sources to the adjacent managed forest areas, and the attractiveness of trees play a major role in the number of trees damaged outside the protected area.
2. Which metamodels are used in an individual-based modeling context, and what are their application purposes?
3. Can sanitation felling alter the course of a beetle mass outbreak on the landscape scale containing a large protected area (national park)?
    a) Increases in the number of bark beetle generations per year due to forecasted increases in mean temperature lead to faster outbreaks and more frequent complete dieback of Norway spruces (*Picea abies*) inside and outside the national park.
    b) Sanitation felling at plot level inside the national park can lower the risk of infestation spread from the protected to adjacent forested areas in the next 20 years but requires a minimum threshold value to be effective.

In order to investigate these questions, an individual-based model is developed and systematically analyzed to investigate the effectiveness of the most common management measure against the spread of *Ips typographus*. After that, a systematic literature review is conducted to identify the most common metamodel applications in an agent-based modeling context and rate these model types' usability and efficiency. Ultimately, the most promising metamodel for spatially and temporally extrapolating individual-based models is applied to facilitate the long-term forecast of bark beetle development in a case study area consisting of a national park and surrounding forest areas. An overview of the specific aspects related to the above research questions, as covered by the main studies of the dissertation, is given in table 1.2.

Table 1.2: Overview of the specific aspects covered by the main studies of the dissertation (Articles 1 - 3 in Chapters 2 - 4).

		Article 1	Article 2	Article 3
Individual-based modeling	infestation pattern reproduction	X		
	sanitation felling efficiency	X		
	spatial configurations & individual traits	X		
Literature review	metamodel types & application purposes		X	
	information quality & applicability		X	
Metamodeling	upscaling of a bark beetle IBM			X
	long-term infestation development			X
	climate change & management scenarios			X

1.2.2 Content

The formulated objectives and research questions reflect the content sequence presented in this dissertation's chapters.

Chapter 2 describes the development, test, and application of a new simulation model on *Ips typographus* dispersal and infestation in a natural landscape of Europe. The concerning individual-based model IPS-SPREADS (Infestation Pattern Simulation Supporting PREdisposition Assessment DetailS) is a novel combination of existing models about the beetles' phenology (PHENIPS), the predisposition of spruce trees (PAS - predisposition assessment systems) and the mechanistic precise dispersal flight in an artificial forest (IPS - Infestation Pattern Simulation). The model is used to investigate the effectiveness of sanitation felling under varying annual beetle generation numbers on five different research areas at the border of a national park in Germany.

Chapter 3 examines the different purposes and types of metamodels applied in an agent-based modeling context and tries to rate and highlight the most promising or most efficient model types for each application purpose. This assessment was done through a systematic literature review that resulted in 27 scientific publications that included 40 different applications of metamodels in an individual-based modeling context. The candidate and a consortium of Ph.D. students and postdoctoral researchers developed and applied a standardized rating instruction to achieve an objective rating of different metamodel applications, such as upscaling agent-based models or performing sensitivity analyses.

In Chapter 4, the results of the new simulation model IPS-SPREADS on the plot level are scaled to a whole national park region and for 20 years into the future.

For this, a metamodel approach is facilitated. A model based on Markov chains is used to scale the findings of the computationally demanding IPS-SPREADS to larger temporal and spatial scales. The amount and timing of infested trees from 2015 to 2017 are used to calibrate and validate the developed metamodel. The model is then facilitated to investigate the effectiveness of sanitation felling to stop a bark beetle mass outbreak from spreading from the national park to adjacent forests until 2038.

After the main studies, Chapter 5 overviews three supervised master theses connected to the candidate's thesis. The first thesis focused on implementing and testing wind speed and direction into the newly developed individual-based model. The second thesis focused on extrapolating individual-based model results on the landscape level through a metamodel approach. The third and last thesis consists of a systematic literature review on the ecology and management of *Ips typographus* as an update to a similar review published in 2004 by Wermelinger (2004).

Chapter 6 summarizes and discusses the significant findings of this thesis and critically evaluates the applied methodology. The chapter closes with an outlook on future research directions.

2 Article I - The Effect of Sanitation Felling on the Spread of the European Spruce Bark Beetle - An Individual-Based Modeling Approach

Summary In this study, the effectiveness of sanitation felling (a method of removing infested trees to prevent the spread of *Ips typographus*) on stopping the spread of a bark beetle population from an unmanaged to a managed forest area is investigated. A dispersal model of the European spruce bark beetle is advanced by adding the influence of wind and importing GIS data on the location and vitality of Norway spruce trees to analyze the management effectiveness. Simulation experiments are then conducted to validate the new model version and find reasonable parameter values by reproducing infestation patterns in 2015, 2016, and 2017 within a national park in Germany. With the calibrated model, the impact of different factors on the damage within the managed forest stand is investigated, and the effectiveness of different levels of sanitation felling is tested. The results show that wind direction and the energy reserve of bark beetles during mass outbreaks are essential factors and that sanitation felling is most effective when performed near the source of the beetles. The model can be used in future studies to test further management measures or to assess the risk of bark beetle infestations in other parts of Europe.

Novelty This study is the first to investigate the impact of sanitation felling, a forest protection measure, against the spread of *Ips typographus* from a protected area to adjacent forests on the individual beetle and tree level through a simulation model. By incorporating GIS data, it is possible to investigate the beetle spread spatially explicitly and under varying management and climate change scenarios.

Key features Despite using a different modeling approach and spatial or temporal resolution to other studies investigating bark beetle infestations, a similar management threshold was found to be met to reduce the beetle spread successfully. Furthermore, to encourage the re-use and application of the developed model, we published the model files, the used data, and the model results freely accessible as a GitHub repository: `https://github.com/bwpietzsch/IPS-SPREADS`. The supplementary material can be freely accessed under the following link: `https://doi.org/10.3389/ffgc.2021.704930`.

Publication type, journal, authors, and the Ph.D. candidates' contribution
This chapter represents a peer-reviewed publication in *Frontiers in Forests and Global Change* from July 2021 entitled 'The Effect of Sanitation Felling on the Spread of the European Spruce Bark Beetle - An Individual-Based Modeling Approach.' It has been compiled along with MSc Felix Johannes Peter and Prof. Dr. Uta Berger, the first supervisor of this Ph.D. study. The candidate of this dissertation developed the model, designed and carried out the experiments, analyzed and interpreted the results, wrote and reviewed the article.

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The Effect of Sanitation Felling on the Spread of the European Spruce Bark Beetle—An Individual-Based Modeling Approach

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Sanitation felling is considered as the main measure to protect managed forests from damage due to outbreaks of the European Spruce Bark Beetle. In this study, we investigate the effectiveness of sanitation felling on stopping the spread of a bark beetle population from an un-managed to a managed forest area. For this, we advance an individual-based dispersion model of *Ips typographus* by adding the influence of wind on the beetle dispersion and by importing GIS data to simulate real world forests. To validate the new model version and to find reasonable parameter values, we conduct simulation experiments to reproduce infestation patterns that occurred in 2015, 2016, and 2017 within the national park Saxon Switzerland, Germany. With the then calibrated model IPS-SPREADS (Infestation Pattern Simulation Supporting PREdisposition Assessment DetailS), we investigate the impact of different factors such as the distance between beetle source trees and the forest border on the amount of damage within the managed forest stand and test the effectiveness of different levels of sanitation felling and its point of action on reducing the amount of damaged trees. As expected, the results of the model calibration show that the direction of wind plays an important role for the occurring infestation patterns and that bark beetle energy reserve is reduced during mass outbreaks. The results of the second experiment show that the main drivers for the amount of damaged trees are the primary attractiveness and the distance to beetle source trees. Sanitation felling effectiveness is highest when performed near the beetle source trees, with considerably high felling intensities and if there is at least some distance to the managed forest. IPS-SPREADS can be used in future studies as a tool for testing further management measures (e.g., pheromone traps) or to assess the risk for bark beetle infestations of forest areas near to wind-felled or already infested trees.

Keywords: *Ips typographus*, management, effectiveness, risk assessment, mass outbreak, active forest protection, agent-based model, individual-based model

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1. INTRODUCTION

There has been a strong increase of biotic (forest pest) and abiotic (droughts) disturbances in central European forests in recent years. With the ongoing climate change and its expected influence on the current and future disposition of these forests to disturbances, there is no weakening of the threat to be expected (Senf et al., 2019). One of the main beneficiaries of climate change and past forest management decisions in Central Europe is the European Spruce Bark Beetle *Ips typographus* L. 1758 that is currently exerting a mass outbreak in Germany. While forest management is constantly trying to minimize the impact of this catastrophe, large areas of un-managed forests such as national parks (NLPs) provide insights in natural factors that influence the starting conditions as well as the development of such a bark beetle mass outbreak (Lausch et al., 2011). On the other hand, forest areas adjacent (ADJ) to such unmanaged areas with ongoing mass outbreaks can be under risk of spreading infestations and timber loss, for which reason an adaptive and thorough management is needed (Zolubas and Dagilius, 2012; Mezei et al., 2017). While sanitation felling can reduce the threat for such forests close to unmanaged areas as it is a desirable measure in regards to forest health, timber yield and economic profit, it is inconsistent with most conservation goals (Kulakowski, 2016) further emphasizing the tension field between large protected areas and managed forest.

To assess the risks of infestations and to support the management of protected area as well as managed forests, a variety of simulation models for the system European spruce bark beetle—Norway spruce tree are available. One main goal of such models lies in the assessment of predisposition or infestation risk ranging from single trees over forest stands up to whole landscapes in dependence of influencing factors such as tree age, soil water supply, or forest management regime (Dutilleul et al., 2000; Netherer and Nopp-Mayr, 2005; Overbeck et al., 2011; Jönsson et al., 2012; Thom et al., 2013; Seidl et al., 2016; Mezei et al., 2017; Blomqvist et al., 2018; Rammer and Seidl, 2019). Other simulation models aim at reproducing and predicting the dispersal and infestation patterns of *I. typographus* (Fahse and Heurich, 2011; Stadelmann et al., 2013b; Kautz et al., 2014, 2016; Doležal et al., 2016; Louis et al., 2016; Økland et al., 2016; Honkaniemi et al., 2018; Koreň et al., 2021), at the prediction of the seasonal brood development (Baier et al., 2007; Jönsson et al., 2007; Ogris et al., 2019) or at the assessment and prediction of population dynamics and its impact as disturbance factor on ecosystem levels (Seidl et al., 2007, 2008, 2009; Marini et al., 2013; Temperli et al., 2013; Rammer and Seidl, 2015). Challenges associated with modeling bark beetle infestation are as diverse as the different model types used. Models on the individual tree or even beetle level often times reach computational cost that forbid their application on scales larger than the local scale or for mass outbreak conditions. On the other hand, models on a higher spatial scale need to make assumptions about mean properties of forest stands, site conditions, or timing, location, and type of forest management measures such as sanitation felling. With all the mentioned simulation models, there is still a lack for assessing the impact and possible effectiveness of forest protection management against the spread of *I. typographus* on very small spatial and temporal scales. With such a fine grained tool, it would be possible to investigate planned management measures on previously assessed risk hot spots in a quasi real time manner and to adapt the intended protection strategy accordingly. To achieve this, we combined the following well known and applied models into one: the pre-disposition assessment systems PAS (Netherer and Nopp-Mayr, 2005), the phenology model PHENIPS (Baier et al., 2007) and, the infestation pattern simulation IPS (Kautz et al., 2014, 2016). PAS generates infestation risks for whole forest stands from forest inventory data and of the forest soil, which can be used to translate given GIS data into a primary attractiveness of spruce trees for bark beetles. PHENIPS estimates the start and duration of *I. typographus* life stages for varying spatial resolutions and can be utilized to calculate the onset of beetle swarming in spring. IPS simulates the beetle dispersal and their infestation pattern in a artificial forest on the individual-based level.

The so derived model is called IPS-SPREADS (Infestation Pattern Simulation Supporting PREdisposition Assessment DetailS) and can be used to simulate the dispersal and infestation of bark beetles within a real forested landscape on the individual-based level on a small spatial resolution (5 × 5 m) under varying management strategies. To calibrate and test ISP-SPREADS, data on infestation patterns of the Saxon Switzerland NLP in Germany is used to reproduce those patterns from 2015, 2016, and 2017. Furthermore, simulation experiments are presented which assess the impact of sanitation felling on the infestation risk of forests adjacent to the NLP on five different research areas as felling infested trees is considered to be one of the main measures against the spread of *I. typographus* (Jönsson et al., 2012; Kulakowski, 2016). For our study, we formulated two hypotheses which we want to investigate: (1) IPS-SPREADS is capable of reproducing the severity and direction of infestation development as observed within the Saxony Switzerland NLP from 2015 to 2017. (2) Sanitation felling at the border of the NLP can effectively reduce the damage in adjacent managed forest areas.

2. MATERIALS AND METHODS

2.1. Model Description: Summary ODD Protocol

A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010, 2020) can be found in **Supplementary Material 1**. The overall *purpose* of our model is to understand and investigate the impact of individual traits of beetles and trees as well as measures of bark beetle management (e.g., sanitation felling) on the spatial pattern of infestations of the Spruce Bark Beetle (*I. typographus*). Specifically, we are addressing the following questions: Which are the main drivers of Spruce Bark Beetle infestation patterns? How does sanitation felling impact the spreading of Bark Beetles to other forests? To consider our model realistic enough for its purpose, we use *patterns* of location, number and progression from 2015, 2016, and 2017 of infested spruce trees (*Picea abies*) within the Saxon Switzerland NLP located in the East of Germany.

The model includes the following *entities*: patches, bark beetles and volatiles. The *state variables* characterizing these *entities* are listed in **Table 1**. The global environment (a forested area) is characterized by wind speed and direction. Patches represent 5 × 5 m areas containing one spruce, one pheromone trap or are empty if neither a spruce tree nor a trap is present.

TABLE 1 | Entities and state variables of the IPS-SPREADS model.

Agent	Variable	Description	Unit
Patches	Infestlev	Infestation level (e.g., 0 if non-infested)	Number
	Primattract	Kairomone-induced attractiveness	Number
	Secattract	Pheromone-induced attractiveness	Number
	Totalattract	Sum of prim- and secattract	Number
	n_{min}	Minimum threshold for successful infestation	Number
	n_{max}	Capacity for infesting beetles	Number
	Height	Tree height	Meter
	n_{start}	Capacity for emerging beetles	Number
	n_{stay}	Beetles attacking the tree	Number
	n_{inf}	Beetles infesting the tree	Number
	n_{lock}	Beetles trapped	number
	$tree_{infestdist}$	Distance to nearest beetle source	Meter
	Spruceprop	Proportion of spruce trees	%
	Delay	Day number of first beetle flight wave (1st of April = 0 etc.)	Number
	Wave-count	Counter for sprouted beetle flight waves	Number
	Inf	Period of real world infestation (e.g., 1 if year before)	Number
	Infestday	Day number of modeled infestation (1st of April = 0)	Number
	Local-speed	Wind speed reduced by forest canopy	$\frac{m}{s}$
	Roughness	Canopy flow index based on tree species	Number
	Neighbor-height	Mean height of surrounding trees	Meter
Beetles	Status	Life status (e.g., dispersing or infesting)	Category
	Energy	Individual energy supply at the beginning of dispersal flight	Number
	t_dispers	Time since dispersal flight began	Ticks
	Staytime	Time since the beetle attacked a tree	Ticks
	Efficiency	Energy efficiency	Number
	Flightdist	Distance flown	Meter
	Starttime	Time when the beetle began its flight	Tick
	Driftdist	Distance drifted by wind	Meter
	Traveldist	Sum of drift- and flightdist	Meter
	Airline	Distance between starting point and final destination	Meter
	Origin	Patch that sprouted the beetle	ID
Volatiles	Flightdist	Distance flown	Meter
	Driftdist	Distance drifted by wind	Meter
	Traveldist	Sum of drift- and flightdist	Meter
	Voattract	Attractiveness of volatile	Number
	Origin	Patch that sprouted the volatile	ID

Characteristics of these patches include their primary and secondary attractiveness for bark beetles, a capacity for infesting and emerging beetles and, a level of infestation: Not infested, infested or, fully occupied. Patches are squares in the horizontal plane with information about tree height stored within, uniform size and shape. Beetles have unique values of energy level and energy efficiency. Volatiles are emitted by beetles infesting trees or by pheromone traps and carry information about the location and the total attractiveness of their source at the time of emission. The *spatial* extent depends solely on the extent of the imported GIS data. If a mass outbreak of *I. typographus* is to be simulated, a maximum extent of a quarter square kilometer is advised. The *temporal* resolution of IPS-SPREADS is defined by time steps, where 200 steps resemble 1 day in reality. The overall length of the simulation depends on the chosen parameter settings (e.g., if one, two, or three generations are to be simulated). The simulation ends as soon as all beetles emerged from the beetle source trees and no more dispersal flight or tree attacks are taking place.

The most important *processes* of the model, which are repeated every *time step* (**Figure 1**), are the emission of volatiles by infested trees and pheromon traps, the beetle flight, the beetle decision to attack a patch and the defense of trees that are attacked by beetles. Each simulation begins with the **model setup** during which GIS data like tree height or the begin of beetle flight is imported and used to create the model world by distributing spruce trees and beetle source trees. After the artificial environment is set up, the first **day** of the simulation starts with the generation of beetles on all beetle source trees and the updating of all plots in the

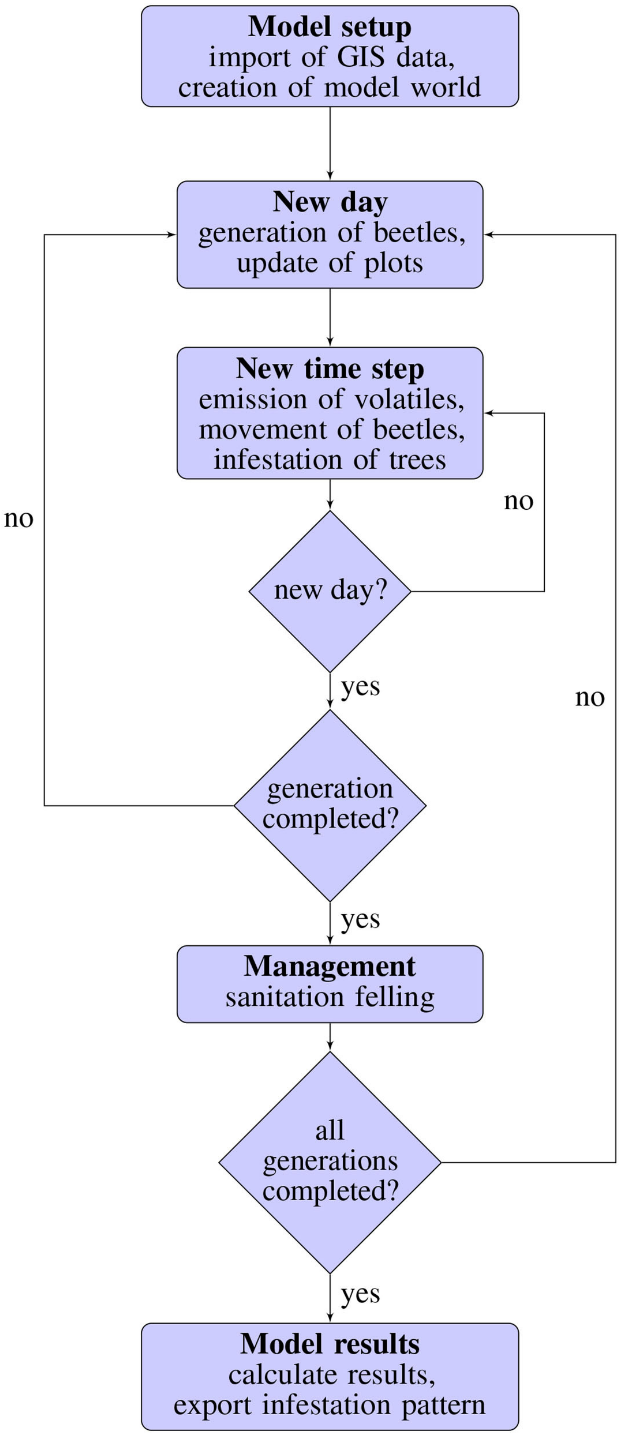

FIGURE 1 | Flow chart showing the schedule for IPS-SPREADS. A new day begins every 200 time steps.

model interface. Then, on each **time step**, volatiles are emitted by infested trees as well as deployed pheromone traps and the beetles are moved either to the source tree of the most attractive volatile within the beetles perception range or to a neighboring patch using a correlated random walk. After all beetles were moved, it is checked if the beetles energy reserve is higher than the total attractiveness of the beetles current patch. If so and if the current patch is a pheromone trap, the beetle is killed by the trap. If the target is an already infested tree, the beetle is added to the infesting beetles on this patch. Otherwise, the beetle will wait on the given tree for 1 day (200 time steps). If enough further beetles attack the same tree within this 1 day, the tree defense will be overcome and the tree will be infested. Otherwise, all beetles waiting on the patch are killed by the tree defense. Every time 1 day (200 time steps) has passed, it is checked if all beetles of the given beetle generation were generated and dispersed. If this is not the case, the next day starts with the generation of beetles and the update of all plots. Otherwise (if the whole beetle generation was simulated), bark beetle **management** is taking place and the predefined proportion (e.g., 50%) of infested trees is removed from the model world by sanitation felling. If more than one beetle generation was defined, all infested trees that were not removed by sanitation felling are shifted to beetle source trees for the next beetle generation. After this, a new day with the same schedule of actions as described above begins (generation of beetles, update of plots, emission of volatiles, movement of beetles and so on). If the predefined amount of generations was simulated and the sanitation felling for each of those generations took place, the **model results** are calculated, the pattern of infested trees is exported as a raster layer (.asc file) and, the simulation stops.

The most important *design concepts* of the model are adaptation, sensing and interaction. Dispersal and infestation patterns are the key results of IPS-SPREADS, which are strongly influenced by the beetles' decision when to attack an attractive patch (adaptation), their sensing of susceptible trees as well as the interaction with other beetles already infesting such trees and fully occupied trees (repelling further attacking beetles). Furthermore, the secondary attractiveness of trees is adapted (zero at the beginning of each simulation) according to the number of beetles attacking (weak increase) or infesting (strong increase) the given tree. If the capacity for infesting beetles of a tree is reached, its primary, secondary and total attractiveness is set to zero, which repels further beetle attacks representing the production of anti-aggregation pheromones by the infesting beetles.

Model dynamics are driven by *input data* representing (1) the location (derived from forest inventory data), size (derived from the digital elevation and surface model provided by the NLP) and attractiveness (calculated with PAS Netherer and Nopp-Mayr, 2005 using stand and site data from the NLP) of susceptible spruce trees; (2) location of beetle source trees (provided by the NLP), (3) day of beetle flight begin [calculated with PHENIPS (Baier et al., 2007) using the digital elevation model provided by the NLP as well as daily air temperature and radiation which were obtained from several climate stations of Germany's federal weather service DWD].

TABLE 2 | Characteristics of research areas used for the calibration of IPS-SPREADS.

Area chr	Year *n*	Beetle source trees *n*	Target trees *n*	Beetles *n*
A	2016	55	186	782,016
B	2016	108	101	1,244,308
C	2016	141	697	1,722,322
D	2017	111	133	1,292,530

The amount of targets refers to the amount of trees infested in the real world on each site. The number of simulated beetles refers to the amount of individuals during the first generation only.

2.2. Model Calibration: Reproduction of Infestation Patterns

To calibrate and test the newly build IPS-SPREADS model, four different study sites with characteristic infestation patterns from the Saxon Switzerland NLP in 2016 and 2017 were selected (**Table 2**) and imported into IPS-SPREADS (**Figure 2**). These research areas were chosen so that a group of infested trees was in the center, no further infested tree groups were within a 500 m radius and the real world infestations of the following year were completely within a 250 m radius.

After testing the impact of all model parameters on the amount and pattern of infested trees (global sensitivity analysis, **Supplementary Material 2**), the parameters swarming time, mean beetle energy, amount of beetle generations, wind direction and speed were investigated during the calibration of IPS-SPREADS as they are the main drivers for the resulting infestation patterns. The range of values for these parameters was retrieved from literature (**Table 3**). The duration of swarming and the amount of generations for the experiments were derived from the application of PHENIPS (Baier et al., 2007) for the NLP in the investigated years 2015–2017. All other parameters received their standard values (**Supplementary Material 1**: ODD Protocol). To achieve a reasonable trade off between amount of simulated parameter combinations and the high computational cost of IPS-SPREADS for the mass outbreak conditions investigated, a random sampling was performed: 200 simulation experiments for each research area were run, where for each run a random value for each parameter out of the displayed ranges was sampled using a uniform distribution. This resulted in 200 different parameter combinations for each site and a total of 800 simulation experiments for the calibration of IPS-SPREADS. All simulation experiments were performed on the high-performance computing machines of the TU Dresden using the BehaviorSpace-Tool of NetLogo version 6.0.4 (Wilensky, 1999).

To calculate the deviation between the model prediction and the real world infestation patterns (the white patches in **Figure 2**), following measure of error was calculated:

$$e\,[\%] = 50 * (|1 - \frac{n\_inf\_real}{n\_inf\_match}| + |1 - \frac{n\_inf\_model}{n\_inf\_match}|), \quad (1)$$

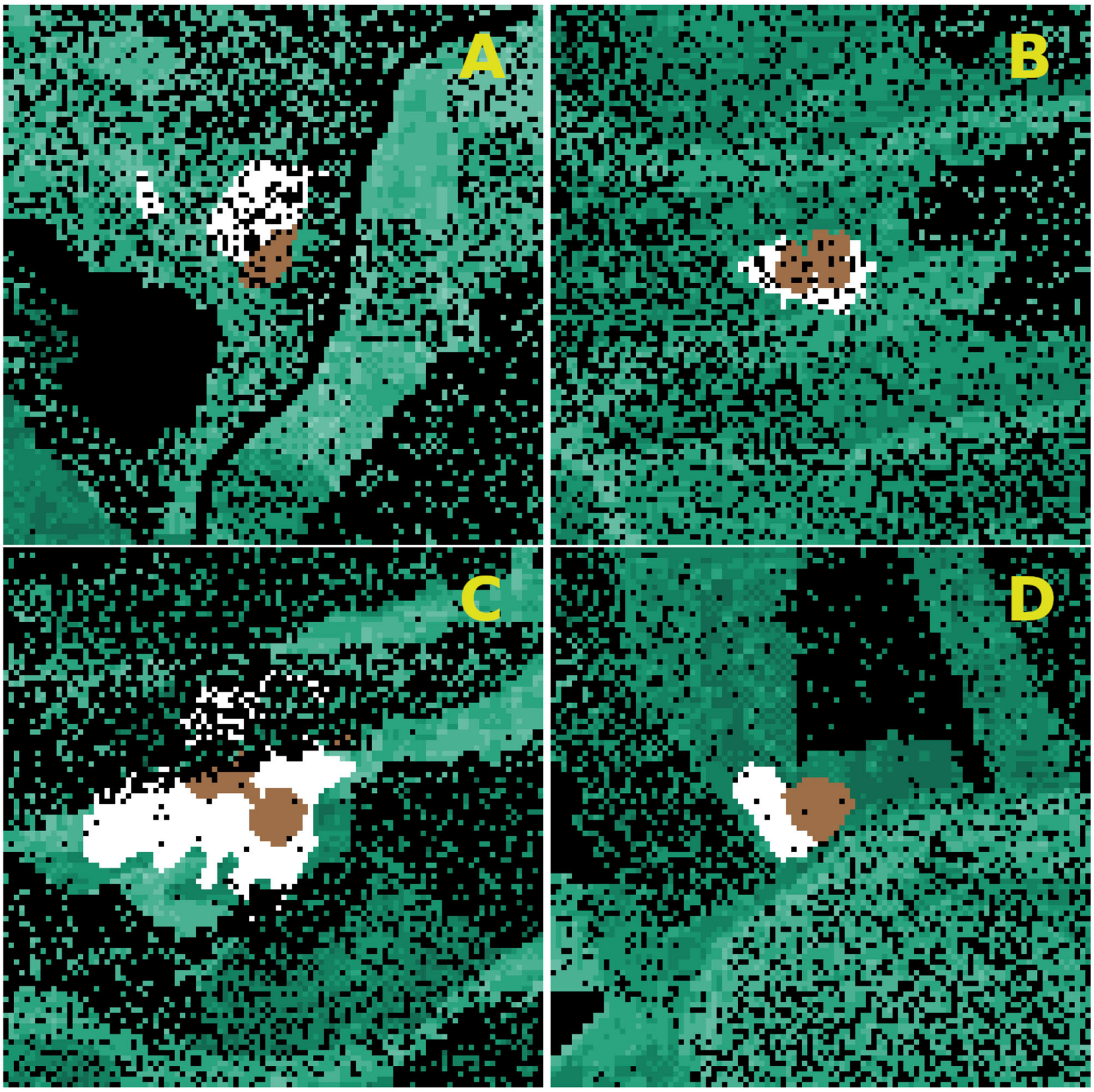

FIGURE 2 | Infestation patterns chosen (research sites **A–D**) for the calibration of IPS-SPREADS. Brown, beetle source trees; green, susceptible spruce trees; white, spruces infested in reality (target trees); black, other (for example other tree species, roads, or rivers).

n_inf_match is the number of infested trees within the model that *match* the real world data, *n_inf_model* is the total number of infested trees within the *model* and, *n_inf_real* is the number of trees infested in the *real* world. If no trees infested within the model run matched the real world data ($n\_inf\_match = 0$), the error *e* was set to 100%. The focus of this particular measure of error was to achieve high numbers of infested trees that match the real world data while keeping the total number of infested trees as low as possible. Other measures of error which focused more or only on the number of matching trees resulted in three or four times the total amount of infested trees within the model. On the other hand, a measure of error focusing on the smallest possible amount of falsefully infested trees resulted in model runs with only one to 10 trees in total. The measure of error (Equation 1) was then used to find the parameter combination with the highest agreement between model prediction and real world data on each research site. Furthermore, this measure was used to derive parameter values for swarming time, beetle

TABLE 3 | Parameter settings for IPS-SPREADS during the model calibration experiments with a reference for the chosen ranges.

Parameter	Unit	Setting		Reference
Swarming	d	7	56	Baier et al. (2007)
Meanenergy	–	6	14	Kautz et al. (2014)
Generations	*n*	1	2	Baier et al. (2007)
Winddirection	°	0.0	360.0	–
Windspeed	$\frac{m}{s}$	0.0	5.5	Hurling (2002)

Parameters not listed received their standard values as listed in the model description.

TABLE 4 | R packages used for the calibration and application of IPS-SPREADS.

R Package	Version	References	Usage
rgdal	1.5–23	Bivand et al. (2021)	Processing GIS data
rgeos	0.5–5	Bivand and Rundel (2020)	Processing GIS data
raster	3.4–5	Hijmans (2020)	Processing GIS data
maptools	1.0–2	Bivand and Lewin-Koh (2020)	Processing GIS data
ggplot2	3.3–3	Wickham (2016)	Visualization of results

energy and wind speed, which provided the highest fits across all research sites. For this, scatter plots and locally estimated scatter-plot smoothing was utilized. To test the robustness of the so derived parameter values, one model run was performed on each research site using these values and the achieved prediction error was compared to the best fit during the random sampling. For all analyses described, the free statistical environment R (R Core Team, 2020) in version 3.6.3 and a variety of packages were used (**Table 4**).

2.3. Model Application: Testing Sanitation Felling Against the Spread of *Ips typographus*

To investigate the impact of sanitation felling onto the risk of spreading of infestations from NLP to ADJ, five research areas were chosen and imported into IPS-SPREADS (**Figure 3**). The areas were chosen so that the center was defined by a group of infested trees and the shortest distance to the outer NLP border was equal or less to 500 m. Possible further cohorts of beetle source trees were removed on each site to set the focus only on the cohort in the center of each research area. The amount of beetle source trees, the amount of beetles starting within the first generation, the direction and distance of the nearest ADJ as well as the susceptibility of the spruces inside and outside the NLP varied between the selected research sites (**Table 5**).

Parameters which were reported as insignificant during the sensitivity analysis of IPS-SPREADS (**Supplementary Material 2**) received their standard values. Influencing factors with a high influence on beetle infestation success as well as on the amount, direction and the distance of infested trees were given values fitted during the model calibration (section 3.1). This included wind speed, beetle swarming time and mean beetle energy. The wind direction and the amount of beetle generations was set to impose a worst case scenario for the forest protection management of the NLP on each investigated research site (**Table 6**).

To depict different scenarios of forest protection management (e.g., a forest protection buffer zone which could be placed inside, outside or on both sides of the border), the intensity of sanitation felling was varied from 0 to 100% in 25% steps. Additionally, the felling intensity inside and outside the NLP was varied simultaneously leading to a total of 25 combinations to be modeled. By repeating each combination 40 times to account for the high stochasticity of individual-based models such as IPS-SPREADS and by using five different research areas, a total amount of 5,000 simulation experiments had to be carried out for the investigation. We chose to simulate 40 repetitions of each combination based on the assumption that the probability of a 41st run to lie outside the range of the previous 40 is 2.5 % (1/40).

To investigate the impact of varying properties of the research sites on the amount of damaged trees without any sanitation felling, the mean amount of trees killed outside the NLP without sanitation felling taking place was used to generate a point plot in dependency of those properties (amount of beetle source trees, amount of beetles within the first generation, distance between beetle source trees and the ADJ, mean primary attractiveness of ADJ as well as NLP). To assess the impact of each property, a linear model was fitted and validated using an ANOVA.

In order to assess the impact of sanitation felling on the amount of damaged trees outside the NLP, the effectiveness after Abbott (1925) was calculated and visualized as tile plot for each research area. For this, we calculated the mean amount of trees killed outside the NLP when no felling took place and used this as the control variant for the calculation of effectiveness. We then calculated the mean number of trees killed outside the NLP for each combination of sanitation felling intensity as well as its point of action and used this number as the treatment for the effectiveness of Abbott (1925). This calculation was done for each of the five research sites individually.

For the experimental setup and all analysis, the free statistical environment R (R Core Team, 2020) in version 3.6.3 and the same packages as during the calibration of IPS-SPREADS were used (**Table 4**).

3. RESULTS

3.1. Model Calibration: Reproduction of Infestation Patterns

While IPS-SPREADS can easily predict the correct amount of infested trees on each investigated research area, predicting the correct location comes along with nearly the same amount of wrongly infested trees even on the best fitting parameter combinations during the random sampling (first four rows of **Table 7**). Nevertheless, the predicted infestations of the fitted parameter values agree well enough with the observed patterns to be used as base setting of IPS-SPREADS during the sanitation felling tests in the second part of this study as they do not underestimate the threat of spreading bark beetle infestations. Interestingly, best agreements between model and reality were

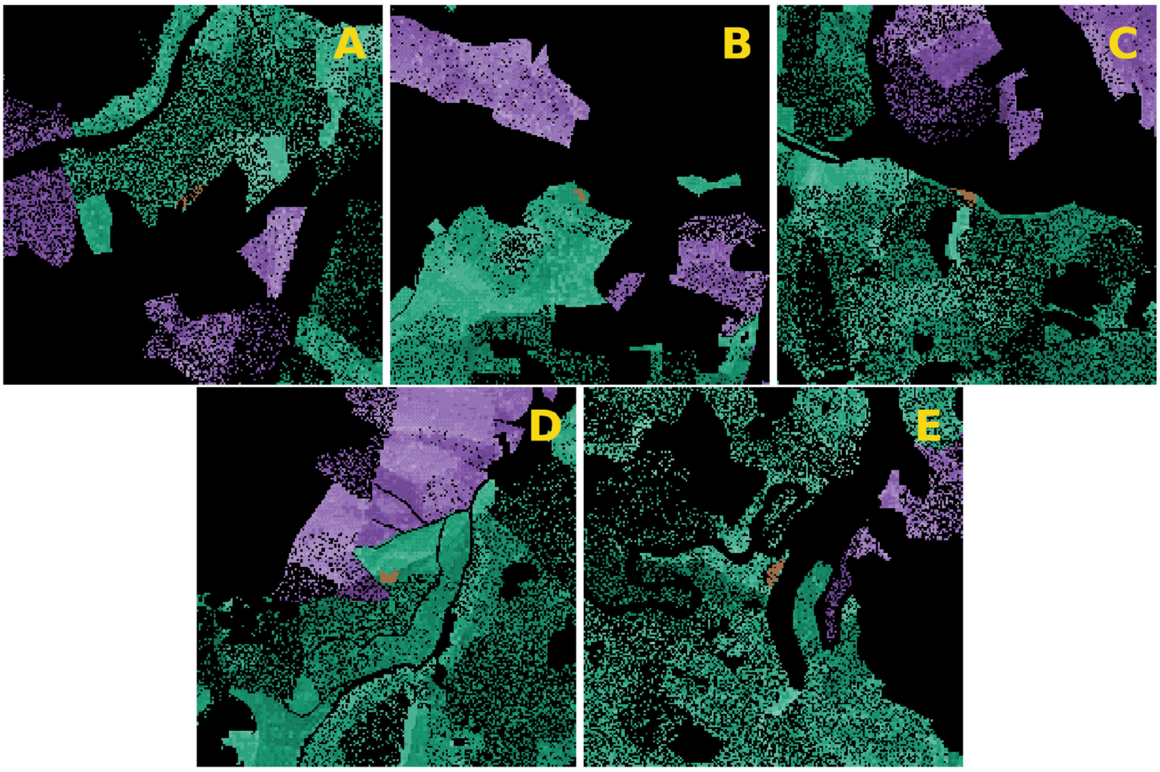

FIGURE 3 | Representation of the five research sites (labeled **A–E**) used for the application of IPS-SPREADS. All spruces outside the NLP (national park) are colored purple. Green, spruce trees inside NLP; brown, beetle sources; black, everything else (meadow, roads, other tree species).

TABLE 5 | Properties of the five research sites investigated during the test of sanitation felling effectiveness on the spread of *Ips typographus* from the national park (NLP) to the adjacent forest area (ADJ).

Area chr	Sources *n*	Beetles *n*	Direction °	Distance m	Attractiveness ADJ μ	Attractiveness NLP μ
A	35	457,571	135.0	192.10	3.99	4.10
B	24	393,372	315.0	128.55	3.27	4.32
C	45	508,346	0.0	149.15	4.76	4.15
D	53	489,970	225.0	29.15	5.02	3.28
E	63	861,765	90.0	152.30	3.87	3.26

Distance and direction of the ADJ are related to the center of the beetle source tree cohort. The attractiveness of ADJ and NLP refers to the mean primary attractiveness of all spruces within the respective areas.

achieved on all sites with decreased beetle energy levels and high swarming durations. The amount of beetle generations varied throughout the investigated research areas, where one generation scored best on sites with fewer and nearer follow-up infestations and vice versa for two generations. The wind speed intensity seems to play only a minor role for the correct reproduction of infestation patterns, but it is still of great importance as it affects the direction of infestation the most.

Using scatter plots and locally estimated scatter-plot smoothing (**Supplementary Material 3**), same parameter values on all sites for beetle energy, beetle swarming duration, and wind speed were chosen (last four rows of **Table 7**) and simulated once on each research area (**Figure 4**). In combination with the best value for wind direction and beetle generation amount on each research site during the random sampling, these derived parameter values scored roughly the same prediction errors as the best fits during the random sampling. With these chosen and robust parameter values for beetle energy, beetle swarming duration and wind speed, simulation experiments investigating the effectiveness of sanitation felling could than be carried out.

Beetle generations and wind direction as varying parameters were set to impose a worst case scenario on each of the given research sites during the model application.

3.2. Model Application: Testing Management Measures

The mean amount of damaged trees outside the NLP of all 40 repetitions of the control variant (no sanitation felling applied) on each research site revealed a high influence of mean primary attractiveness and distance between beetle source trees and ADJ (**Figure 5**). The amount of beetle source trees as well as the primary attractiveness of spruces within the NLP had only a small impact while the amount of beetles emerging within the first beetle generation had none at all. Performing a ANOVA analysis on the displayed linear models revealed that only for the primary attractiveness of ADJ a significant influence on the amount of damaged trees without sanitation felling could be proven.

The calculated effectiveness highlights the possible reduction of damaged trees outside the NLP by applying sanitation felling after each beetle generation (**Figure 6**). While felling infested trees inside the NLP always exhibited a strong reduction of damaged trees, felling outside the NLP was only effective on 60% of all sites. This behavior is in direct relationship to the amount of NLP forest area between the beetle source trees and ADJ: On sites B and E, where the sanitation felling outside the NLP has no impact at all, there is some distance with spruces between the beetle source trees and the NLP border. On sites with no NLP forest between the beetle sources and ADJ, the sanitation felling outside the NLP becomes much more important and reaches reduction levels of up to 69% without felling a single tree inside the NLP. The overall mean effectiveness (bottom right panel of **Figure 6**) shows that only with the removal of 75% or more of infested trees inside the NLP or in combination with felling outside the NLP can achieve noteworthy damage reduction effects.

TABLE 6 | The settings of all parameters with high influence on direction, distance and amount of infested trees as used for the simulation experiments on testing the effectiveness of sanitation felling.

Parameter	Unit	Site	Setting
Wind direction	°	A	315.0
		B	135.0
		C	180.0
		D	45.0
		E	270.0
Wind speed	$\frac{m}{s}$	–	4.0
Generations	*n*	–	2
Swarming	d	–	56
Mean energy	–	–	8.0

The wind direction was varied between all sites to always exhibit a worst case scenario (drifting the beetles directly to the nearest forest area outside the NLP, ***Figure 3****).*

4. DISCUSSION

In this study, we introduce the newly developed IPS-SPREADS, a combination of three well accepted models on the European spruce bark beetle (*I. typographus*): the predisposition assessment systems PAS (Netherer and Nopp-Mayr, 2005), the phenology model PHENIPS (Baier et al., 2007) and, the individual-based model IPS (Kautz et al., 2016). By incorporating the ability to utilize GIS data, IPS-SPREADS is applicable on any real world landscape and is capable of investigating the impact of different management measures as well as climate change on the dispersal and infestation patterns of *I. typographus*. By using patterns of real world infestations of a NLP inside Germany, we test our model (sensitivity analysis), calibrate its most important parameters and investigate the effectiveness of sanitation felling against the spread of the European spruce bark beetle. In the following paragraphs, the results of the model calibration as well as its application are discussed.

Decreased energy due to high intra-specific competition plays a major role in populations of *I. typographus* (Salle et al., 2005). Results of Botterweg (2009) show that the mean relative

TABLE 7 | Parameter combinations with the lowest prediction error for each research area during the random sampling (first four rows) and derived parameter combinations with their prediction errors (last four rows).

Area code	Energy –	Swarming d	w-direction °	gen *n*	w-speed $\frac{m}{s}$	inf_model *n*	inf_real *n*	inf_match *n*	error %
A1	7.3	56	148.8	2	1.2	344	186	141	87.94
B1	8.8	53	356.3	1	4.0	260	101	99	82.32
C1	6.0	55	129.4	2	4.0	937	697	528	54.73
D1	8.3	55	71.6	1	5.2	289	133	104	102.88
A2	8.0	56	148.8	2	4.0	360	186	141	93.62
B2	8.0	56	356.3	1	4.0	262	101	99	83.33
C2	8.0	56	129.4	2	4.0	1,010	697	553	54.34
D2	8.0	56	71.6	1	4.0	288	133	103	104.37

The corresponding results of one model run with the respective parameter values can be found in ***Figure 4****. w-direction, wind direction; gen, generations; w-speed, wind speed; inf_model, number of infested trees within the model; inf_real, number of infested trees in the real world; inf_match, number of infested trees in the model that match the real world data.*

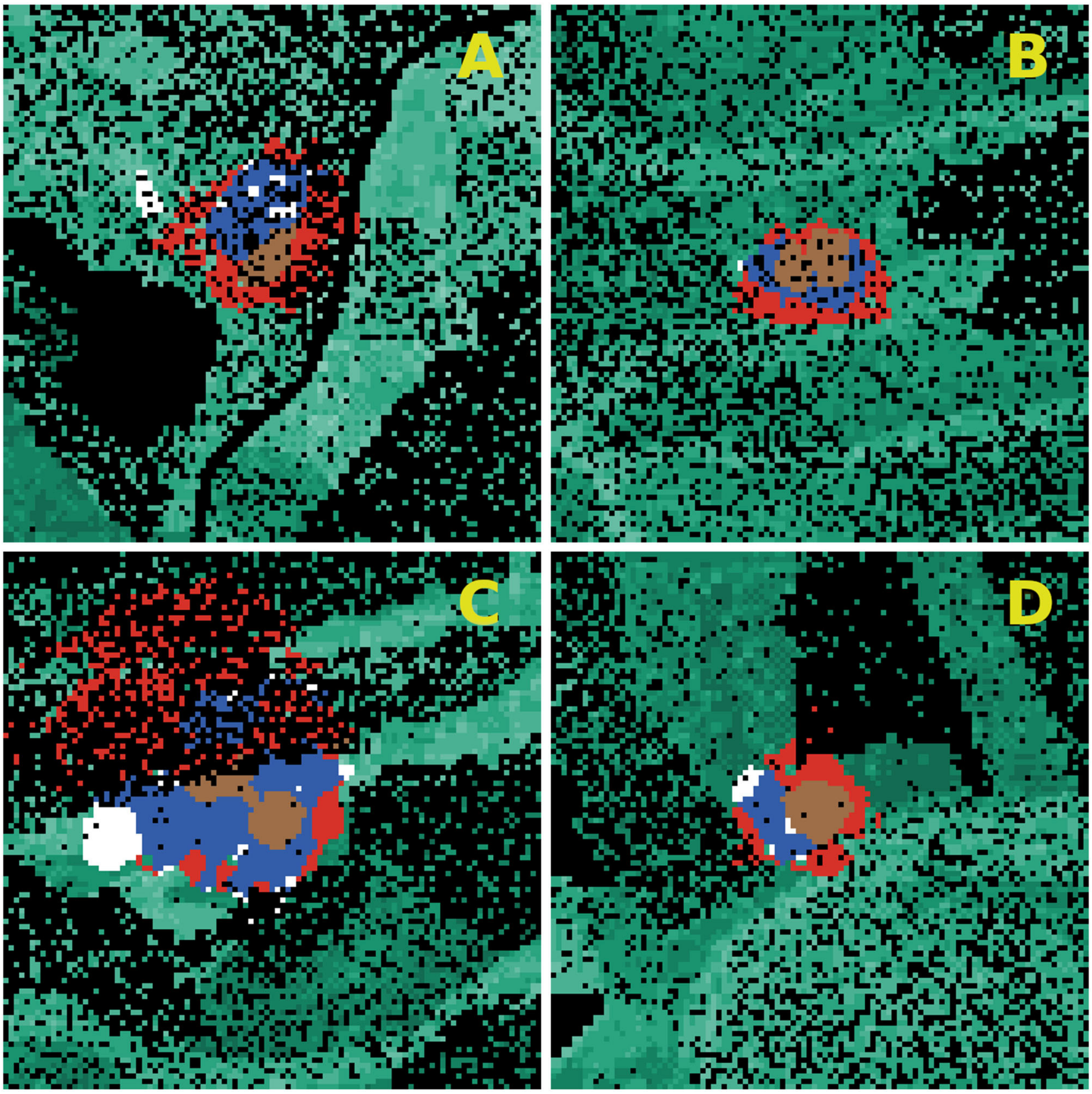

FIGURE 4 | Simulation results for the fitted parameter combinations on the four research sites **(A–D)**. The values for beetle energy, wind speed, and beetle swarming duration are the same on each research site while the values of wind direction and beetle generation amount are taken from the best fits during random sampling. The corresponding parameter values and prediction errors can be found in **Table 7**. Brown, beetle source trees; red, trees infested only in the model; white, trees infested only in reality; blue, trees infested in the model matching the real world data; green, spruce trees; black, everything else (e.g., other tree species, meadow, roads).

fat content of emerging beetles decreased to 86.5% when the breeding density was doubled. These findings support the results of the calibration of IPS-SPREADS, where reduced mean beetle energy levels scored the smallest errors. Relating the fitted value for beetle energy to the standard value of the original model IPS (Kautz et al., 2014, 2016), a reduction of 20% can be expected when mass outbreaks of *I. typographus* take place. The relatively high swarming duration can be explained with the overall dry and hot weather that was observed in the simulated years (2016 and 2017). The online version of PHENIPS (Baier et al., 2007) for the German federal state Saxony, in which the NLP is located, calculated for the years 2016, 2017, and 2018 theoretical

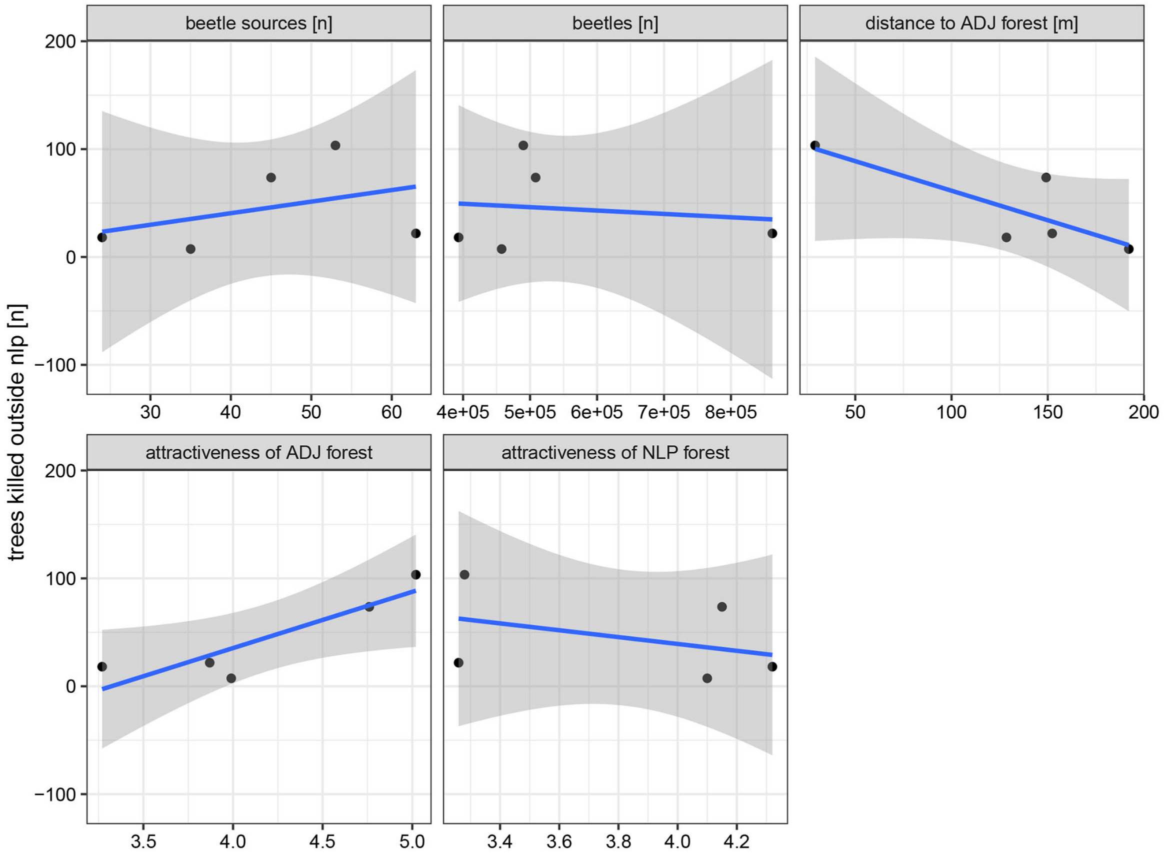

FIGURE 5 | Mean amount of damaged tress [n] outside the national park (NLP) for the control variants (no sanitation felling applied) of each research area. Each panel displays a different property (from top left to bottom right): Amount of beetle source trees, amount of emerging beetles during the first generation, distance between source trees and adjacent forest area (ADJ), mean primary attractiveness of ADJ and mean primary attractiveness of the NLP. Blue lines display a linear model fitted with the smooth function of the R package *ggplot2* and gray areas highlight the 95% confidence interval.

swarming durations of 100, 101, and 120 days, respectively for the NLP[1]. Distributed on two beetle generations, a theoretical swarming duration between 50 and 60 days is achieved and in accordance with the values fitted during the calibration of IPS-SPREADS. The differences in the number of beetle generations between the investigated research sites could be connected with different elevations of those sites (Baier et al., 2007; Wermelinger et al., 2012; Jakoby et al., 2019) or the presence and absence of forest protection management. Nevertheless, as the data provided by the NLP does not state when in the course of the year the infestation took place, all trees from 1 year are considered as beetle source trees for the following year. Because of this, even trees infested in early spring are considered as beetle source trees for the next year, which should lead to an overestimation of beetles emerging during the first beetle generation. Because of that, sites with fewer and nearer infested trees achieve lower errors with only one beetle generation as the number of beetles within this one generation is sufficient to infest the same amount of trees as observed in reality. More precise data on the timing of infestation or at least the affiliation to spring or summer infestation would result in better fits and probably lead to a fitted amount of two generations on all investigated sites. The impact of wind direction and intensity on the distance and direction of infested trees in relation to the beetle source trees is directly linked to the general impact of wind on the dispersion of airworthy insects as mentioned by Johnson (1969) and Pasek (1988) as well as on the impact on the pheromones produced by the beetles to attract more individuals to already infested trees (Mankin et al., 1980; Strand et al., 2009). The wind speed does not exert an influence as big as the wind direction, which can be explained with the overall low wind speeds that are reached within the forest canopy. The average wind speed (*local-speed* in the model) never exceeded 1 m per second on all research sites. As the beetles do not (yet) stop their dispersal flight due to high

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[1] https://ifff-server.boku.ac.at/wordpress/index.php/language/de/phenips-online-monitoring/phenips-online-deutschland/phenips-sachsen/

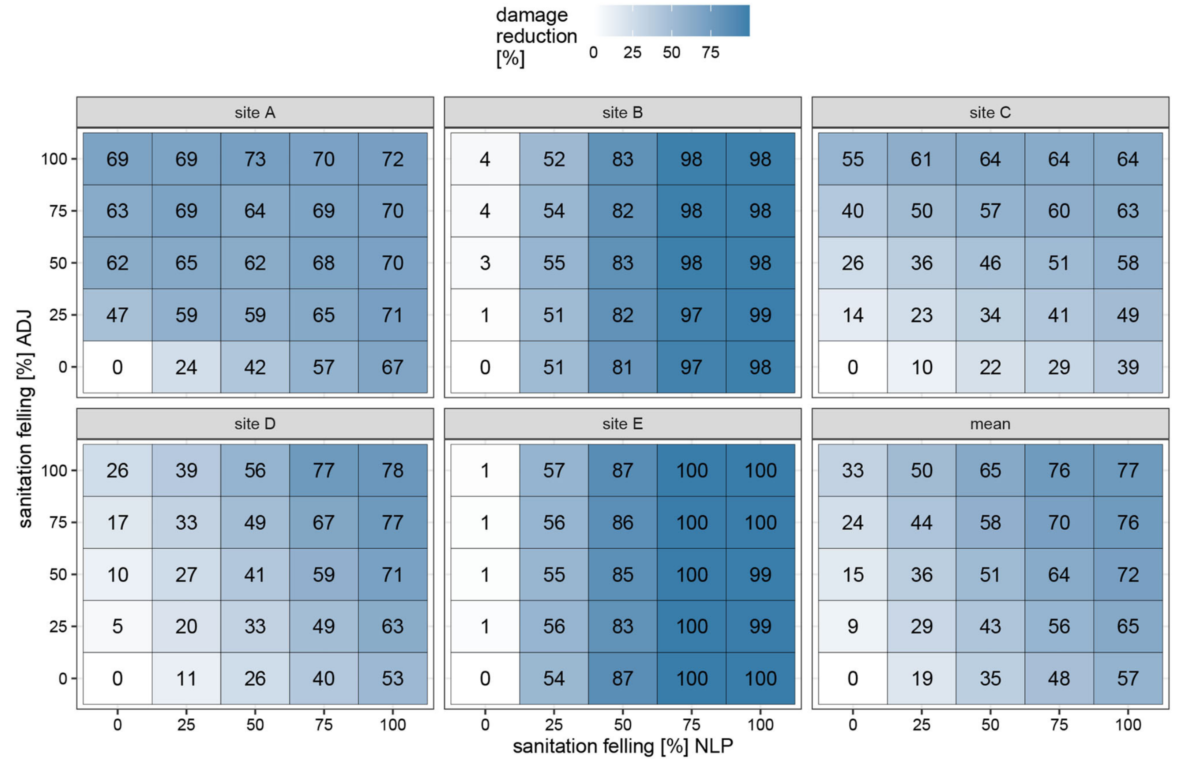

FIGURE 6 | Mean effectiveness of reduction of damaged trees outside the NLP [%] of the 40 repetitions in dependency of sanitation felling intensity inside the NLP (x axis) and outside the NLP (y axis). Each panel displays the effects on one of the five research sites and the mean over all sites combined. The effectiveness is calculated following (Abbott, 1925).

wind speeds, the maximum wind speed was not set beyond 5.5 m per second, which is reported to be the maximum wind speed in which *I. typographus* still disperses (Hurling, 2002). The overall fit could have been improved if another calibration cycle with reduced parameter sections would have been performed. As the overall fit was reasonable and the simulation cost considerably large, further model runs were not performed. One of the main limitations for IPS-SPREADS to reproduce real world infestation patterns lies within the modified PAS for calculating the primary attractiveness of each tree. Firstly, the data provided by the NLP is limited in its temporal and spatial resolution. For example, the variation of important factors for spruce tree vitality such as acute drought stress (Netherer et al., 2019) are not taken into account as only long term means are used for the calculation in this study. Secondly, the original PAS was developed to calculate predispositions for whole forest stands and not for the individual trees. Factors influencing the individual composition of spruces can vary greatly between each 5 × 5 m patch and those small scale differences were not taken into account. Further improvements could be achieved by using open accessible sentinel radar data which provide a high temporal resolution or by using promising analysis methods such as machine learning, which could improve the results of the predisposition assessment while using the same base data as done in the presented study (Rammer and Seidl, 2019).

The increase of damaged trees outside the NLP with increasing primary attractiveness of those trees is a logical consequence as the tree defense is directly calculated from the primary attractiveness. As such, higher primary attractiveness results in lower tree defense and therefore lower beetle densities are needed to inflict a successful infestation (Kautz et al., 2014, 2016). As the primary attractiveness was calculated based on the PAS (Netherer and Nopp-Mayr, 2005), high levels of primary attractiveness imply worse conditions for the trees outside the NLP such as low water supply or poor nutrient availability. With higher distances between beetle source trees and the ADJ forest area lower amounts of damaged trees occurred. This connection between distance to infested trees and infestation risk is often reported: New infestations occur mostly within 100 and up to 500 m around old infestations (Wichmann and Ravn, 2001; Kautz et al., 2011; Zolubas and Dagilius, 2012; Potterf et al., 2019), which is in turn connected to decreasing beetle densities with higher distances from beetle sources (Angst et al., 2012; Hinze and John, 2020). The amount of beetle source trees as well as the amount of beetles starting in the first generation from those trees had no impact on the amount of damaged trees outside the NLP. This phenomenon can be understood as indication that the resulting beetle densities in the ADJ forest areas were always high enough generate a damage there. If smaller amounts of beetle source trees or starting beetles would have been tested on the same research sites, there would have been a minimum amount necessary for damage outside the NLP to happen. With this, it would be possible to determine critical amounts of beetle source tree cohorts for damages to occur and highlight further possibilities to facilitate IPS-SPREADS as a risk assessment tool. As most infestations occur in the direct surroundings of previous infested trees, higher primary attractiveness and therefore lower tree defenses of spruces within the NLP reduce the risk of damage outside the NLP. This is in direct relationship to the aforementioned lower beetle densities which are further lowered if a given amount of beetles is attracted to susceptible trees before they can reach the ADJ forest area.

The applied sanitation felling happened only between the two simulated beetle generations as this is reported to be the optimal timing (Wichmann and Ravn, 2001) and to depict realistic frequencies that could be applied to a whole NLP and its surrounding forest areas. A complete reduction of damage outside the NLP was only achieved on sites with appropriate amount of NLP forest area between the beetle source trees and the NLP border. On the one hand, this is directly related to the aforementioned higher infestation emergence near old infestations or wind-thrown trees (Wichmann and Ravn, 2001; Kautz et al., 2011; Zolubas and Dagilius, 2012; Havašová et al., 2017; Potterf et al., 2019), as this leads to fewer damaged trees outside the NLP to begin with. On the other hand, trees cut during the sanitation felling outside the NLP were also counted as damaged trees in this study. Therefore, even with a removal of 100% of infested trees outside the NLP, there were still trees being damaged. In accordance with Stadelmann et al. (2013a) the results of the presented model application indicate, that increasing sanitation felling reduces the amount of damaged trees. It is also reported that sanitary felling of more than 80% or more than 95% is needed to substantially reduce bark beetle disturbances (Dobor et al., 2020a,b), further validating the model results. Similar intensities are needed relating to the amount of individual beetles, where more than 80% of the population should be killed to avoid bark beetle outbreaks (Fahse and Heurich, 2011).

The advantages of IPS-SPREADS in comparison to other simulation models for *I. typographus* are in its high spatial and temporal resolution, which allows it to be applied as a tool to assess the effects of different management strategies in any given real world forest on a daily bases. For example, it is possible to test the planned management strategy for a given infestation cohort and revise it according to the model results and to achieve the lowest possible damage for the next days, weeks, or month. This also emphasizes the possibility of IPS-SPREADS to be used as a risk assessment tool. As an older version of the model was used to calibrate the implementation of pheromone traps using results of mark recapture experiments similar to the model of Doležal et al. (2016), it is possible to extract the relation between the number of trapped beetles and the total size of the beetle population within a given forest. This relation could then be used to improve the estimation of bark beetle activity throughout the year more accurately in the given area. Disadvantages of the presented model are in the high computational cost which exceed the capabilities of average computers if mass outbreak conditions are to be simulated like during our model calibration. For such conditions other, less computational intensive models are to be preferred to analyze the dispersal and infestation patterns (Fahse and Heurich, 2011; Honkaniemi et al., 2018) or to perform risk assessment on larger scales (Dutilleul et al., 2000; Overbeck et al., 2011; Blomqvist et al., 2018). Nevertheless, if IPS-SPREADS is applied for initial infestations or the development of early outbreak stages, thanks to thorough code optimization the model performs well even simulating all beetles individually. For longer study periods or broader areas IPS-SPREADS is not suitable as it does not take into account changes in forest structure, water household or weather throughout the year or between years and it does not account for disturbances such as wind, fire or management and their impact on host tree availability, population dynamics and management in return. For this, other available simulation models (Seidl et al., 2007, 2008, 2009; Temperli et al., 2013; Rammer and Seidl, 2015, 2019) are far more appropriate. Another shortcoming of IPS-SPREADS is in the dependency on the availability of various base data to be applicable in a given forest, such as digital elevation model, daily temperature and irradiation, canopy closure, spruce proportion, or soil properties. For future applications of IPS-SPREADS it is therefor planned to make full use of publicly available and globally present data such as from the European Union's earth observation program Copernicus.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in an online repository: https://github.com/bwpietzsch/IPS-SPREADS.

AUTHOR CONTRIBUTIONS

BP developed the model, designed and carried out the experiments, analyzed and interpreted the results, and wrote the article. FP developed parts of the model and commented on the article. UB supervised the whole project and revised the article. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.704930/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

3 Article II - Metamodels for Evaluating, Calibrating and Applying Agent-Based Models: A Review

Summary The use of metamodels in agent-based modeling is expanding, and there is a growing demand for applications that mimic the input-output behavior of these models. This paper provides an overview of common metamodel types and the purposes for their use in an agent-based modeling context. These metamodels' implementation efforts and performance are assessed to guide modelers' selection and application. This review provides information about the most suitable metamodel types for each purpose and forms a first guidance for implementing and validating metamodels for agent-based models.

Novelty This study is the first systematic literature review on metamodels used in an agent-based modeling context. In addition, we illustrate and analyze the different metamodel types and purposes used in this context and provide a novel rating methodology to assess the applicability, usability, or information quality of the reviewed metamodels.

Key features As we intended this publication not only to be a systematic overview of metamodel types used and application aims pursued but also to be a guide for Ph.D. students and postdocs in choosing the most suited metamodel type for their application, we provide the full rating methodology as well as all data used in this open access publication as freely accessible supplementary material under the following link: `https://www.doi.org/10.18564/jasss.4274`.

Publication type, journal, authors, and the Ph.D. candidates' contribution This chapter represents a peer-reviewed publication in the *Journal of Artificial Societies and Social Simulation* (JASSS) from March 2020, entitled 'Metamodels for Evaluating, Calibrating and Applying Agent-Based Models: A Review.' It has been compiled with MSc Sebastian Fiedler, Dr. Kai G. Mertens, MSc Markus Richter, Dr. Cedric Scherer, MSc Kirana Widyastuti, MSc Marie-Christin Wimmler, Dr. Liubov Zakharova as well as with Prof. Dr. Uta Berger, the first supervisor of this Ph.D. study. The candidate of this dissertation designed and carried out the literature search, designed the rating methodology, analyzed and interpreted the results, and wrote and reviewed the article.

Metamodels for Evaluating, Calibrating and Applying Agent-Based Models: A Review

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Abstract: The recent advancement of agent-based modeling is characterized by higher demands on the parameterization, evaluation and documentation of these computationally expensive models. Accordingly, there is also a growing request for "easy to go" applications just mimicking the input-output behavior of such models. Metamodels are being increasingly used for these tasks. In this paper, we provide an overview of common metamodel types and the purposes of their usage in an agent-based modeling context. To guide modelers in the selection and application of metamodels for their own needs, we further assessed their implementation effort and performance. We performed a literature research in January 2019 using four different databases. Five different terms paraphrasing metamodels (approximation, emulator, meta-model, metamodel and surrogate) were used to capture the whole range of relevant literature in all disciplines. All metamodel applications found were then categorized into specific metamodel types and rated by different junior and senior researches from varying disciplines (including forest sciences, landscape ecology, or economics) regarding the implementation effort and performance. Specifically, we captured the metamodel performance according to (i) the consideration of uncertainties, (ii) the suitability assessment provided by the authors for the particular purpose, and (iii) the number of valuation criteria provided for suitability assessment. We selected 40 distinct metamodel applications from studies published in peer-reviewed journals from 2005 to 2019. These were used for the sensitivity analysis, calibration and upscaling of agent-based models, as well to mimic their prediction for different scenarios. This review provides information about the most applicable metamodel types for each purpose and forms a first guidance for the implementation and validation of metamodels for agent-based models.

Keywords: Individual-Based Model, Surrogate Model, Emulator, Calibration, Sensitivity Analysis, Review

Introduction

1.1 Essentially, a metamodel (MM) is a model which describes the behaviour of an original model on a higher hierarchical level (Moorcroft et al. 2001; Urban 2005; Gore et al. 2017). In the context of mechanistically detailed and therefore often computationally expensive agent-based models (ABM) or individual-based models (IBM [1]), MMs provide an efficient way to facilitate profound model analysis and prediction of ABM behaviour over a wide range of parameter combinations.

1.2 The term MM originates from the *Design of Experiments* literature (Wang & Shan 2007; Montgomery 2009). It was originally developed to study the effects of a set of explanatory variables on a response variable. Therein, optimization via response surface MMs was the most widely performed application (Barton 1988). Both terms, surrogate models (Dey et al. 2017) or emulators (Conti & O'Hagan 2010), can also be understood as MMs. Most commonly, they all treat a particular ABM as a white, grey or black box (Papadopoulos & Azar 2016) and link the input and output values by aggregated functions (Barton 1988; Friedman & Pressman 1988; Friedman 1996; Barton & Meckesheimer 2006). As a result, MM significantly reduce simulation costs in terms of computational time and allow easier communication and understanding of simulation models' behavior (Kleijnen & Sargent 2000; Mertens et al. 2018). This review will not consider other related concepts of MMs such as the model framework of concepts (Goldspink 2000).

1.3 The aim of this review is to condense available information about common MM types used for various tasks related to ABM analysis and applications to guide modelers in choosing an appropriate MM type for their research problem. For detailed information on specific MMs and their applications, it is advised to look for reviews or tutorials elsewhere like Barraquand & Murrell (2013), Barton (1988), Gore et al. (2017), Heard et al. (2015), Kalteh et al. (2008), Mertens et al. (2018), O'Hagan (2006), Oakley (2002) or Urban (2005). A methodology for rating MM quality and implementation effort in an ABM context was developed and applied for the reviewed publications by eight different raters with varying mathematical skills and scientific backgrounds. This was done to support readers in their selection and application of a metamodel in an ABM context.

Methods

Searching procedure

2.1 We conducted a literature survey in Open Access databases (see Table 1) on the 17th, 18th, 21st and 24th of January 2019 and considered only peer-reviewed papers. For each database used, we performed ten searches combining the terms *agent-based model* and *individual-based model* with each of the following keywords: *Approximation*, *emulator*, *metamodel*, *meta-model* and *surrogate*. We did not limit the time frame of the results but took only a maximum of 50 results per search into account, sorted by their relevance. Papers containing a single or combinations of keyword(s) in their title, abstract, or keywords section were selected for review.

Database	Website
Academic Search Complete	`ebscohost.com/academic/academic-search-complete`
Web of Science Core Collection	`apps.webofknowledge.com`
Google Scholar	`scholar.google.de`
Scopus	`elsevier.com/solutions/scopus`

Table 1: Complete list of all databases used for the review presented. The survey was conducted in January 2019 without limiting the years of publication.

Categorization of MMs and purpose of application

2.2 In contrast to Papadopoulos & Azar (2016), we do not sub-classify MMs into white (reduced order), gray (both physical equations and stochastically estimated parameters) and black box (Machine Learning) surrogate models. Instead, we simply distinguish them according to their approach to describe the link between input and output variables as deterministic (e.g. Differential Equation) and stochastic (e.g. Machine Learning) MMs, respectively. We thus assign, for example, a Partial Differential Equation used for upscaling (e.g. Moorcroft et al. 2001) to the family of deterministic MMs, whereas Bayesian Emulators applied for calibration (e.g. Bijak et al. 2013) are considered as stochastic MMs.

2.3 The MMs were first subdivided into two main **classes** namely *deterministic* and *stochastic* models depending on whether they consider probability distributions linked to the input, output, or processes described by the ABM. The classes were further subdivided into six model **families** that comprise different MM **types** (Table 2). In this sense, all MM family names resemble the so-called suitcase phrases and do not necessarily share all attributes or requirements of their namesake in a mathematical context. The names of the model types were directly

Model Class	Model Family	Model Type
Deterministic	Ordinary Functional Equation	Difference Equation, Equation-free Modeling, System Dynamics Model
	Differential Equation	Compartment Ordinary Differential Equation (CODE), Ordinary Differential Equation (ODE), Partial Differential Equation (PDE)
Stochastic	Regression	First-order Regression, Linear Regression, Polynomial Regression, Weighted Ordinary Least Squares Regression
	Bayesian Emulator	Approximate Bayesian Computation (ABC), Dynamic Linear Model Gaussian process, Gaussian Process, Spatial Correlation (Kriging), Parametric Likelihood Approximation
	Machine Learning	Decision Tree, Decision Tree Ensemble, Feature Selection, Radial Basis Function Network, Random Forest, Support Vector Regression, Symbolic Regression
	Markov chain	Transition Matrices

Table 2: MM classification derived from the accepted papers with MM applications in an ABM context. The differentiation between *deterministic* and *stochastic* models depend on whether probability distributions of input, output or processes described by the emulated ABM were taken into account. Model families represent the so-called suitcase phrases, which are not necessarily mathematical definitions for all MM types included in the family.

extracted from the accepted papers without any adjustments. Appendix A provides complete information about the reviewed papers and the corresponding model families and types.

2.4 We categorized the purpose of each MM exclusively based on the declaration of the particular authors (Table 3). Notably, we understand parameter fitting as calibration incorporating calibration, parameterization or optimization in accordance to Railsback & Grimm (2012).

Assessment of MM quality and implementation effort

2.5 In the following paragraphs, we briefly describe how we rated the MM's quality and implementation effort. For more in-depth information on the procedure as well as for some examples of each rating criterion, see Appendix C. This guide was used to rate each MM application and to calculate the mean quality and implementation effort. An inter-rater reliability was calculated using the *icc* function of the R package *irr* version 0.84.1 (Gamer et al. 2019). Following Koo & Li (2016), we applied a *two-way* mixed effects model (all selected raters were the only

Purpose	Description
Calibration	Find reasonable values for input parameters (Friedman & Pressman 1988; Barton 1988; Friedman 1996; Kleijnen & Sargent 2000; Barton & Meckesheimer 2006).
Prediction	Predict model behavior for new scenarios or parameter values while replacing the simulation model (Kleijnen & Sargent 2000). Also known as exploratory analysis (Bigelow & Davis 2002), what-if analysis (Barton & Meckesheimer 2006) or exploration / inverse exploration (Friedman & Pressman 1988; Friedman 1996).
Sensitivity analysis	Explore model output sensitivity to changes in parameter values (Railsback & Grimm 2012; Thiele et al. 2014; Ligmann-Zielinska et al. 2020).
Upscaling	Scale the model to a coarser spatial resolution (Cipriotti et al. 2016) or from individuals to populations (Campillo & Champagnat 2012).

Table 3: Common purposes of emulating ABMs by means of MMs.

Criteria	**MM Quality**			**Key Questions**
	Low	**Medium**	**High**	
Consideration of Uncertainty **(CU)**	no	yes	with evaluation	Did the authors give any assessment on the uncertainties of the MM assumptions or results?
Suitability Assessment **(SuA)**	none or bad	good (qualitatively)	good (quantitatively)	How did the authors state the suitability of the MM for the given purpose?
Number of Evaluation Criteria **(NE)**	1	2	> 2	How many different criteria were provided by the authors for evaluating the MM suitability?

Table 4: Criteria applied for assessing the MM quality for the given purpose of emulating the ABM.

one of interest), using *average* as type (we want to use the mean ratings for each MM application) and *agreement* as definition since we had sought to evaluate the agreement among the raters.

2.6 The quality of MM was assessed based on the assessment of the respective source authors using three different criteria (Table 4): Consideration of Uncertainty **(CU)**, Suitability Assessment by Source Authors **(SuA)**, and Number of Evaluation Criteria **(NE)**. With the **CU** criterion, we evaluated how the authors considered uncertainties in the inputs and outputs of the respective MM family. In this criterion, the term *no* means that there was no explicit consideration of uncertainty given by the authors using the MM, while *yes* refers to those where they used at least some (quantitative) measures (e.g. error bars or R^2). We assigned a *high* quality if the source authors had presented measures of uncertainty with a corresponding evaluation of such measures. The term suitability in **SuA** refers to the applicability of the given MM type (e.g., Approximate Bayesian Computation) to fulfill the particular purpose (e.g., calibration of an ABM). A good MM evaluation by the authors was regarded as *medium* if the assessment is only based a qualitative statement (e.g., "The MM performed extremely well."). We adjudged suitability as *good* in those cases where the ABM emulation was quantitatively assessed with a positive result. The third criteria **NE** is self-explaining. For example, a basic linear regression model provides two criteria for evaluating suitability (R squared for the goodness of fit and p-value for evaluating the significance of the linear relationship between the input and output variables) and, thus, would receive a *medium* assessment for this specific criterion if the authors presented those criteria within their peer-reviewed research paper. Example statements like, *the MM had a 61% probability of selecting a parameter set that fitted all investigated outputs*, or *this procedure was successful in 92% of cases, revealing its great potential to assess parameters difficult to measure in nature*, were considered as **SuA** = *good* with **NE** = *low*.

2.7 The implementation effort of each MM family was assessed by the following three criteria (Table 5): Availability of Open Access Guiding Sources **(AG)**, R Coverage **(RC)**, and Out-of-the-Box Applicability **(OA)**. Since we focus exclusively on the effort to implement MMs, computational cost has been absent in our consideration. The **AG** criterion evaluates the effort of finding help or further information for the potential MM application to own needs. If no sources could be found by performing a search in Google Scholar and Google.com using the MM type name as search query, the MM was regarded with a *high* implementation effort, while multiple usable sources (e.g. a page on Wikipedia.org and a mathematical blog entry) were considered as a *medium* implementation effort. *Low* efforts were assessed if there was one source giving a comprehensive tutorial on implementing the respective MM. The **RC** criterion focused on the free available statistical language R (R Core Team 2018). If one dedicated package is available to implement the whole MM, it was rated with a *low* implementation effort. If multiple R packages were necessary, a *medium* effort was given. We assigned a *high* implementation effort if the entire MM had to be developed from scratch. The last criterion **OA** assessed the possibility of MMs to be immediately usable (partly depends on the existing software). MMs were evaluated at a high implementation effort if the derivation of specific equations was required or some important assumptions had to be investigated for it's use. Little adjustments correspond, for example, to the derivation of a linear model equation for the corresponding R function, while the application of an unsupervised artificial neural network was considered as a *low* implementation effort.

2.8 Using the average value of all raters of each criterion, we conducted an overall assessment of quality and implementation effort of each MM application. Mean ratings were then analyzed separately for quality and implementation effort using the five-level classification (*low*, *low-medium*, *medium*, *medium-high* and *high*) displayed in

Criteria	**Implementation Effort**			**Key Questions**
	Low	**Medium**	**High**	
Availability of Open Access Guiding Sources **(AG)**	1 good source	multiple sources	none	Are there any openly accessible sources like books or blogs that give an implementation guideline for the MM family of interest?
R Coverage **(RC)**	1 good package	multiple packages	none	Are there any dedicated R packages to implement the given MM?
Out-of-the-Box Applicability **(OA)**	no adjustments	little adjustments	need for full recreation	Is it necessary to develop an own equation from scratch for the MM to be applicable?

Table 5: Criteria applied for assessing the MM implementation effort for the given application aims.

Amount of Scores in			**Overall MM Quality / Implementation Effort**
High	**Medium**	**Low**	**Level**
3	0	0	high
2	1	0	high
2	0	1	medium-high
1	2	0	medium-high
1	1	1	medium
0	3	0	medium
1	0	2	low-medium
0	2	1	low-medium
0	1	2	low
0	0	3	low

Table 6: The overall MM quality and implementation effort was calculated for each application according to the mean ratings of each of the three criteria for quality (CU, NE and SuA) and effort (AG, OA and RC).

Table 6. If, for example, a MM application received a high **SuA**, a high **NE** and a medium **CU**, a high overall MM quality was given. These overall assessments were used to generate a plot for each application aim (Table 3) depicting the MM quality in the dependency of the MM implementation effort. Within these plots a bisecting line was drawn for visualizing the 1 : 1 ration of quality and implementation effort and highlight favorable MMs scoring above this line and less favorable MMs staying below this line.

Results and Discussion

3.1 Following the previously described selection criteria (see method section), 27 different peer-reviewed journal papers published from 2005 to 2019 (Figure 1) were accepted for the review (see Appendix B. With this we could extract 40 different MM applications in an ABM context (see Appendix A).

Sensitivity analysis

3.2 For sensitivity analyses, Bayesian Emulators and Regressions have the highest MM quality indicating accessible implementation efforts (Figure 2). Half of the reviewed publications with focus on Machine Learning scored above the bisecting line indicating a broad MM usage, while the remaining applications were either on or below the bisecting line.

3.3 Overall, we found the implementation effort for the three MM families (Bayesian Emulators, Machine Learning and Regression) to be reasonable due to a predominantly high RC (R coverage) and the broad AG (availability

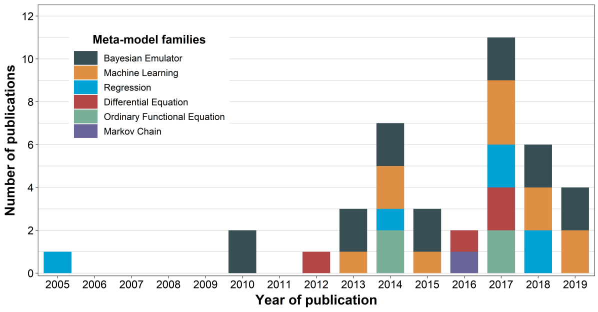

Figure 1: Number of reviewed papers and categorized MM families according to the publication year.

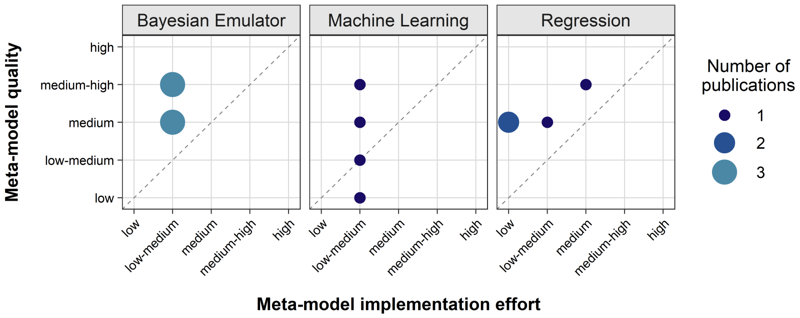

Figure 2: Results of the MM quality and implementation effort assessment for the application aim of sensitivity analysis.

of Open Access guiding sources) on these MMs. However, a shortcoming in the application of these three MM families for sensitivity analysis is their need for adjustments to be applicable for another ABM: There was not a single MM type within those MM families that could be reused without any changes. The superior qualities of Bayesian Emulators and Regression MMs result from the moderate to good SuA (Suitability Assessment by Source Authors) in addition to their moderate to good CU (Consideration of Uncertainty). The applied Machine Learning MMs for sensitivity analysis never exceeded a moderate NE (Number of Evaluation Criteria) while their CU and the SuA increased in the following order: Decision Tree Ensemble, Support Vector Regression, Symbolic Regression and Random Forest.

Calibration

3.4 For calibration, Bayesian Emulators, Machine Learning and Regression MMs seem to be the preferable MM families since they constantly stay above the bisecting line (or thereon) indicating a beneficial MM quality to implementation effort ratio (Figure 3). In contrast, Differential Equation and Ordinary Functional Equation MMs do not exceed or even reach the bisecting line and therefore seem to be less favorable MM families to be applied for the purpose of calibrating ABMs.

3.5 The overall low-medium implementation efforts of the three best scored MM families such as Bayesian Emulator, Machine Learning and Regression can be explained with their good to at least medium RC (R Coverage) as well as the good to moderate AG (Availability of Guiding Sources). Their OA (Out-of-the-Box Applicability) was never rated as low and always received medium or high assessments regarding their implementation efforts.

3.6 High implementation efforts of Differential Equations and Ordinary Functional Equations are due to considerably low OA because they have to be rebuilt entirely for every new ABM. Their AG and RC remain good to medium, emphasizing their broad usability.

3.7 The superior MM qualities of Bayesian Emulators are due to their high NE as well as in-depth CU (Consideration of Uncertainty). Only SuA (Suitability Assessment of Source Authors) was poor to medium, indicating that not every MM type of this family suited the task of calibration as good as the others. Machine Learning MMs always achieved a good SuA while their CU and NE (Number of Evaluation Criteria) varied from medium to high.

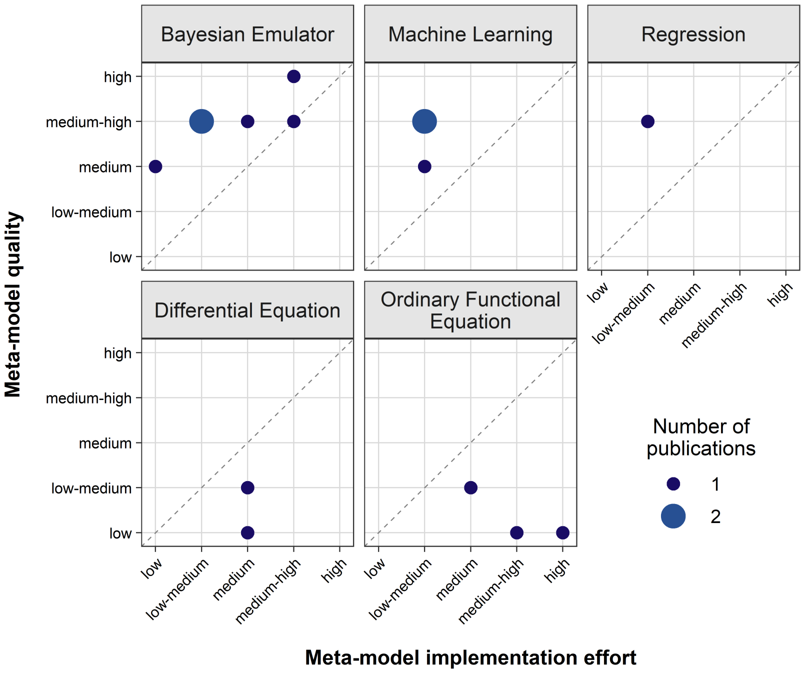

Figure 3: Results of the MM quality and implementation effort assessment for the application aim of calibration.

3.8 The considerably poor qualities achieved by Differential Equations and Ordinary Functional Equations result from their low CU and NE. Nevertheless, the respective source authors assessed the suitability of these MMs qualitatively as good.

Prediction

3.9 In order to predict the behavior of ABMs, Bayesian Emulators and Machine Learning MMs seem to be the most favorable MM families since they continually exceed the bisecting line of 1 : 1 ratio for MM quality and implementation effort (Figure 4). While the only Regression application for predicting ABMs achieves a low-medium MM quality as well as implementation effort signaling a trade-off between prediction and implementation, Differential Equations as well as Ordinary Functional Equations consistently remain below the bisecting line.

3.10 For predicting ABMs behavior, Bayesian Emulators scored the best quality rating with varying implementation efforts. The low-medium effort of Gaussian Process Emulator originates from very good RC (R Coverage) as well as medium OA (Out-of-the-Box Applicability) and AG (Availability of Guiding Sources). The medium-high effort of the dynamic linear model Gaussian Process is due to worse OA, AG as well as RC. The latter two criteria should be considered critically as we used the exact name presented here as a key phrase in our online research while looking for R packages and guiding sources. We could expect a lower implementation effort had we used a more flexible search term for this kind of MM type.

3.11 The second best MM family for prediction of ABMs are Machine Learning models. Their considerably low implementation efforts are due to their broad RC and AG. OA varies around a medium ranking with decision trees achieving the highest rating. The varying quality within this MM family is because differentiating SuA (Suitability Assessment) by the respective source authors, while CU (Consideration of Uncertainty) is overall low and NE (Number of Evaluation Criteria) scores between low and medium. The highest quality is achieved by Random Forest for its comparable higher CU and NE.

3.12 The Regression MM applied for predicting ABMs is a First Order Regression receiving lower quality ratings while still being good at SuA. The implementation effort consists of a medium OA (the formula of the linear model has to be adapted for every ABM) and a moderate RC, which could be caused by using the whole and exact model name for our online research of R packages.

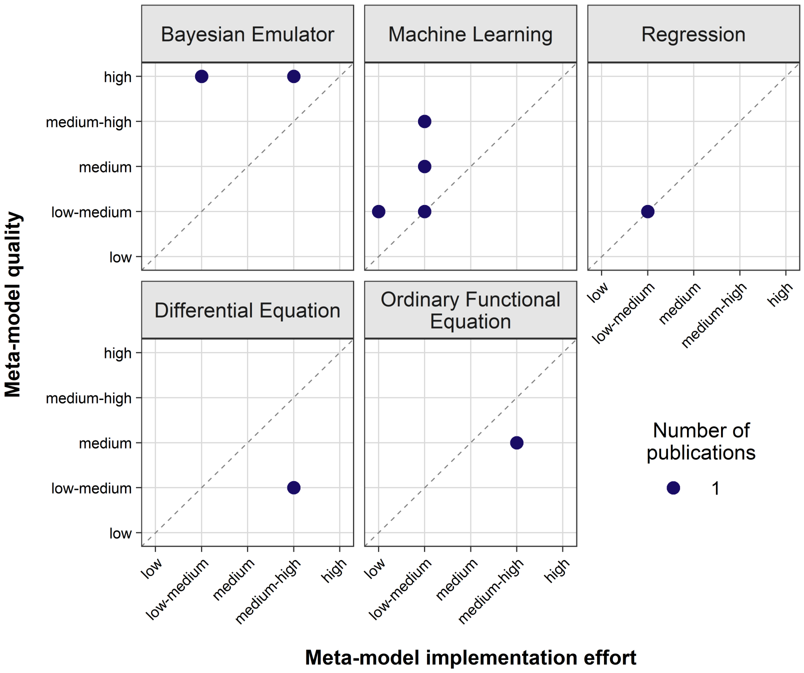

Figure 4: Results of the MM quality and implementation effort assessment for the application aim of Prediction.

3.13 The overall high implementation efforts of Differential Equations (Compartment Ordinary Differential Equation) and Ordinary Functional Equations (Systems Dynamic Model) while scoring only low-medium to medium qualities are due to their really low OA, since these MM families have to be rebuild anew entirely for each ABM applied. Furthermore, their CU as well as their NE is low, which together with only a qualitatively good SuA add up to medium qualities at best.

Upscaling

3.14 For upscaling ABMs only the Markov Chain MM exceeded a neutral MM quality and implementation effort ratio (Figure 5). The Differential Equation MM stayed below the bisecting line, making it a less favorable choice of MM for upscaling ABMs.

3.15 The Markov Chain MM reached a medium quality because of the considerably high SuA (Suitability Assessment by Source Authors), low-medium CU (Consideration of Uncertainty) and NE (Number of Evaluation Criteria). The implementation effort is dominated by its poor OA (Out-of-the-Box Applicability), meaning many adjustments are required to adapt this kind of MM to another ABM. The only accepted Differential Equation (Partial Differential Equation) scored a low OA since a new equation has to be derived for every application in ABMs.

MM rating method and inter-rater reliability

3.16 The inter-rater reliability never fell below a fair level and even achieved excellent evaluation for CU (Consideration of Uncertainty) and OA (Out-of-the-Box Applicability) (Table 7).

3.17 With eight raters and a sample size of 40 MM applications, the requirements suggested by Koo & Li (2016) are met and exceeded, emphasizing the robustness of the inter-rater reliability results and therewith the results of the MM rating. Nevertheless, the calculated fair intra-class correlation coefficients for SuA (Suitability Assessment of Source Authors), AG (Availability of Guiding Literature) and RC (R Coverage) (Table 7) indicate a necessity to further improve the clarity of the rating instruction for these criteria.

3.18 One reason for the stronger variation inside the MM implementation effort criteria AG and RC lies within the diverse backgrounds of the raters which participated in the MM assessment. Since the individual knowledge,

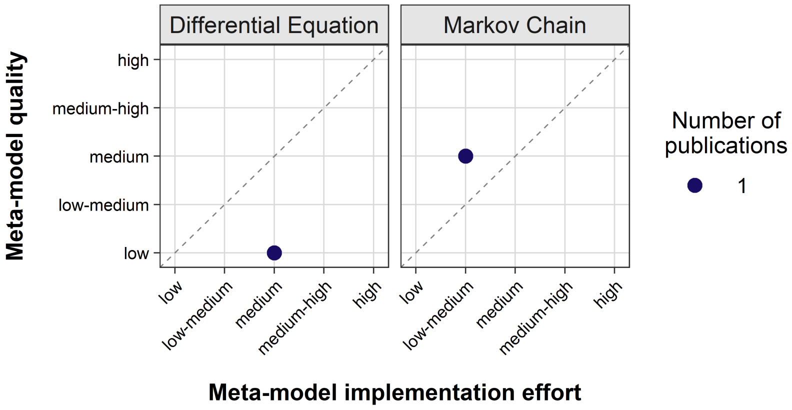

Figure 5: Results of the MM quality and implementation effort assessment for the application aim of upscaling.

the experiences with the corresponding MM types as well as the statistical software R were different (Appendix D), the assessment of a number of R packages needed to apply a given MM varied among reviewers.

3.19 The only fair agreement within the MM quality criterion SuA could be because of the unclear instruction for cases in which the authors provided empirical proof for the suitability but never directly assessed it themselves qualitatively. In these cases, some raters gave a medium rating and others a high. Additional divergences emerged when the source authors did not provide any assessment but some raters were able to identify a good or bad fit by themselves while investigating the provided plots, highlighting disparities in certain instances. A more fine grained analysis (e.g. five or seven scale evaluation) might reveal a clustering around high, medium and low with some within variations.

Rating Category	Rating Criterion	Inter-Rater Reliability	Evaluation
MM quality	Consideration of Uncertainty (CU)	0.859	excellent
	Suitability Assessment (SuA)	0.556	fair
	Number of Evaluation Criteria (NE)	0.721	good
MM implementation effort	Availability of Open Access Guiding Sources (AG)	0.461	fair
	R Coverage (RC)	0.509	fair
	Out-of-the-Box Applicability (OA)	0.773	excellent

Table 7: Calculated inter-rater reliability for the rating criteria with evaluation following Cicchetti (1994).

Conclusions

4.1 Metamodelling is a promising approach to facilitate ABM calibration, sensitivity analysis, prediction and upscaling. We conducted a review that overviews the MM types used among their purposes. Within the 27 papers analysed, we identified 40 different MM applications. For each of them, we (PhD students and Postdocs with none up to moderate mathematical background) assessed the performance quality and the implementation effort. The methodology applied MM rating in this paper was validated by the fair to excellent intra-class correlation coefficients during the inter-rater reliability assessment.

4.2 Our goal was to support MM selection for the various needs of daily ABM problems by highlighting the currently most promising MM types with an example each serving as a practical application guide:

- **Sensitivity analysis**: The easiest MMs to implement with a medium performance are Regression models (e.g. Polynomial Regression Model). Several examples with step-wise guidance for implementation in R (Team 2018) are provided by Thiele et al. (2014).
- **Calibration**: Approximate Bayesian Computation from the Bayesian Emulator family provides a good balance of effort and performance. Thiele et al. (2014) provides several basic implementation examples

of ABM calibration with step-by-step guidance in R (Team 2018).

- **Prediction**: Gaussian Processes from the Bayesian Emulator MM family provide the best quality while offering low-medium implementation effort. In contrast, Random Forest MMs (Machine Learning family) offer low-medium effort but only medium-high quality. An example on predicting new parameter combinations like an inverted calibration can be found in Peters et al. (2015).
- **Upscaling**: Transition Matrices from the Markov Chain MM family seem to be the most promising tool for scaling up ABMs. Note that we reviewed only two MMs on this application aim. The corresponding application can be found in Cipriotti et al. (2016).

4.3 This review was intended as a "first aid" for agent-based modelers who seek to improve the performance, optimization or analysis of their simulation model using a metamodel. Our motivation for this work ensued from our day-to-day modeling tasks. Please note that the review presented here can only provide an initial overview, which is primarily meant to stimulate and guide a potential reader through a self-exploration of the wide field of metamodels with ease. The examples presented here are not exhaustive and the field of metamodeling itself is constantly and rapidly developing. Particularly, the application of the potentials offered by various methods of artificial intelligence (with the branches of machine learning or deep learning) is just beginning to emerge. We would therefore like to motivate our readers to stay abreast on new developments in applying metamodeling approach to ABMs, and above all, try out metamodels in their own ways.

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Appendix A: MM classification and evaluation

For the results of MM classification and assessment of implementation effort as well as information quality, see the CSV file labelled "*results-rating.csv*".

Appendix B: Peer-reviewed papers accepted for this review

The complete list of references accepted for this review can be retrieved from the PDF file labelled "*reviewed-paper.pdf*".

Appendix C: MM rating instructions

The methods used for the MM quality and implementation effort rating can be found in the PDF file labelled "*rating-instructions.pdf*".

Appendix D: Rater background information

Information on the background of each rater highlighting their field of expertise, their experiences with R, modeling in general as well as with MMs in detail can be found in the CSV file labelled "*background.csv*".

Notes

[1] We refer to both individual- and agent-based models synonymously as ABM.

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4 Article III - Nonparametric upscaling of bark beetle infestations and management from plot to landscape level by combining individual-based with Markov chain models

Summary The European spruce bark beetle benefits from climate change, which complexly impacts forest health by weakening trees and promoting insect pest activity. Individual-based simulation models like IPS-SPREADS have been used to understand the long-term risks of beetle infestation better. However, the computational costs of these models limit their spatial scale of application. This paper introduces a two-step approach to address this challenge: using IPS-SPREADS to simulate bark beetle dispersal at a local scale and then applying a metamodel framework to upscale the results to the landscape level. The metamodel is based on Markov chains and is validated by comparing its predictions with observed infestations in a national park in Germany. The metamodel forecasts indicate an increase in the risk of infestation for adjacent forest areas. In a mass outbreak, sanitation felling at 80 percent or above intensities seem to mitigate further outbreak progression.

Novelty The study is the first to investigate the outbreak propagation of *Ips typographus* across spatial and temporal scales: it uses simulation results of an individual-based model on a small scale to develop a metamodel based on Markov chains that can be readily applied on a whole landscape and for two centuries into the future. For the first time, this enabled us to investigate the emergent patterns and effects of individual traits on the long-term and the large-scale development of a mass outbreak of *Ips typographus* under varying management and climate change scenarios.

Key features Despite using a different modeling approach and spatial or temporal resolution to other studies investigating bark beetle infestations, a similar management threshold was found to be met to reduce the beetle spread successfully. Furthermore, to encourage the re-use and application of the developed models, we published the model files, the used data, and the models' results freely accessible as a GitHub repository: `https://github.com/bwpietzsch/IPS-UPS`. The supplementary material can be freely accessed under the following link: `https://doi.org/10.1007/s10342-022-01512-1`.

Publication type, journal, author, and the Ph.D. candidates' contribution This chapter represents a peer-reviewed publication in the *European Journal of Forest Research* from October 2022 entitled 'Nonparametric upscaling of bark beetle infestations and management from plot to landscape level by combining individual-based with Markov chain models.' It has been compiled along with MSc Chris Wudel and Prof. Dr. Uta Berger, the first supervisor of this Ph.D. study. The candidate of this dissertation developed both models, designed and carried out the experiments, analyzed and interpreted the results, and wrote and reviewed the article.

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ORIGINAL PAPER

Nonparametric upscaling of bark beetle infestations and management from plot to landscape level by combining individual-based with Markov chain models

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Abstract

Linked to climate change, drivers such as increased temperatures and decreased water availability affect forest health in complex ways by simultaneously weakening tree vitality and promoting insect pest activity. One major beneficiary of climate-induced changes is the European spruce bark beetle (*Ips typographus*). To improve the mechanistic understanding of climate change impacts on long-term beetle infestation risks, individual-based simulation models (IBM) such as the bark beetle dispersion model IPS-SPREADS have been proven as effective tools. However, the computational costs of IBMs limit their spatial scale of application. While these tools are best suitable to simulate bark beetle dynamics on the plot level, upscaling the process to larger areas is challenging. The larger spatial scale is, nevertheless, often required to support the selection of adequate management intervention. Here, we introduce a novel two-step approach to address this challenge: (1) we use the IPS-SPREADS model to simulate the bark beetle dispersal at a local scale by dividing the research area into 250 × 250 m grid cells; and (2) we then apply a metamodel framework to upscale the results to the landscape level. The metamodel is based on Markov chains derived from the infestation probabilities of IPS-SPREADS results and extended by considering neighbor interaction and spruce dieback of each focal cell. We validated the metamodel by comparing its predictions with infestations observed in 2017 and 2018 in the Saxon Switzerland national park, Germany, and tested sanitation felling as a measure to prevent potential further outbreaks in the region. Validation showed an improvement in predictions by introducing the model extension of beetle spreading from one cell to another. The metamodel forecasts indicated an increase in the risk of infestation for adjacent forest areas. In case of a beetle mass outbreak, sanitation felling intensities of 80 percent and above seem to mitigate further outbreak progression.

Keywords *Ips typographus* · Risk assessment · Long-term forecast · Agent-based model · Metamodel · Upscaling

Introduction

European forests are under accelerated effects of climate change, showing decreasing intervals between extreme events, as well as increased drought risks (Lindner et al. 2010). Interactions among such change drivers might potentialize negative impacts (Seidl et al. 2017). Drought-induced mortality (Allen et al. 2010), for example, may not only lead to changes in tree growth due to altered intra- and inter-specific competition (Piao et al. 2011; Sánchez-Salguero et al. 2012) but also to changes in species distribution (Delzon et al. 2013). Rainfall deficits in combination with extreme summer heat, as observed in 2003, lead to a decrease in primary production and could convert temperate ecosystems into carbon sources (Ciais et al. 2005). The effects of extreme events and increased drought risk on current and future biotic and abiotic disturbances are also not expected to subside with time (Allen et al. 2010; Dale et al. 2001; Seidl et al. 2020; Senf et al. 2019; Thiele et al. 2017). Warmer and drier conditions, as well as increased disturbances such as windthrow also favor pests such as the European spruce bark beetle *Ips typographus* L. (Seidl et al. 2016, 2017; Temperli et al. 2013). In recent years, beetle mass outbreaks have been observed in both managed and

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unmanaged forests. Although outbreaks in large protected areas without management interventions, such as national parks, might provide valuable insights into its starting conditions and development (Lausch et al. 2011), these sites can provide an infestation risk for managed surrounding forests, requiring an adaptive management to avoid negative impacts on non-protected areas (Mezei et al. 2017; Zolubas and Dagilius 2012). On the other hand, while felling infested trees is inconsistent with most conservation goals of national parks (Kulakowski 2016), it is suggested as one of the most effective measures against *Ips typographus* outbreaks (Jönsson et al. 2012; Kulakowski 2016).

We apply the novel individual-based model IPS-SPREADS (Pietzsch et al. 2021) to investigate the impacts of climate change and forest protection management on the long-term development of bark beetle outbreaks and spreading risk from the Saxon Switzerland national park, Germany, to adjacent managed forests. A mass outbreak of *Ips typographus* was observed from 2015 to 2018 in this area (Fig. 1). IPS-SPREADS was developed from the IPS model (Kautz et al. 2014, 2016) by implementing GIS import capabilities to promote its application to real forests. This model describes beetle spreading mechanistically, considering explicitly the energy of each beetle, the energy costs during their flights, and the attractivity of trees among others, which is an advantage over statistical models. Like most individual-based models (IBMs), emerging model results and patterns arise from the simulated individuals' traits (Railsback and Grimm 2011). Therefore, the forecasted dispersal and outbreak patterns in the IPS-SPREADS model depend on the individual traits of both beetles and trees. The model can be applied, for instance, to test the effects of sanitation felling on the outbreak, beetle population fitness and the number of damaged trees. As most IBMs, however, the IPS-SPREADS model is computationally expensive and applicable only for smaller forest plots. Upscaling from plot to landscape level, as well as forecasting spatio-temporal dynamics of bark beetle outbreaks 20 years into the future requires a metamodel (MM) approach, based on a general nonparametric framework (Cipriotti et al. 2016).

Such MM describes the behavior of an underlying model on a higher hierarchical level (Gore et al. 2017; Moorcroft et al. 2001; Urban 2005), providing an efficient way to facilitate the predictions of the behavior of the

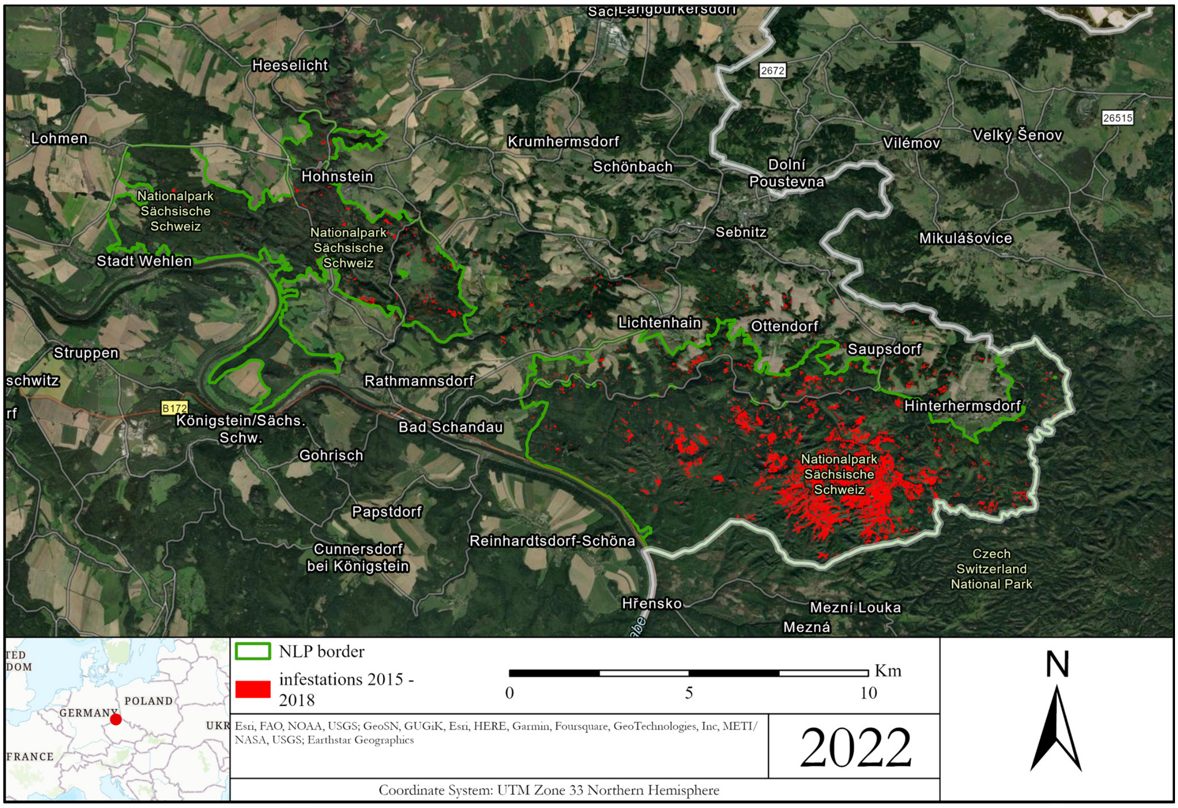


Fig. 1 Map of areas infested from 2015 to 2018 in the research area (Saxon Switzerland national park, Germany)

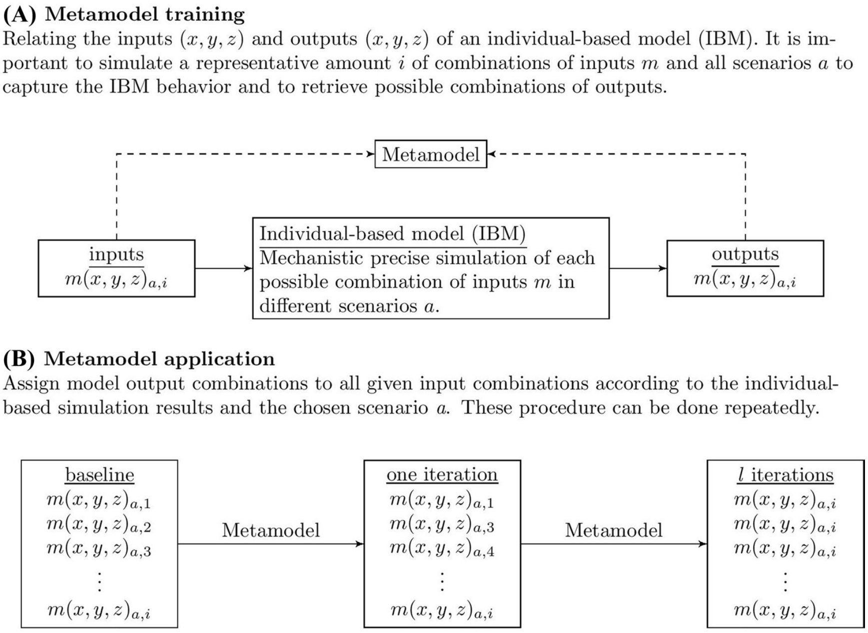
individual-based model (IBM, Fig. 2) over a wide range of parameter combinations and scenarios (Pietzsch et al. 2020). The use of MMs reduces simulation costs and promotes communication and understanding of simulation models' behavior (Kleijnen and Sargent 2000; Mertens et al. 2017). Regression, Bayesian emulators, machine learning, differential equation and Markov chain (Pietzsch et al. 2020) are the most common types of MMs used in an IBM context, being used as prediction tools, as well as are applied for sensitivity analysis, calibration and upscaling (Pietzsch et al. 2020). We used the Markov chain MM developed by Cipriotti et al. (2016) as a template for our MM, as this model type has proven effective for IBM upscaling (Pietzsch et al. 2020). This applies in particular when considering land cover transitions and neighbor interactions, which are of importance for the development and spread of a bark beetle mass outbreak (e.g., Seidl et al. 2016; Wildemeersch et al. 2019).

We hypothesize that (1) increases in number of bark beetle generations per year due to forecasted increases in mean temperature leads to faster outbreaks and more frequent complete dieback of Norway spruces (*Picea abies*) inside and outside the national park. We also propose that (2) sanitation felling (i.e., removal or debarking of infested trees) at plot level inside the national park can lower the risk of infestation spread from the protected to adjacent forested area in the next 20 years, but requiring a minimum threshold value to be effective.

Materials and methods

Data processing

First, a representative selection of grid cells from the research area was chosen using a shapefile of forest stand polygons (Saxon Forest State enterprise; Staatsbetrieb Sachsenforst). We then selected 7524 grid cells of 250 × 250 m cells to model beetle outbreak within the approximately 14,100 ha of forested area. The relatively small size of the chosen area was representative of heterogeneity of the landscape, while limiting the maximum number of beetles to be simulated during possible mass outbreaks to a tractable number. Of the selected area, 2257 cells had spruce trees and 170 of them exhibited an initial infestation in 2015, being used to simulate the outbreak development in the following year using the IBM IPS-SPREADS. To choose the grids used for beetle outbreak simulation, a classification of the three main features of all grid cells was performed and allowed the selection of a reasonable number of representative areas. Therefore, we calculated the mean kairomone-induced primary attractiveness of trees to beetles, and both the proportion of spruces and the number of trees already infested by beetles in each site. The frequency distributions of these three features (Fig. 3) were used as classification criteria, so that the number of grid cells within each class was approximately the same (ranging from 53 to 61 cells for each class). This ensured we selected at least one grid cell


(A) Metamodel training

Relating the inputs (x, y, z) and outputs (x, y, z) of an individual-based model (IBM). It is important to simulate a representative amount i of combinations of inputs m and all scenarios a to capture the IBM behavior and to retrieve possible combinations of outputs.

(B) Metamodel application

Assign model output combinations to all given input combinations according to the individual-based simulation results and the chosen scenario a. These procedure can be done repeatedly.

Fig. 2 Concept of training (**A**) and applying (**B**) a metamodel in an individual-based context

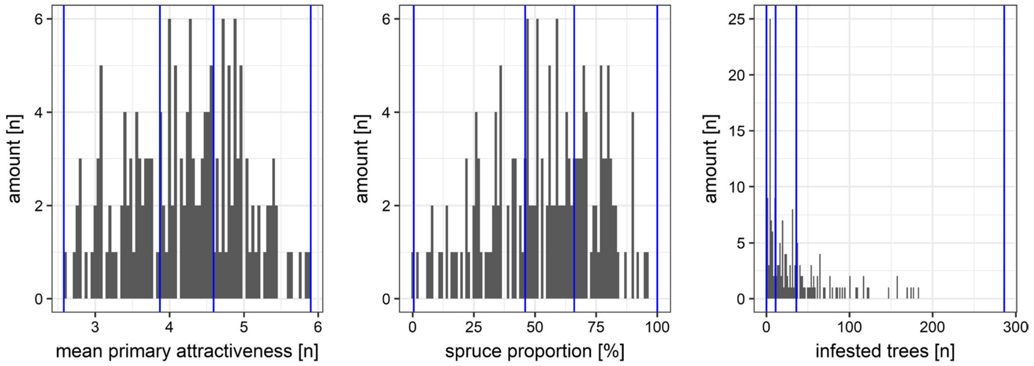


Fig. 3 Frequency distribution of the main features of all 250×250 m grid cells in the research area, which were used as the baseline for the classification. The derived boundaries of the classification levels are visualized as blue lines. The resulting number of grid cells in each level ranged from 53 to 61. Primary attractiveness relates to the kairomone-induced attractiveness of each tree to bark beetles (Kautz et al. 2014, 2016)

for each possible combination of mean primary attractiveness, spruce proportion and infested tree amount.

The classification of features resulted in 36 possible combinations (3 classes for primary attractiveness, 3 classes for spruce proportion and 4 classes for infestation level), with at least one grid cell per combination (see supplementary material, Table S1). For each grid cell of the research area, the mean deviation of its features was calculated and used to identify which combination of grid cells was closest to the respective classification level mid. This was done to ensure that effects associated with each feature were as close as possible to a given classification level.

For all data processing, MM development, result summarization, and visualization, the free statistical programming language R (RCoreTeam 2020) was used. For the GIS data processing, the packages raster 3.4–5 (Hijmans 2020), maptools 1.0–2 (Bivand and Lewin-Koh 2020), rgdal 1.5-23 (Bivand et al. 2021), terra 1.5-12 (Hijmans 2022) and rgeos 0.5-5 (Bivand and Rundel 2020) were applied. For visualizing the simulation results, the package ggplot2 3.3.5 (Wickham 2016) was used. Maps presented were created using ArcGIS Pro (version 3.0.0).

Individual-based simulations

We followed the ODD protocol (Grimm et al. 2020) to describe the applied individual-based model IPS-SPREADS. The IPS-SPREADS model has been described by Pietzsch et al. (2021) and was used here with small modifications. The random placement of spruce trees was done beforehand during the data processing with R, instead of during the setup of the IPS-SPREADS model and incorporated into the imported raster file PAS.asc to ensure that the amount and placement of spruces was equal for all model runs. We also introduced a new global result in the form of number of trees cut after each generation: ncut1, ncut2 and ncut3. The full ODD protocol with adjustments to the original from Pietzsch et al. (2021) can be found in GitHub (linked in the data availability statement) section.

The overall purpose of using IPS-SPREADS was to understand and investigate the impact of individual traits of beetles and trees as well as measures of bark beetle management (e.g., sanitation felling) on the spatial pattern of outbreaks of the spruce bark beetle. We used patterns of location, number and progression from 2015, 2016, and 2017 of infested spruce trees (*Picea abies*) within the Saxon Switzerland national park to model beetle outbreaks from real data.

The model includes patches, bark beetles and volatiles as entities. The global environment (a forested area) is characterized by wind speed and direction. Patches represent 5×5 m areas containing one spruce or are empty. Characteristics of these patches include their primary and secondary attractiveness for bark beetles, a capacity for infesting and emerging beetles and, one of three levels of infestation: not infested, infested or, fully occupied. Patches are squares in the horizontal plane with data about tree height, tree species and capacity for infesting bark beetles. Beetles have unique values of energy level and energy efficiency. Volatiles are emitted by beetles infesting trees and carry information about the location and the total attractiveness of their source at the time of emission. The spatial extent is constrained to the imported GIS data. If a mass outbreak should be simulated, a maximum extent of a quarter square kilometer is advised. The temporal resolution of IPS-SPREADS is defined by time steps, where 200 steps are contained in one day. The overall length of the simulation depends on the chosen parameter settings (e.g., if one, two, or three generations are to be simulated). The simulation ends as soon as all beetles emerged from the beetle source trees and no more dispersal flight or tree attacks are taking place.

The most important processes of the model, which are repeated every time step, are the (1) emission of volatiles by infested trees, (2) beetle flight, (3) beetle's decision to attack a patch, and (4) defense of attacked trees. Each simulation begins with the model setup during which GIS data like tree height or the begin of beetle flight is imported and used to create the model world by distributing spruce trees and assigning trees as beetle sources. After the artificial environment is set up, the first day of the simulation starts with the generation of beetles on all beetle source trees and the updating of all plots in the model interface. Then, on each time step, volatiles are emitted by infested trees and the beetles move either to the source tree of the most attractive volatile within the beetle's perception range, or to a neighboring patch using a correlated random walk. After all beetles have moved, it is checked if the beetle's energy reserve is higher than the total attractiveness of the beetle's current patch. If the target is an already infested tree, the beetle is added to the infesting beetles on this patch. Otherwise, the beetle will wait on the given tree for one day. If enough beetles attack the same tree within one day, the tree defense is overcome and the tree becomes infested. Otherwise, all beetles waiting on the patch are killed by the tree defense. At the end of each day, it is checked if all beetles of the given beetle generation were generated and dispersed. If not all beetles were generated and dispersed, the next day starts with the generation of beetles and the update of all plots. Otherwise, bark beetle management takes place and a predefined proportion (i.e., 50%) of infested trees is removed from the model world by sanitation felling. This is done before brood emergence or sister brood establishment can take place to simulate an optimal timing of management action. If more than one beetle generation was defined, all infested trees that were not removed by sanitation felling are shifted to beetle source trees for the next beetle generation. After this, a new day with the same schedule of actions as described above begins. When the predefined number of generations has been simulated and the sanitation felling for each of those generations has taken place, model results are calculated, the pattern of infested trees is exported as a raster layer (.asc file) and the simulation stops.

Simulation experiments

After processing, the grid cells chosen for simulating the 36 combinations of mean primary attractiveness, spruce proportion and number of infested trees (Table S1) were imported into IPS-SPREADS. During the simulation experiments parameters were set to the expected values, while both wind speed and duration of beetle flight activity were modified: the wind speed was set to zero to avoid beetle drifting out of the relatively small grid cells, and the duration of beetle flight activity was set to 40. The latter was done, as the online version of the phenology model PHENIPS (Baier et al. 2007) recorded for the weather station within the research area (Lichtenhain-Mittelndorf) 80–100 swarming days in years with two beetle generations and 120 possible days in 2018 where three full generations took place. For the sake of simplicity, we therefore used 40 days of swarming for each simulated beetle generation in the IPS-SPREADS model.

The number of infested trees, the number of living spruce trees, the number of trees cut during sanitation felling if applied and the mean primary attractiveness of all living spruce trees were measured at the end of each simulation experiment. The number of infested trees was used as number of beetle source trees for the following year and to calculate the proportion of dead trees on each site. This proportion was used to assess the impact of management and climate-induced increase in number of beetle generations on the development of the long-term outbreak.

To account for a possible impact of climate changes on the bark beetle population and outbreaks, we varied the number of beetle generations per year from two to three, where more generations per year suggested a stronger increase in mean annual temperature (hereby climate change scenarios). Using such approach ensured that climate-induced increases in mean temperatures on beetle development, flight activity duration and tree susceptibility were considered. In addition, forest management scenarios were investigated. We varied the intensity of sanitation felling (removal or debarking of infested trees) from zero to 100 percent in 10% steps after each beetle generation. As both sanitation felling and climate change scenarios per year were applied simultaneously, a total of 22 combinations were simulated on the selected grid cells ($n = 27$). Performing ten replicates each, the total number of runs with IPS-SPREADS added up to 5940. Only 27 of the selected 36 grid cells were simulated, as nine cells did not exhibit any prior infestation prohibiting beetle emergence and spread in the IPS-SPREADS model.

The results of the simulation experiments with IPS-SPREADS were stored as a data table for each combination of climate change and management scenario. These data tables contained the mean primary attractiveness, spruce proportion and number of infested trees at the end of the simulation with IPS-SPREADS separated by simulated grid cell. If at least one level of the three aforementioned features changed during the simulations, a new combination label was assigned based on the new combination of features and the previously applied labeling of all possible combinations (Table S1). By using the ten replicates for each grid cell and scenario, we determined the probability of each combination of features to either be converted into another combination, or to remain unchanged (Table 1). These determined probabilities were used as the foundation for the Markov chain MM adapted from Cipriotti et al. (2016), described

Table 1 Theoretical example of transition probabilities and destinations for all combinations of features (mean primary attractiveness, spruce proportion and number of infested trees) as retrieved from the IPS-SPREADS simulations

Combination chr	Destination 1 chr	Probability %	Destination 2 chr	Probability 2 %
A	A	100.0	–	0.0
B	B	33.3	A	66.7
C	D	43.5	X	56.5
⋮	⋮	⋮	⋮	⋮
ZK	ZK	12.0	–	0.0

While the displayed destinations and probabilities are theoretical examples, the number of destinations for each combination of features is representative of the actual simulation results (there were no cases with more than two possible destinations)

in the following section. The resulted data tables are openly accessible from the GitHub repository referenced in the data availability statement section.

Metamodel

For the development, first we imported the data table containing the combination of features (mean primary attractiveness, spruce proportion and number of infested trees) for all 7524 grid cells of the research area into R (Fig. 4). We then imported the processed simulation results of IPS-SPREADS (Table 1), which contain the possible destinations and corresponding transition probabilities for each combination of features.

In the next step, the MM checks if interactions between neighboring cells in the form of beetle spread should be considered or not (N is TRUE in Fig. 4). If this is the case, the model searches for all grid cells with at least one neighbor with an infested tree amount level of 286 (the highest possible amount). All of these cells simultaneously increase their level of infested tree amount by one level for each beetle generation simulated, according to the climate change scenario. With this MM extension, the spread of bark beetles from one grid cell to another is represented and directly correlated with the given amount of beetle generations during one year.

The baseline MM consisting of Markov chains based on (Cipriotti et al. 2016) is then applied (Fig. 5): Depending on the combination of features (primary attractiveness, spruce proportion and number of infested trees), each grid cell is assigned a new combination based on the simulation results with IPS-SPREADS and the chosen scenario of climate change and management (Table 1). If there is more than one possible destination for a combination of features, a random number is drawn to decide the new combination for the given grid cell according to the pre-calculated transition probabilities.

In the next step, the model checks if the grid cells' dieback of spruce trees should be considered or not (C is TRUE in Fig. 4). If this is the case, then the model applies the spruce dieback extension, in which the amount of living spruce trees is updated for all grid cells by removal of infested or felled trees. If the amount of living spruce trees reaches or falls below zero, then the corresponding cell is marked as 'dead' by setting mean primary attractiveness, spruce proportion and number of infested trees to 500 each. Furthermore, the MM calculates the proportion of dead trees over the total number of living spruces at the beginning of the simulation. This relation is later used for analyzing the impact of management and climate change scenarios on the long-term outbreak development in the research area.

The model then exports the data table containing the new combination of features for each grid cell as a CSV file, labeled with the climate change and management scenarios, and the simulated year.

At last, the MM increases the counter of simulated years by one ($a+1$) and checks if the total number of years (i.e., 20) were already simulated. If not, the MM begins the next year by checking if the beetle spread extension should be applied (N is TRUE in Fig. 4) and so on. Once the total number of years is reached, the MM stops its calculations.

Model validation: reproduction of outbreak development in 2017 and 2018

To validate the performance of the developed MM and assess if the introduced beetle spread and spruce dieback extensions improve the predictions of outbreaks development, observations from outbreaks dating from 2017 and 2018 in the Saxon Switzerland national park were used as a measure of agreement. Data of both years were processed as described in *Data processing* and used to compare the MM predicted number of infested trees for each of the 7524 grid cells. To evaluate the goodness of agreement between model prediction and observations, the macro-averaged F1 score was applied. This score is defined as the harmonic mean of precision and recall, and is commonly used for evaluation of classification models or algorithms (Sammut and Webb 2010) as well as an optimization criterion (Yang 1999). As the F1 score is calculated for each class separately, the global mean of the per-class F1 scores (macro-averaged F1 score) was used for comparison of model predictions (Yang 1999).

To also validate the introduced extensions of beetle spread and spruce dieback, four different MM variants were used to predict the infestation development of 2017 and 2018 in the Saxon Switzerland national park: (1) MM without any extension (MM), (2) MM with spruce dieback (MM-C), (3) MM with beetle spread (MM-N) and (4) MM

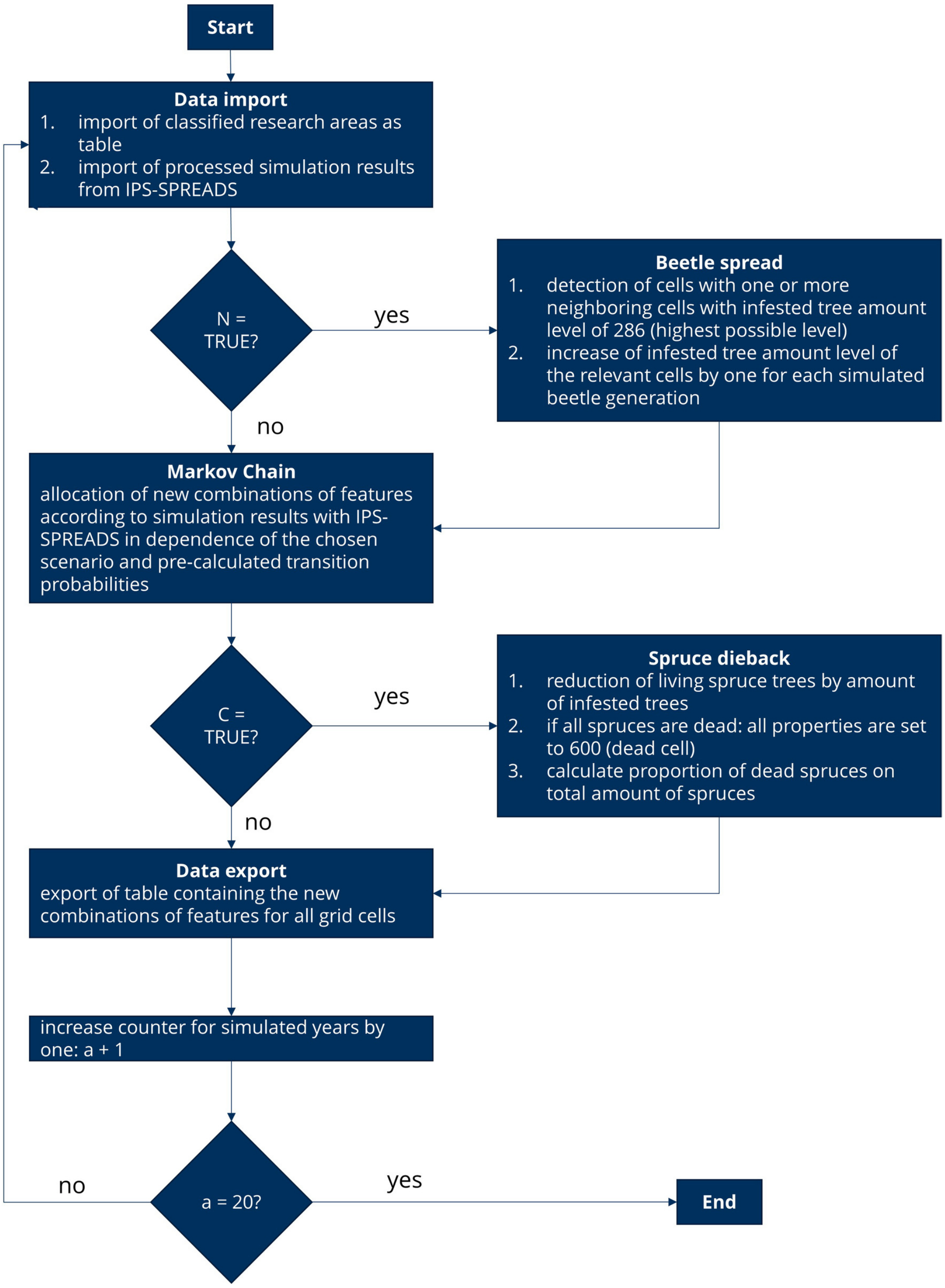


Fig. 4 Flowchart showing the process schedule of the developed metamodel. The left column describes the simulation of one year by using the baseline metamodel consisting of data import and export as well as the assignment of new feature combinations using Markov chains. The right column contains the metamodel extension of beetle spread to neighboring grid cells as well as spruce dieback on all cells

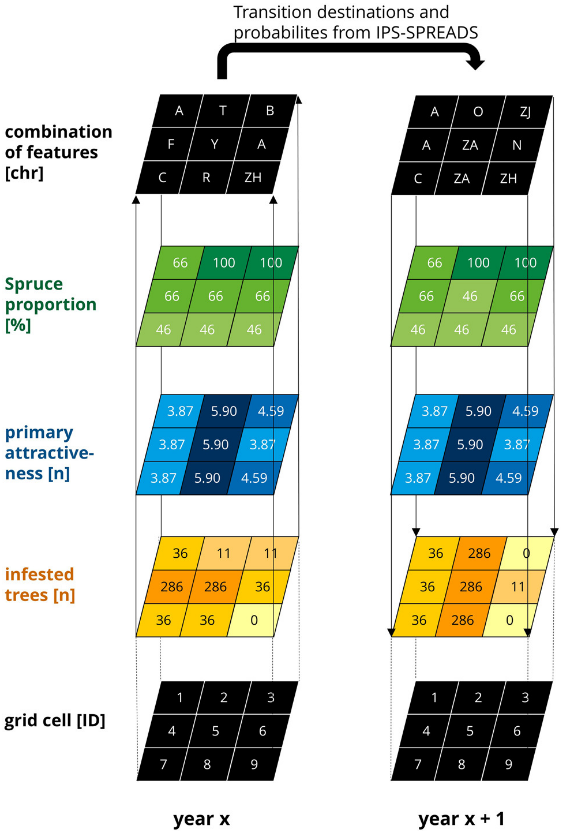


Fig. 5 Scheme of the developed metamodel modified from Cipriotti et al. (2016). Each grid cell starts with one of the 36 possible combinations defined by number of infested trees, mean primary attractiveness and spruce proportion (all stages are explained and labeled in Table S1). By using the transition probabilities and possible destinations of stages derived from simulation experiments with the IBM IPS-SPREADS (Table 1), new combinations of spruce proportion, mean primary attractiveness and infested trees are assigned to all grid cells of the research area per time step

with spruce dieback and beetle spread (MM-C-N). For each of these variants and for each possible combination of climate change and management scenarios a macro-averaged F1 score was calculated and visualized as tile plot. We then visually inspected the MM variants' results and data, and determined the variant with highest agreement. The intensity of sanitation felling was also varied during the metamodel validation because no information on location, timing or intensity of felling inside and outside the national park was available. Sanitation felling in the MM was applied in the same intensity on all grid cells inside and outside the national park alike.

Long-term forecast of outbreak development

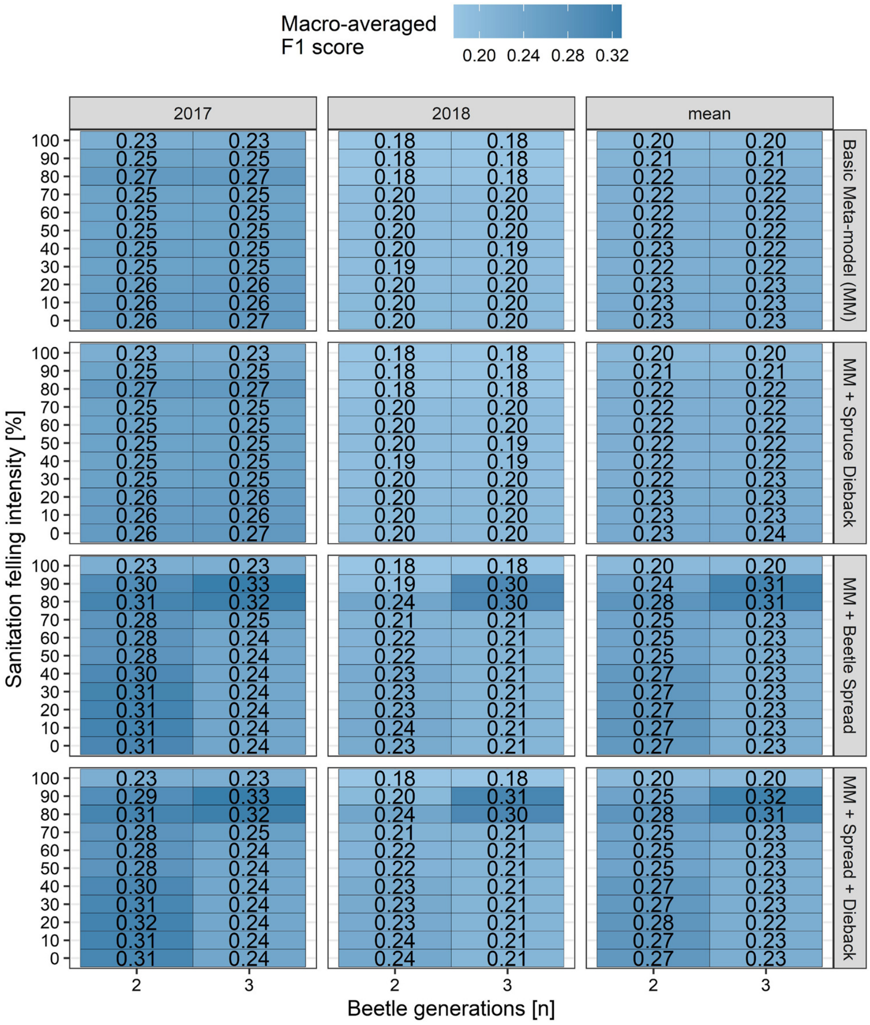
For the long-term forecast of the outbreak development in the Saxon Switzerland national park, the MM variant with the highest overall macro-averaged F1 score during model validation (Section *Metamodel Validation*) was applied for 20 consecutive years. To investigate possible impacts of climate change and forest protection management on the outbreak development, the amount of yearly beetle generations was varied from two to three and the intensity of sanitation felling from zero to 100% in 10 percent steps. As the interaction between these two scenarios was also from interest, a total of 22 different combinations had to be simulated. A bar plot was generated to visualize the number of sites with 0, 25, 50, 75 or 100% of spruce dieback inside and outside the national park in dependency of the chosen combination of climate change and management scenario. With this bar plot it was possible to detect thresholds where sanitation felling was able to avoid the spread of infestations from the national park to adjacent forest areas or when no mass outbreak happened in the protected area at all. A map was generated for each scenario showcasing the proportion of dead spruces of each grid cell for the research area as an index of outbreak risks.

Results

Model validation: reproduction of outbreak development in 2017 and 2018

The calculated macro-averaged F1 scores of the four different MM variants showed that the highest mean agreement between model prediction and observations was achieved by the model version with both beetle spread and spruce dieback extensions (Fig. 6). While the introduction of spruce dieback only marginally improved the prediction, the introduction of beetle spread raised the agreement substantially. The full model version however was used for the long-term forecast because of its capability to also assess both the impact of climate and management scenarios on the dieback of spruces inside and outside the national park. In general, the agreement between model prediction and observations was higher for 2017 than 2018, regardless of the chosen scenario or MM type. The validation of MM variants using the macro-averaged F1 score also revealed that scenarios with zero to 90% sanitation felling intensity achieved the highest agreement between model prediction and observations regardless of the chosen amount of beetle generations. Lowest agreements were reached when a sanitation felling intensity of 100% was applied.

Fig. 6 Macro-averaged F1 scores (harmonized mean of prediction and recall) for rating the agreement between metamodel predictions and observed European spruce bark beetle (*Ips typographus*) outbreak development in 2017 and 2018 in Saxon Switzerland national park, Germany. Columns represent the investigated years, rows the applied metamodel variants. The higher the scores are (the darker the blue color), the better the agreement is



Basic Meta-model (MM)

Sanitation felling intensity [%]	2017, 2	2017, 3	2018, 2	2018, 3	mean, 2	mean, 3
100	0.23	0.23	0.18	0.18	0.20	0.20
90	0.25	0.25	0.18	0.18	0.21	0.21
80	0.27	0.27	0.18	0.18	0.22	0.22
70	0.25	0.25	0.20	0.20	0.22	0.22
60	0.25	0.25	0.20	0.20	0.22	0.22
50	0.25	0.25	0.20	0.20	0.22	0.22
40	0.25	0.25	0.20	0.19	0.23	0.22
30	0.25	0.25	0.19	0.20	0.22	0.22
20	0.26	0.26	0.20	0.20	0.23	0.23
10	0.26	0.26	0.20	0.20	0.23	0.23
0	0.26	0.27	0.20	0.20	0.23	0.23

MM + Spruce Dieback

Sanitation felling intensity [%]	2017, 2	2017, 3	2018, 2	2018, 3	mean, 2	mean, 3
100	0.23	0.23	0.18	0.18	0.20	0.20
90	0.25	0.25	0.18	0.18	0.21	0.21
80	0.27	0.27	0.18	0.18	0.22	0.22
70	0.25	0.25	0.20	0.20	0.22	0.22
60	0.25	0.25	0.20	0.20	0.22	0.22
50	0.25	0.25	0.20	0.19	0.22	0.22
40	0.25	0.25	0.19	0.19	0.22	0.22
30	0.25	0.25	0.20	0.20	0.22	0.23
20	0.26	0.26	0.20	0.20	0.23	0.23
10	0.26	0.26	0.20	0.20	0.23	0.23
0	0.26	0.27	0.20	0.20	0.23	0.24

MM + Beetle Spread

Sanitation felling intensity [%]	2017, 2	2017, 3	2018, 2	2018, 3	mean, 2	mean, 3
100	0.23	0.23	0.18	0.18	0.20	0.20
90	0.30	0.33	0.19	0.30	0.24	0.31
80	0.31	0.32	0.24	0.30	0.28	0.31
70	0.28	0.25	0.21	0.21	0.25	0.23
60	0.28	0.24	0.22	0.21	0.25	0.23
50	0.28	0.24	0.22	0.21	0.25	0.23
40	0.30	0.24	0.23	0.21	0.27	0.23
30	0.31	0.24	0.23	0.21	0.27	0.23
20	0.31	0.24	0.23	0.21	0.27	0.23
10	0.31	0.24	0.24	0.21	0.27	0.23
0	0.31	0.24	0.23	0.21	0.27	0.23

MM + Spread + Dieback

Sanitation felling intensity [%]	2017, 2	2017, 3	2018, 2	2018, 3	mean, 2	mean, 3
100	0.23	0.23	0.18	0.18	0.20	0.20
90	0.29	0.33	0.20	0.31	0.25	0.32
80	0.31	0.32	0.24	0.30	0.28	0.31
70	0.28	0.25	0.21	0.21	0.25	0.23
60	0.28	0.24	0.22	0.21	0.25	0.23
50	0.28	0.24	0.22	0.21	0.25	0.23
40	0.30	0.24	0.23	0.21	0.27	0.23
30	0.31	0.24	0.23	0.21	0.27	0.23
20	0.32	0.24	0.23	0.21	0.28	0.22
10	0.31	0.24	0.24	0.21	0.27	0.23
0	0.31	0.24	0.24	0.21	0.27	0.23

Long-term forecast of outbreak development

Applying the MM variant with beetle spread and spruce dieback extensions for 20 years using climate and management scenarios revealed the possible risks of complete dieback of spruce forests in nearly all grid cells outside the national park under the warmer climate change scenario (i.e., three beetle generations per year) and without sanitation felling (Fig. 7). This risk was diminished by sanitation felling of 80% and more, leading to nearly no dead trees outside the national park. For the scenario with two beetle generations per year, even without management intervention only a small proportion of the grid cells located outside the national park were affected by infestations. Inside the national park, nearly half of the grid cells populated with spruces died completely when no management intervention took place. With increasing sanitation felling intensity, the proportion of completely dead grid cells inside the national park was reduced and reached zero percent when a felling intensity of 90 or more percent was applied. The proportion of grid cells with complete spruce dieback outside the protected area also decreased with increasing management intervention and reached zero with 80% felling intensity. A direct comparison of both climate scenarios (two and three beetle generations per year) revealed that an outbreak with complete dieback of all spruces in forests adjacent to the national park did not occur regardless of management intervention when only two beetle generations were simulated. In both scenarios, a felling intensity of 80% and more substantially decreases or diminishes the amount of dead spruces inside and outside the national park. While low management intervention activities had no effect on the outbreak with three beetle generations, the amount of dead spruces linearly decreased with sanitation felling intensity when two beetle

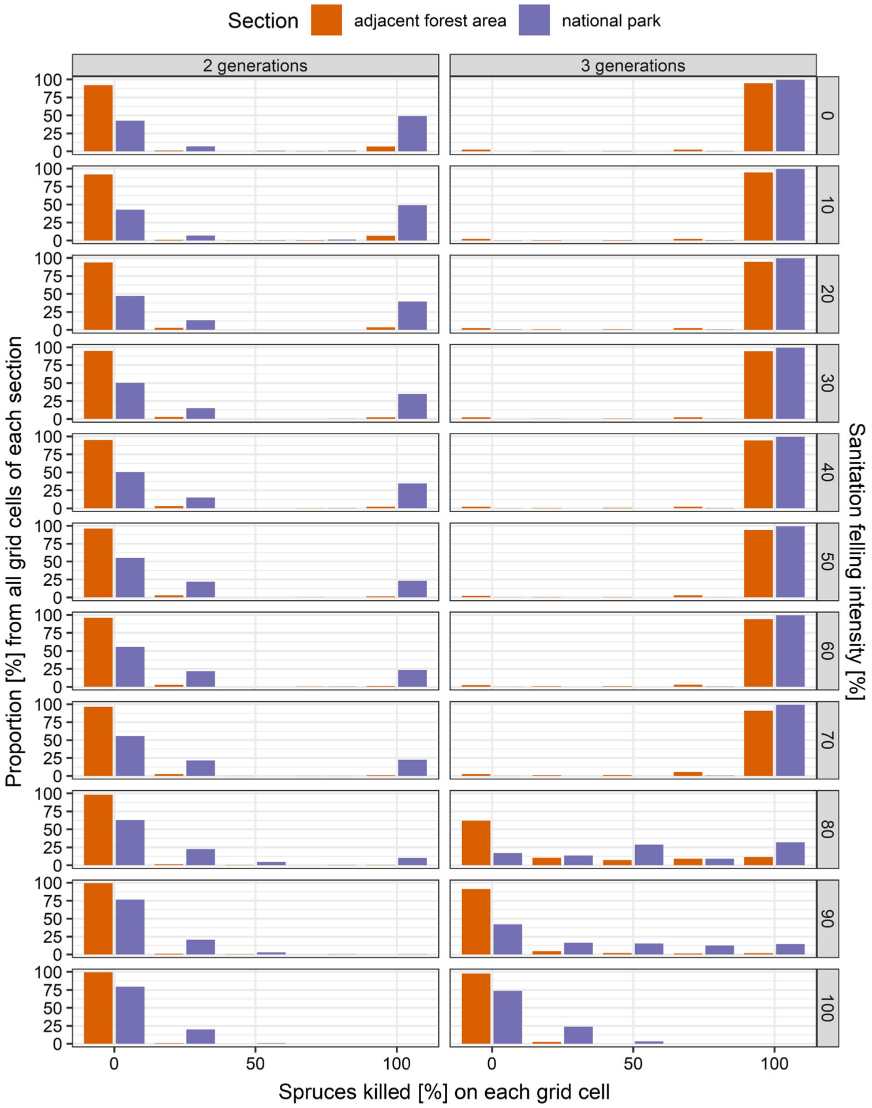


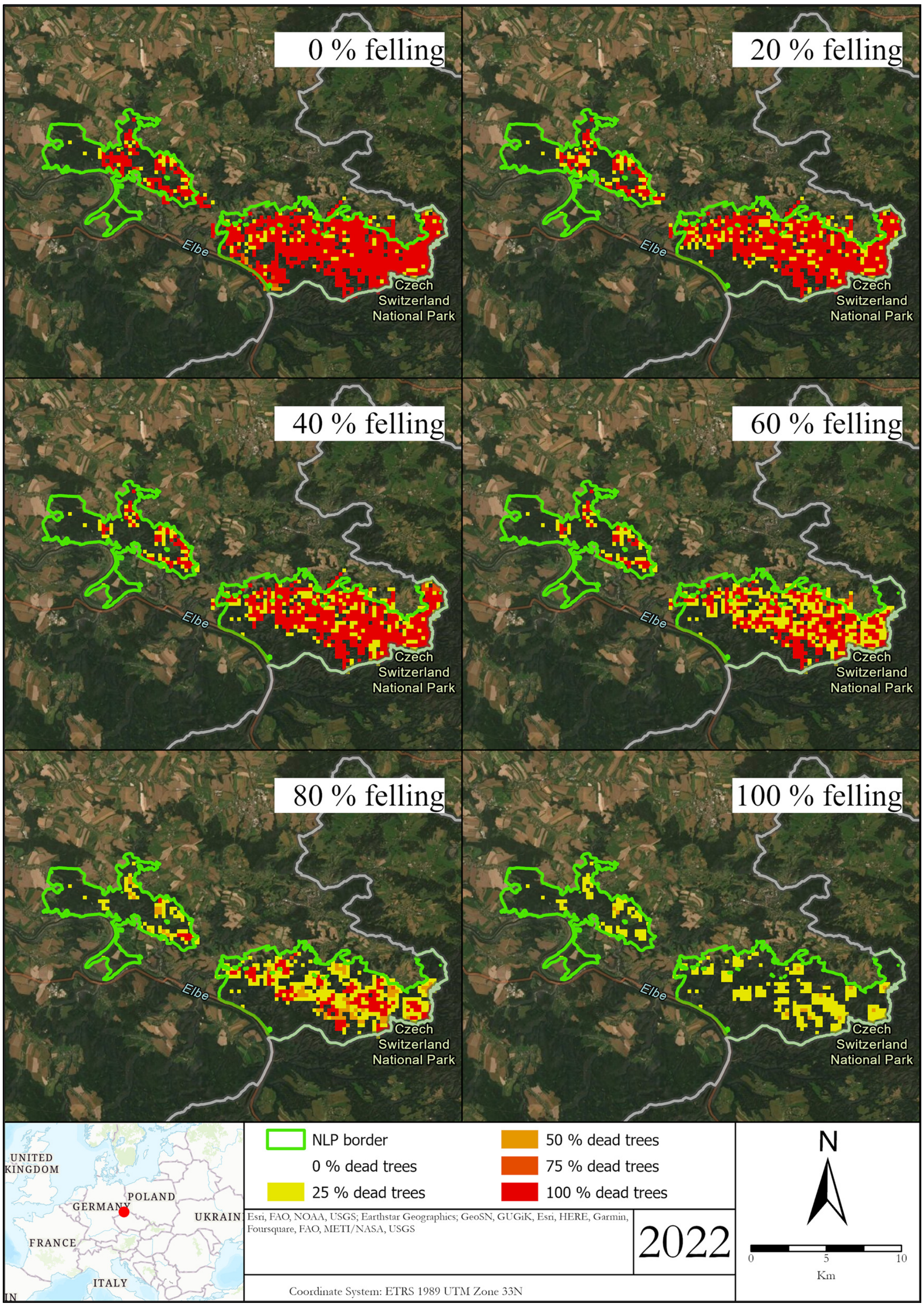
Fig. 7 Proportion of grid cells with zero to 100% dead spruce trees of all grid cells present in the research area in dependency of the chosen management scenario (rows) and amount of induced beetle generation mimicking climate change (columns) after 20 simulation years. Coloring differentiates between the location of the grid cells: orange—grid cells outside the national park, purple—grid cells within the national park

generations were present. The maps on spruce dieback risk generated from the 20-year simulation show hotspot areas with high risk for infestations spreading from the national park to adjacent forests located in the north of the eastern part as well as in the northeast of the western part of the protected area (Figs. 8, 9).

Discussion

In this study, we tackled a core problem of forest ecology and management: upscaling from tractable small-scale observations to forecasting large-scale patterns. We used the metamodel framework, MM, adapted from Cipriotti et al. (2016) to scale a computationally intensive yet mechanistic precise bark beetle model to a whole landscape encompassing a national park. Our study introduced a novel analysis of forest pests using simulation models. The approach focuses on defining important state variables (i.e., plot) using a small-scale model to design a state space that is partitioned into a finite number of discrete states. The transition probabilities from one state to the next (i.e., from a non-infested state to an infested state) are then determined by monitoring extensive simulation runs of the small model, which covers the entire range of initial conditions and state combinations.

We introduced two extensions to the MM approach, which incorporate both the spread of beetles from one grid cell to another, as well as the possible dieback of spruce individuals



Esri, FAO, NOAA, USGS; Earthstar Geographics; GeoSN, GUGiK, Esri, HERE, Garmin, Foursquare, FAO, METI/NASA, USGS

Fig. 8 Percentage of dead spruce trees in the Saxon Switzerland national park region after simulations of 20 consecutive years with two annual bark beetle generations and varying sanitation felling intensities

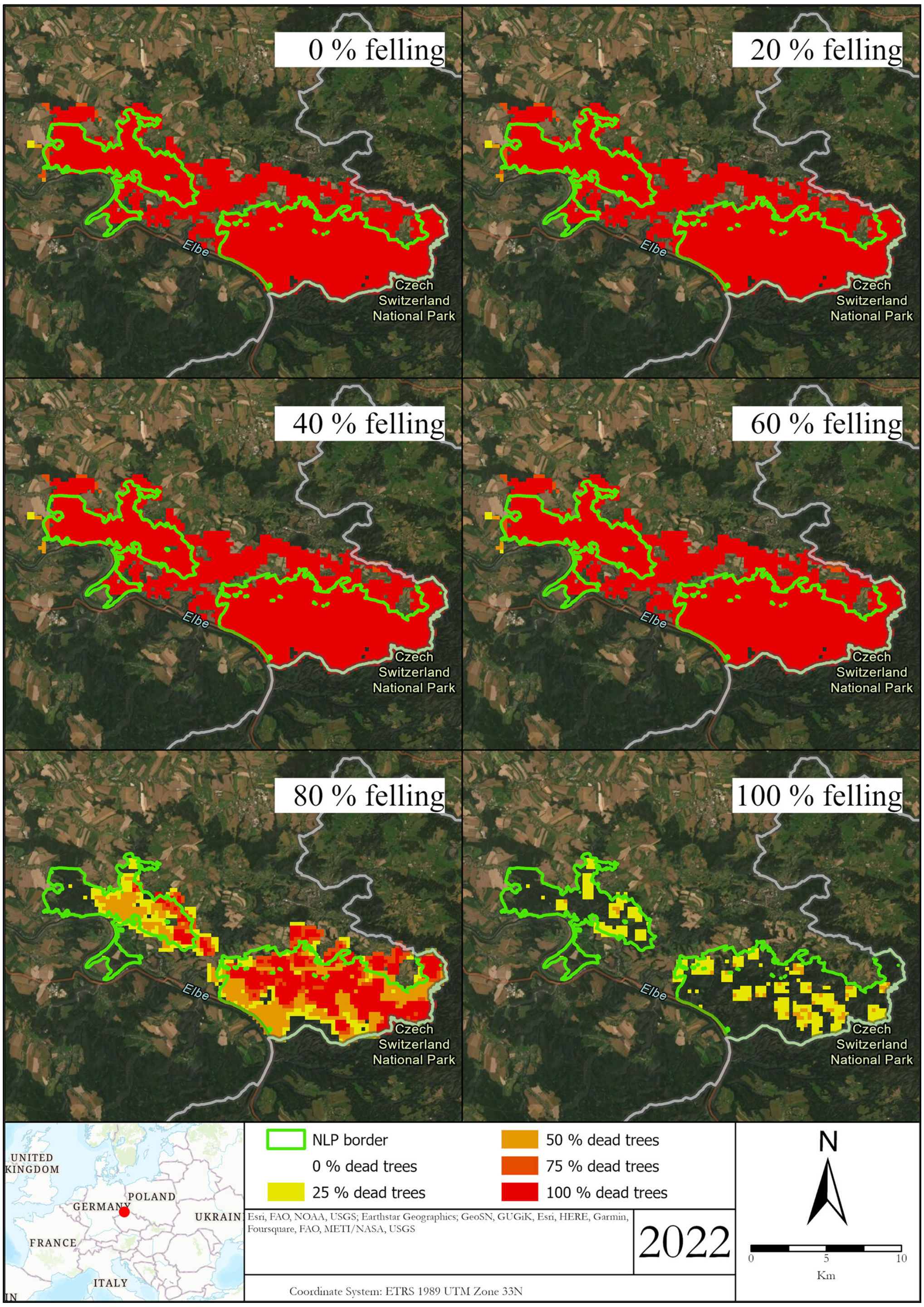


Fig. 9 Percentage of dead spruce trees in the Saxon Switzerland national park region after simulations of 20 consecutive years with three annual bark beetle generations and varying sanitation felling intensities

on all grid cells. Our proposed extension of beetle spread substantially improved the agreement between model predictions and observations during the 2017 and 2018 bark beetle outbreak in the Saxon Switzerland national park, Germany. With this MM we then investigated the impact of climate change and of management on the long-term development of outbreaks on a landscape level through an increase in yearly beetle generation numbers and sanitation felling, respectively.

The validation of four different MM variants revealed that the baseline model version (i.e., without beetle spread or spruce dieback extension) was not sufficient to hindcast the outbreak development of 2017 and 2018 in the national park. Particularly, the introduction of an indirect interaction of neighboring grid cells by the spreading of beetle infestations substantially improved model predictions. Sites with weakened spruces have been reported as step stones for successful infestation of neighboring and more robust areas, eventually leading to mass outbreaks at regional scale (Křivan et al. 2016), which can include highly resilient forests. Furthermore, connecting habitats has a particularly driving role in facilitating and producing mass outbreaks of European spruce bark beetle (Kärvemo et al. 2016; Seidl et al. 2016; Wildemeersch et al. 2019). The higher agreement between model scenarios and observations from 2017 and 2018 are compatible with two to three yearly beetle generations, suggesting that climate-induced changes to temperature and rainfall regimes in the region might have been already benefitting beetle outbreaks. An increased number of yearly beetle generations have the potential to lead to more disturbances and to a two- to threefold increase in damaged timber volume (Dobor et al. 2020; Seidl et al. 2008). This highlights the importance of forecasting climate change scenarios on both short- and long-term bark beetle outbreak development modeling. Even though the combination of beetle spread and spruce dieback extensions did not substantially improve the agreement between model prediction and observations in comparison to the use of the beetle spread extension alone, by combining both extensions we were able to depict and assess the risks of infestation of adjacent forests through the proportion of dead spruce trees per grid cell and the proportion of grid cells with completely dead spruces. Nevertheless, we suggest that the marginal impact of the spruce dieback extension on the agreement between models and observations might be related to the short simulation period and/or, more likely, to the lack of data on sites with 100% spruce dieback; grid cells with most spruce trees killed were still classified as the highest level of infestations and no consideration of complete dieback was done during the rating of agreement between model results and observations. Another possible reason for the discrepancy between model predictions and observations may lie on weather. The year of 2018 was one of the hottest and driest years observed and resulted in three beetle generations and two sister broods by the end of September (IFFF 2022). This might have promoted the ongoing mass-outbreak in the national park, leading to a potential underestimation of infestations by the MM. It is also possible, that the MM extension of beetle spread from grid cell to neighboring cells may not be enough to capture the speed and intensity of the outbreak development sufficiently. Most new infestations occur within 100 m (Kautz et al. 2011; Wichmann and Ravn 2001) to 500 m (Kautz et al. 2011; Stadelmann et al. 2013) around initial infested trees. Therefore, further research could focus on testing whether including beetle spreading from a high infested grid cell to both direct and secondary neighbors could improve agreement between model outputs and observations.

While two annual bark beetle generations imposed only a marginal risk for forests adjacent to the national park, an increase to three generations per year due to drier and hotter years as associated with climate change might have shifted the predictions to complete diebacks within the national park (Dobor et al. 2020; Seidl et al. 2008), as well as to high infestation risks for adjacent forests. To address the outbreak risk and decrease potential risks for forests surrounding the national park, a timely removal of at least 80% of infested trees might be needed. Similar magnitudes for a successful reduction in infestation risk were found with ≥ 95% for salvage logging (Dobor et al. 2020) and with 80% for bark beetle mortality in general (Fahse and Heurich 2011). Such a high reduction is difficult to achieve and only feasible if damage is limited to small areas (Dobor et al. 2020) as the removal of infested trees might not effectively stop a mass outbreak once it reached a large scale (Kulakowski 2016). Nonetheless, timely removal or debarking of infested trees is still considered to be the most efficient measure against the spread of bark beetles (Jönsson et al. 2012; Stadelmann et al. 2013; Wermelinger 2004). Our study results support this assessment: with 80% or more sanitation felling intensity the infestations are reduced substantially regardless of the amount of yearly beetle generations present. Although further studies could consider other measures used in bark beetle management, such as pheromone traps, we did not include it in our study as these might not be suited for the reduction in infestations, being mostly used for monitoring of seasonal flight activity (Dimitri et al. 1992; Lobinger and Skatulla 1996; Wichmann and Ravn 2001). The almost complete dieback of spruce trees inside the national park, with low sanitation felling and two or three beetle generations might be related to the large bark beetle population within parts of the national park where no management intervention took place. There, population densities are reached, that cause infestation of nearly all spruces of a given dimension regardless of climatic factors or individual tree conditions (Marini et al. 2017). As a consequence of this mass outbreak and the resulting reduction in spruce individuals at a regional scale, we suggest that a collapse of the beetle population could be expected, similarly to what has been observed for spruce beetle (*Dendroctonus rufipennis)* interacting with Engelmann spruce (*Picea engelmannii*) across the Southern Rocky Mountains of northwestern Colorado, USA (Hart et al. 2015).

A possible reason for the low infestation risk of adjacent forests with only two yearly beetle generations could lie within the missing connectivity of forested grid cells between the national park and its surrounding forests. Beetle spread was simulated in the MM as interaction between grid cells in direct neighborhood, which neglected the possibility of beetle flight from grid cells farther away. Furthermore, in reality sister broods happen regularly in national park region and lead to higher beetle densities and to more infestations than the IPS-SPREADS model or the MM predicted. In addition, as we used the infestation maps from 2016 as baseline for our model predictions, we had no information on the beetle population present outside the protected area at the beginning. Therefore, infestations predicted by the model could only originate from the infested trees inside the national park, which again leads to an underestimation of infestation risk in forests adjacent to the protected area.

While our simulation results indicate possible reductions in infestation spread, sanitation felling in our model was implemented in a near perfect manner: detection and removal of infested trees always took place right after the last beetle of a generation finished its dispersal flight and right before sister brood establishment or brood emergence could take place. As this procedure is considered as using an optimal timing with the highest effectiveness (Kautz et al. 2022), our model application possibly overestimated the effects of sanitation felling. Further challenges influencing the effectiveness of sanitation felling include the delay in visual detection of infestations, limitation of technical and human resources, high costs of debarking or challenging terrain conditions (Wermelinger 2004). With such challenges, sanitation felling intensities practice are unlikely to reach 100% with level of even 75% not being feasible on larger scales (Dobor et al. 2020). Nevertheless, while lower felling intensities did not stop the beetle spread from the national park to adjacent forests entirely, sanitation felling can be a valid option for small high-risk areas that could potentially serve as a bridge for infestation spread to adjacent forests.

The implementation of a buffer zone at the border of the national park as an outbreak contention measure might be a next step to be tested within our proposed MM framework on upscaling an IBM on bark beetle outbreak. In other national parks in Germany it was shown that such a buffer zone between 100 m (Niemeyer et al. 1995) and 1500 m (Heurich 2001) could be enough to substantially reduce the spread of infestations from protected to adjacent forest areas (Wermelinger 2004). This buffer zone could be implemented in the model to test the impact of different sanitation felling intensities in this zone as well as different widths of the buffer on the beetle spread. Implications from such modeling studies could then be used for the national park management to identify areas with high risks and to focus management actions accordingly.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-022-01512-1.

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Author's contribution BP developed both models, designed and carried out the experiments, analyzed and interpreted the results, and wrote the article. CW developed parts of the metamodel and commented on the article. UB supervised the whole project and revised the article. All authors contributed to the article and approved the submitted version.

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Availability of data and materials The datasets generated and analyzed for this study can be fully accessed in the GitHub repository under https://github.com/bwpietzsch/IPS-UPS.

Code availability The applied model files (individual-based model as well as metamodel) for this study can be fully accessed in the Github repository under https://github.com/bwpietzsch/IPS-UPS.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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5 Supervised Master theses

5.1 Implementierung und Untersuchung des Windeinflusses auf das Schwärmverhalten des Buchdruckers (*Ips typographus* L. 1758) in das individuen-basierte Modell IPS-SPREADS

This study aims to implement and test the influence of wind speed and direction on the dispersal of *Ips typographus* and its aggregation pheromones in the individual-based model IPS-SPREADS. It has been designed and supervised by the author of this doctoral study. In the following, (1) the author of this doctoral study gives a summary of the thesis, (2) the outline of tasks written by the author of this doctoral study is presented, and (3) the title page and abstract of the master thesis from the master student himself are shown.

Summary This Master thesis investigates the impact of wind on the dispersal and infestation patterns of the European Spruce Bark beetle (*Ips typographus* L.). A systematic literature review was done, and its findings were discussed. Afterward, according to the literature review findings, wind speed and direction were implemented into the individual-based model IPS-SPREADS. A thorough analysis of parameter influences on the model results (sensitivity analysis) was performed to detect the most influential model parts on the amount and location of infested trees. Data on the time and location of infested spruce trees within the Saxony Switzerland national park were then used to calibrate the wind extension and to test if the fit of model predictions and real-world data improved due to the introduction of wind.

The thesis shows that the dispersal and infestation patterns of *Ips typographus* are strongly affected by wind speed and direction and that applying both improve the model predictions substantially.

TECHNISCHE
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Fakultät Umweltwissenschaften Institut für Waldwachstum und Forstliche Informatik

17. April 2018

Angebot für eine Masterarbeit

Erweiterung des individuenbasierten Modells IPS-SPREADS 0.x für die Untersuchung des Einflusses von Wind auf die Ausbreitungs- und Befallsmuster des Buchdruckers *Ips typographus* L.

Das übergeordnete Ziel besteht darin, das individuenbasierte Modell IPS-SPREADS („Infestation Pattern Simulation - Supporting PREdisposition Assessment DetailS“) mit dem Submodell „Windausbreitung“ zu erweitern und deren Effetkt auf den simulierten Borkenkäferbefall systematisch zu überprüfen. Im Anschluss soll die neue Modellversion mittels Befalls- und Monitoringdaten aus dem NLP Sächsische Schweiz parametrisiert und validiert werden.

Dazu soll zunächst eine systematische Literaturrecherche zum Einfluss des Windes auf die Ausbreitung des Buchdruckers (*Ips typographus* L.) sowie auf die kairomonale und pheromononale Kommunikation im System Fichte-Buchdrucker durchgeführt werden. Ziel dieser Recherche ist es, Implementierungsmöglichkeiten zu entwickeln, sowie Forschungshypothesen aufzustellen, die mit dem erweiterten Modell im Rahmen der Masterarbeit beantwortet werden können.

Vorschläge für mögliche Forschungsfragen:

1. Wird das Flugverhalten des Buchdruckers durch Wind (Intensität und Richtung) beeinflusst? Wenn ja, in welcher Form?
2. Wie wirkt sich ein Verdrift der Pheromone / Kairomone auf die Ausbreitungs- und Befallsmuster des Buchdruckers aus?
3. Können die Befallsmuster aus dem NLP Sächsische Schweiz durch die Implementierung einer windbeeinflussten Ausbreitung in IPS-SPREADS genauer reproduziert werden?

LITERATURHINWEISE

Railsback, S. F. & Grimm, V. (2012): Agent-based and individual-based modeling - a practical introduction. Princeton University Press, Princeton.

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zur

Erlangung des akademischen Grades

Master of Science (M.Sc.)

die Masterarbeit mit dem Thema

Implementierung und Untersuchung des Windeinflusses auf das Schwärmverhalten des Buchdruckers (*Ips typographus* L. 1758) in das individuen-basierte Modell IPS-SPREADS

vorgelegt.

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Verantwortlicher Hochschullehrer: Prof. Dr. rer. Nat. Uta Berger

Verantwortlicher Betreuer: Herr Bruno Pietzsch

Institut/Professur: Institut für Waldwachstum und forstliche Informatik:

Professur für forstliche Biometrie und Systemanalyse

Für die Ausleihe zugelassen/nicht zugelassen

Dresden, den ....

Vorsitzender des Prüfungsausschusses

8. Zusammenfassung

Die vorliegende Arbeit befasst sich mit der Implementierung des Windeinflusses auf das Schwärmverhalten des Buchdruckers (*Ips typographus* L. 1758) in das individuen-basierte Modell IPS-SPREADS von PIETZSCH (unveröffentlicht) und der anschließenden Auswertung von Simulationsexperimenten.

Als Grundlage kam das in NetLogo erstellte IBM IPS-SPREADS in der Version 1.1 zum Einsatz. Dieses Modell beschreibt das Schwärmverhalten des Buchdruckers und die Interaktion zwischen diesem und seinem Wirtsbaum der gemeinen Fichte (*Picea abies* (L.) H. KARST. 1753).

Dieses Modell wurde um Volatile und Windeinfluss erweitert. Die als Agenten implementierten Volatile ersetzen die bereits im Modell vorhandene Eingabegröße der Wahrnehmungsentfernung und tragen Informationen über die Attraktivität der Fichten im Modell.

Der Windeinfluss wurde neu in das Modell eingefügt. Die Windgeschwindigkeit berechnet sich aus Baumhöhe, Baumart und Daten des DWD. Die Verteilung der Windrichtungen wurde ebenfalls den Daten des DWD entnommen. Sowohl Borkenkäfer als auch Volatile werden im erweiterten Modell vom Wind verdriftet. Ab einer Windgeschwindigkeit von 5,5 m*s^-1 stellen die Käfer allerdings ihr Schwärmaktivität ein.

Eine anschließende Simulationsstudie hat ergeben, dass die Anzahl und räumliche Verteilung der neu besiedelten Fichten sowie die von Käfern zurückgelegte Distanz durch Wind beeinflusst werden. Die Implementierung des Windeinflusses erlaubt es dem Modell z. T. genauere Aussagen über die Realität zu treffen.

Die im Modell abgebildeten Käfer reproduzieren in der Natur beobachtete Verhaltensweisen in Bezug auf das durch den Wind beeinflusste Schwärmverhalten.

Das IBM IPS-SPREADS legt einen Grundstein für das tiefere Verständnis des Dispersionsverhaltens von Borkenkäfern und künftige Risikoeinschätzungen.

5.2 Extrapolation des individuen-basierten Modells IPS-SPREADS zur Erzeugung von Risikokarten des Buchdruckerbefalls (*Ips typographus* L.) auf Landschaftsebene mittels Metamodell

This study uses a metamodel to scale the individual-based model IPS-SPREADS to the landscape level. It has been designed and supervised by the author of this doctoral study. In the following, (1) the author of this doctoral study gives a summary of the thesis, (2) the outline of tasks written by the author of this doctoral study is presented, and (3) the title page and abstract of the master thesis from the master student himself are shown.

Summary In this thesis, a metamodel framework for IPS-SPREADS was conceptualized, built, and applied to scale the infestation patterns from the individual-based model to the landscape scale. While many different metamodel types were applied previously in an individual-based context, Markov chains seemed to be the most suited for this task. Therefore, the master student developed his version of a previously applied Markov chain metamodel and enhanced it with several extensions, such as neighbor and capacity rules. Furthermore, the developed metamodel was calibrated and validated using real-world infestation patterns from the Saxony Switzerland national park. In the end, the calibrated metamodel was applied to forecast the infestation development for the next 30 years in the national park region under different scenarios of forest protection management and climate change intensity.

The thesis shows that the metamodel framework is a promising tool to apply individual-based model findings on broader temporal and spatial scales. Furthermore, incorporating extensions considering the neighborhood of grid cells in the research area increased the model predictions substantially, which could not have been considered with the individual-based model alone.

TECHNISCHE
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DRESDEN

FOREST BIOMETRICS
& SYSTEMS ANALYSIS

Fakultät Umweltwissenschaften Institut für Waldwachstum und Forstliche Informatik

13. August 2019

Angebot für eine Masterarbeit

Metamodell-basierte Extrapolation des individuen-basierten Modells IPS-SPREADS auf die Landschaftsebene für die Untersuchung der Befallsentwicklung des Buchdruckers *Ips typographus* L. unter Berücksichtigung verschiedener Management- und Klimaszenarien

Das übergeordnete Ziel besteht darin, das individuenbasierte Modell IPS-SPREADS („Infestation Pattern Simulation - Supporting PREdisposition Assessment DetailS"), das sich vor allem für Flächen von 1,5km x 1,5km eignet, auf die gesamte Region des Nationalparks Sächsische Schweiz zu extrapolieren. Hierfür soll ein sogenannter Metamodellansatz verfolgt werden, bei dem ein übergeordnetes Modell (das Metamodell wie z.B. ein künstliches neuronales Netz) mit den Input- und Outputdaten von IPS-SPREADS trainiert und unter verschiedenen Szenarien des Klimas und des Waldschutzmanagements auf die gesamte Nationalparkregion angewendet wird.

Für das Vorhaben stehen die Daten des Nationalparks Sächsische Schweiz, das individuenbasierte Modell IPS-SPREADS samt Dokumentationen sowie eine bereits durchgeführte systematische Literaturrecherche zu Metamodellen bei individuen-basierten Modellen zur Verfügung (Pietzsch & Berger, 2019; unveröffentlicht). Basierend auf diesen Grundlagen sollen die Möglichkeiten zur Extrapolation recherchiert und die aussichtsreichste getestet werden. Am Ende sollen Szenarien zu Klimawandel und Managementmaßnahmen simuliert und analysiert werden. Die Durchführung der Metamodellkonzeption und -berechnung soll dabei in der Statistiksoftware R (RCoreTeam, 2019) erfolgen.

Spezifische Vorkenntnisse, z.B. in individuen-basierter Modellierung sind willkommen, aber keine Voraussetzung für diese Arbeit. Wichtig sind Spaß an einer interdisziplinären Arbeit sowie Offenheit und Wille, sich in die Thematik einzuarbeiten. Bei Interesse oder Fragen wenden Sie sich bitte direkt an: bruno.pietzsch@tu-dresden.de.

Mögliche Forschungsfragen:

1. Welche Metamodelltypen eignen sich besonders für die Extrapolation des individuen-basierten Modells IPS-SPREADS?
2. Wie wirken sich zunehmende mittlere Temperaturen auf die zu erwartende Befallsdynamik des Buchdruckers (*Ips typographus* L.) in der Nationalparkregion Sächsische Schweiz aus?
3. Wie stark können Managementmaßnahmen diese Befallsentwicklung beeinflussen?

Verweise

Pietzsch, B. & Berger, U. (2019, unveröffentlicht): Meta-Models Used to Evaluate, Calibrate and Apply Agent-Based Models: A Review. *Journal of Artificial Societies and Social Simulation* (x): X - X.

RCoreTeam (2019): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

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Master of Science (M.Sc.)

die Masterarbeit mit dem Thema

Extrapolation des individuen-basierten Modells IPS-SPREADS zur
Erzeugung von Risikokarten des Buchdruckerbefalls (*Ips typographus* L.)
auf Landschaftsebene mittels Metamodell

vorgelegt.

Tag der Einreichung: ....

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Für die Ausleihe zugelassen/nicht zugelassen

Dresden, den ....

....
Vorsitzender des Prüfungsausschusses

Abstrakt

Der Klimawandel führt zu einem gravierenden Anstieg der mittleren Jahrestemperatur. Damit verbunden ist die Zunahme von extremen Ereignissen wie Stürmen und Dürren. Dies führt zu besonders hochdisponierten Wäldern gegenüber Schadinsekten, wie dem Buchdrucker (*Ips typographus* L. 1758) und zu enorm hohem Schadholzaufkommen von vielen Millionen Festmetern. Darunter sind besonders nicht-standortgerecht begründete Fichtenbestände (*Picea abies* (L.) H. Karst., 1881) betroffen. Ziel dieser Arbeit ist es, mittels eines Metamodells ein Upscaling von IPS-SPREADS auf Ebene der Nationalparkregion Sächsische Schweiz durchzuführen und Langzeitprognosen in Form von rasterbasierten Befallskarten für die Befallsentwicklung unter Berücksichtigung von verschiedenen Klimaszenarien und Managementintensitäten zu simulieren. Beim Upscaling liegt das Metamodell „über" dem eigentlichen Grundmodell (IPS-SPREADS) und ermöglicht durch eine rechenextensive Anwendung eine gröbere räumliche Auflösung (CIPRIOTTI et al. 2016). So soll den Bewirtschaftern des Nationalparks und denen der angrenzen Waldflächen ein effektives Managementinstrument zur Einschätzung der Befalls-dynamik und zur Ausweisung von Gefährdungsschwerpunkten zur Verfügung gestellt werden, um hohe Schäden in zum Nationalpark angrenzenden Wirtschaftswäldern zu vermeiden. Die Ergebnisse zeigen, dass realistische Befallsentwicklungen von *Ips typographus* als Rasterkarten der Nationalparkregion Sächsische Schweiz abgebildet werden können, was besonders interessant für den Staatsbetrieb Sachsenforst, die Nationalparkverwaltung und die Eigentümer der angrenzenden Wirtschaftswälder ist. Denn diese können so, Befallsschwerpunkte lokalisieren und ausweisen sowie daraufhin ein effektives Management ausrichten. Besonders hervorzuheben ist, dass sich die Erweiterung um Nachbarschaftsbeziehung und exponentielles Populationswachstum am besten für Langzeitprognosen eignet. Dabei ist zu erkennen, dass der Klimawandel eine zeitliche Beschleunigung der Befallsintensität bewirkt. Eine weitere wichtige Erkenntnis ist, dass mindestens eine Bekämpfungsintensität von 50 % benötigt wird, um ein vollständiges Absterben der Fichten in der Nationalparkregion Sächsische Schweiz zu verhindern.

5.3 Ökologie und Management des Buchdruckers (Ips typographus L.) - eine systematische Literaturstudie der Jahre 2004 - 2021

This study aims to update a review on the ecology and management of *Ips typographus* from 2004 with a systematic review on the same topic but for 2004 to 2021. It has been designed and supervised by the author of this doctoral study. In the following, (1) the author of this doctoral study gives a summary of the thesis, (2) the outline of tasks written by the author of this doctoral study is presented, and (3) the title page and abstract of the master thesis from the master student himself are shown.

Summary Climate change significantly impacts forest loss. Environmental conditions influenced by climate change can impact the development of harmful insects such as *Ips typographus* and the health of its host trees. This development puts pressure on those involved in forest resource management. This thesis summarizes the knowledge on *Ips typographus* as a matter of a systematic literature review of 2004 to 2021 based on a literature review from 2004 by Wermelinger. It functions as an update on the knowledge of ecology and management of this forest pest. It can be used to inform management decisions and aid in consideration of alternatives for bark beetle control.

The thesis shows differences in knowledge, affirmations of information, or new research directions in contrast to the review from 2004. It summarizes possible implications based on these changes for forest protection management.

TECHNISCHE
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DRESDEN

FOREST BIOMETRICS
& SYSTEMS ANALYSIS

Fakultät Umweltwissenschaften Institut für Waldwachstum und Forstliche Informatik

2. Dezember 2021

Angebot für eine Masterarbeit

Ausbreitungs- und Befallsmuster des Buchdruckers (Ips typographus L.) - eine systematische Literaturstudie der Jahre 2004 - 2021

Das übergeordnete Ziel besteht darin, die von Wermelinger (2004) angefertigte Literaturstudie zur Ökologie und zum Management des Großen Achtzähnigen Fichtenborkenkäfers *Ips typographus* L. zu aktualisieren. Dabei soll eine systematische Literaturstudie der Jahre 2004 bis 2021 durchgeführt werden, welche sich am Aufbau und Inhalt der oben genannten Publikation orientieren soll und ein sogenanntes Update einer Literaturstufe zu bearbeiten sein wird (Cumpston & Chandler, 2021).

Vorkenntnisse in der Benutzung einer Literaturverwaltungssoftware sind von Vorteil, wobei die Wahl der Software dem Kandidaten vorbehalten ist. Bei Interesse oder Fragen wenden Sie sich bitte direkt an: bruno_walter.pietzsch@tu-dresden.de.

Verweise

Wermelinger, B. (2004): Ecology and management of the spruce bark beetle Ips typographus—a review of recent research. Forest Ecology and Management, 202(1–3), 67–82. `https://doi.org/10.1016/j.foreco.2004.07.018`

Cumpston, M. & Chandler, J. (2021): Chapter IV: Updating a review. In: Higgins, J.P.T., Thomas, J., Chandler, J., Cumpston, M., Li, T., Page, M.J., Welch, V.A. (Editoren): Cochrane Handbook for Systematic Reviews of Interventions - version 6.2 (updated February 2021). Cochrane. `https://training.cochrane.org/handbook`

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Masterarbeit mit dem Thema

Ökologie und Management des Buchdruckers (Ips typographus L.) – eine systematische Literaturstudie der Jahre 2004–2021

zur

Erlangung des akademischen Grades

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Abstrakt

EN: Environmental conditions influenced by climate change act as a driver of extensive forest loss. Their occurrence influences both the physiological performance of harmful insects and the vitality of the host trees. The interaction of climatic changes and the resulting altered development of *Ips typographus* (L.) puts high pressure on the actors in the field of forest resource management. Based on a publication by the Swiss forest scientist Beat Wermelinger from 2004, a compilation of knowledge about the relevant processes and driving factors was developed in the form of a systematic literature study and supplemented with additions on the current state of knowledge in the respective subject areas. The focus of the work was placed on the ecology and management of the insect. The findings from the literature study correspond to those from the source and can prove them. The knowledge condensed in this way is not only intended to encourage further investigations in the subject areas, but it can also be consulted as an integral part of management decisions and help to weigh up alternatives in bark beetle control.

DE: Durch den Klimawandel veränderte Umweltbedingungen wirken als Treiber flächendeckender Waldverluste. Deren Auftreten nimmt sowohl Einfluss auf die physiologische Leistung von Schadinsekten als auch auf die Vitalität der Wirtsbäume. Durch das Zusammenspiel klimatischer Veränderungen und der daraus resultierenden veränderten Entwicklung des *Ips typographus* (L.) entsteht ein hoher Druck auf die Akteure im Bereich des Waldressourcenmanagements. Nach dem Vorbild einer Publikation des Schweizer Forstwissenschaftlers Beat Wermelinger aus dem Jahre 2004 wurde eine Zusammenstellung der Kenntnisse über die relevanten Prozesse und treibenden Faktoren in Form einer systematischen Literaturstudie entwickelt und mit Ergänzungen zum aktuellen Wissensstand in den jeweiligen Themenfeldern vervollständigt. Dabei wurden die Schwerpunkte der Bearbeitung auf Ökologie und Management des Insekts gelegt. Die Erkenntnisse aus der Literaturstudie decken sich mit denen aus der Bezugsquelle und können diese belegen. Das so komprimierte Wissen soll nicht nur dazu anregen, weitere Untersuchungen in den Themengebieten anzustellen, sondern es kann darüber hinaus auch als integraler Bestandteil bei Managemententscheidungen zurate gezogen werden sowie dabei unterstützen, Alternativen in der Borkenkäferbekämpfung abzuwägen.

6 Discussion

6.1 Major findings

This work adds to a series of previous studies investigating several aspects of the Norway spruce (*Picea abies*) and European spruce bark beetle (*Ips typographus*) system, such as risk assessment (Netherer and Nopp-Mayr, 2005; Seidl et al., 2008), beetle development (Baier et al., 2007), dispersal and infestation patterns (Kautz et al., 2014, 2016; Potterf and Bone, 2017), the effectiveness of forest protection measures against the beetle spread (Fahse and Heurich, 2011), or the impact of bark beetle disturbance on the forest system as well as its interaction with other disturbances (Seidl et al., 2012). In order to combine multiple of these simulation tools and to apply them on different spatial and temporal scales in a novel and rigorous way, a metamodel approach is facilitated: A metamodel is a model of a model and allows for a faster and more easily application of resource-demanding and precise mechanistic models such as individual-based models (Peters et al., 2015). In the following paragraphs, the significant findings of the studies presented in Chapters 2 to 4 of this thesis will be discussed in the context of the research questions first presented in Chapter 1.

The first study of the thesis focused on the following research questions, as was first described in the section 'objectives and content' of the dissertation:

1. How effective is sanitation felling on a local scale, and what parameters influence its effectiveness?
    a) The individual-based model IPS-SPREADS can reproduce the severity and direction of infestation development observed within the Saxony Switzerland national park from 2015 to 2017.
    b) Sanitation felling at the border of a national park can effectively reduce the damage in adjacent and managed forest areas.
    c) Parameters such as the number of beetle sources, number of beetles, the distance of beetle sources to the adjacent managed forest areas, and the attractiveness of trees play a major role in the number of trees damaged outside the protected area.

According to the results of model calibration of IPS-SPREADS, there was a decrease in beetle energy levels during mass outbreaks, which may be attributed to intra-specific competition (Salle et al., 2005) or to a decrease in the beetles' relative body fat, which is possibly due to increased breeding intensity (Botterweg, 2009). This relationship, in turn, affirms the assumption that traits of the individual beetle or tree influence the emerging dispersal and infestation patterns in *Ips typographus* and *Picea abies* systems of Europe. If more calibration cycles with decreasing parameter sections had been carried out, the overall fit could have been enhanced. However, no further runs were conducted since the overall infestation severity and direction fit was already satisfactory, and additional model simulations would have been expensive. Sanitation felling could not stop the European spruce bark beetle from spreading from the national park to adjacent forest areas. Even with 100 % felling intensity, trees were still damaged outside the national park. Nevertheless, the simulation experiments suggest a felling intensity threshold of 75 % and more to reduce the beetle and infestation spread effectively. Comparable magnitudes were reported with 95 % and more for salvage logging (Dobor et al., 2020) and 80 % for bark beetle mortality in general (Fahse and Heurich, 2011). For a mountain pine beetle population to decline, a mortality of 97.5 % and more must be achieved to decline the population accordingly (Safranyik and Carroll, 2006). Despite the high threshold and the possible enormous consequences of missing even a few trees (Trzcinski and Reid, 2008), sanitation felling in the form of a timely removal or debarking of infested trees is still considered one of the most efficient measures against the spread of bark beetles (Jönsson et al., 2012; Stadelmann et al., 2013; Wermelinger, 2004). Other options, such as pheromone trapping, do not seem to reduce economic damages at the local scale even when combined with sanitation felling and could even induce new attacks by attracting but not necessarily neutralizing bark beetles at the site (Kuhn et al., 2022). While results of Lindmark et al. (2022) suggest trap logs in sufficient numbers as a possible control measure to reduce tree mortality at forest edges, additional use of chemical cues did not improve the efficiency of trap logs. The authors also stated that their findings do not imply evidence of protection on a large scale. The simulation experiments showed a positive relationship between the primary attractiveness of spruce trees and the infestation amount, which is related to the fact that trees with higher primary attractiveness exhibit lower defenses against infestation in the Infestation Pattern System model and therefore require fewer beetles to cause a successful infestation Kautz et al. (2014, 2016). As the primary attractiveness of the IPS-SPREADS model was determined using the predisposition assessment systems (Netherer and Nopp-Mayr, 2005), it is indicative of poor tree conditions, such as low water supply or inadequate nutrient availability. The impact of tree distance on beetle source trees is supported by other studies that found that the risk of infestations decreases with increasing distances from the beetle source trees (Wichmann and Ravn, 2001; Kautz et al., 2011; Zolubas and Dagilius, 2012; Potterf et al., 2019). One possible explanation is that beetle densities decrease with greater distances from the infestation sources (Angst et al., 2012; Hinze and John, 2020). The simulation results affirmed the findings of other studies that showed that the risk of infestation is highest near previously infested trees (Kautz et al., 2011; Stadelmann et al., 2013; Wichmann and Ravn, 2001). Along with this, it could be shown that spruce trees within the national park with higher primary attractiveness and, therefore, lower defenses reduced the risk of damage to trees outside the national park: These susceptible trees acted as a beetle sink and resulted in lower beetle amounts outside the national park during the simulated year. It has to be emphasized that this effect will likely be inverted in the following year when beetles will emerge from these trees and spread to the surrounding forests. While several other modeling studies on *Ips typographus* and *Picea abies* such as Fahse and Heurich (2011); Seidl et al. (2012); Kautz et al. (2014, 2016); Potterf and Bone (2017) already exist, the model presented in this study is the first to spatially explicit describe both the beetles and the trees as real individuals with traits, sensing, and interaction and incorporate management measures such as sanitation felling and pheromone trapping.

Like many other individual-based models, the IPS-SPREADS model generates results and patterns based on the characteristics of the simulated individuals (Railsback and Grimm, 2012). Consequently, the dispersal and outbreak patterns projected by the model are reliant on the traits of the beetles and trees in the simulation. However, like other individual-based models, the IPS-SPREADS model is computationally expensive and can only be used for smaller forest areas on the plot level. An upscaling of the model was necessary to apply the individual-based model to more extensive spatial, temporal, or population scales. In this regard, applying a so-called metamodel, which is a model of an individual-based model, seemed promising. In order to choose a meaningful and efficient model type for the upscaling of IPS-SPREADS, a systematic literature review was done in Chapter 3 of this thesis investigating the following research question:

2. Which types of metamodels are used in an individual-based modeling context, and what are their application purposes?

The systematic literature review revealed six different metamodel families and associated model types that were commonly used in an individual-based modeling context: Ordinary equations (e.g., difference equation), differential equations, regressions, Bayesian emulators such as approximate Bayesian computation, machine learning such as random forests and Markov chains such as transition matrices. As primary application purposes of such metamodels in an individual-based context, the following four were identified: calibration - find reasonable values for input parameters (Friedman and Pressman, 1988; Barton, 1994; Kleijnen and Sargent, 2000; Barton and Meckesheimer, 2006); prediction - predict model behavior for new scenarios or parameter values while replacing the simulation model (Kleijnen and Sargent, 2000); sensitivity analysis - explore model output sensitivity to changes in parameter values (Railsback and Grimm, 2012; Thiele et al., 2014; Ligmann-Zielinska et al., 2020); and upscaling - scale the model to a coarser spatial resolution (Cipriotti et al., 2016) or from individuals to populations (Campillo and Champagnat, 2012). It has to be emphasized that the term prediction in this regard also includes exploratory analysis (Bigelow and Davis, 2002), what-if analysis (Barton and Meckesheimer, 2006) and exploration / inverse exploration (Friedman and Pressman, 1988; Friedman, 1996). The rating of metamodel information quality and implementation effort by a group of Ph.D. students and postdoctoral researchers revealed for each of the application purposes mentioned above the most promising metamodel types: sensitivity analysis - linear regression; calibration - approximate Bayesian computation; prediction - Gaussian processes; and upscaling - transition matrices. In addition to these significant findings, the study presented in Chapter 2 is the first to describe and apply a methodology in order to rate the metamodel quality and implementation effort in an individual-based context. The rating was done using three criteria for quality (consideration of uncertainty, suitability assessment, and the number of evaluation criteria) and implementation effort (availability of open access guiding sources, R coverage, and out-of-the-box applicability). While other publications on guiding fellow researchers in choosing and applying metamodels for specific purposes already exist (e.g. Thiele et al., 2014; Ligmann-Zielinska et al., 2020), the presented study is the first to systematically review all purposes of metamodeling in an agent-based modeling context. In addition, it is the first to give an objective rating of metamodel quality and implementation effort for the given application purposes to guide fellow researchers in choosing and applying a promising metamodel type for their intended goal.

As described in Chapter 2 of this thesis, the IPS-SPREADS model as an individual-based model generates results and patterns based on the characteristics of the simulated individuals (Railsback and Grimm, 2012) and, like many other individual-based models, is computationally expensive. In order to apply and investigate the effects of individual traits of trees and beetles on more extensive spatial, temporal, or population scales, a computationally less demanding upscaling of the individual-based model was necessary. In Chapter 4 of this thesis, such an upscaling through a metamodel was done in order to investigate the following research questions:

3. Can sanitation felling alter the course of a beetle mass outbreak on the landscape scale containing a large protected area (national park)?
    a) Increases in the number of bark beetle generations per year due to forecasted increases in mean temperature lead to faster outbreaks and more frequent complete dieback of Norway spruces (*Picea abies*) inside and outside the national park.
    b) Sanitation felling at plot level inside the national park can lower the risk of infestation spread from the protected to adjacent forested areas in the next 20 years but requires a minimum threshold value to be effective.

In contrast to the study presented in Chapter 2, which described, validated, and applied the individual-based model IPS-SPREADS on the plot level, the study in Chapter 4 introduces a new metamodel that can extrapolate the outcomes of the individual-based model to the landscape level. This application addresses a key challenge in forest ecology and management: using small-scale observations to predict large-scale patterns (Denny and Benedetti-Cecchi, 2012). Introducing a beetle spread between neighboring grid cells improved the agreement between metamodel predictions and real-world observations. This finding follows other studies which found that weakened spruces can act as step stones for infestations of neighboring and more robust areas, eventually leading to a mass outbreak at the regional scale (Křivan et al., 2016). In addition, connections between habitats play a significant role in enabling and developing mass outbreaks of *Ips typographus* (Kärvemo et al., 2016; Seidl et al., 2016b; Wildemeersch et al., 2019). Climate change could cause drier and hotter years, leading to three bark beetle generations per year instead of two. According to the results of this study, this might change the forecasts of bark beetle infestations to total forest loss in the national park and high infestation threats for nearby forests, which were only slightly at risk from two beetle generations. This finding follows studies by Seidl et al. (2008) or Dobor et al. (2020), which found that more beetle generations each year could cause more disruptions and double or triple the amount of wood damage. The presented study also found that removing or debarking at least 80 % of the infested trees might be necessary to reduce the potential risks for the forests near the national park and manage the outbreak risk. Similar thresholds are reported for salvage logging with $\geq$ 95 % (Dobor et al., 2020) and for general bark beetle mortality with 80 % (Fahse and Heurich, 2011). Achieving such a high reduction is complex and only possible if the damage is confined to small areas (Dobor et al., 2020) because cutting down infested trees may not stop a mass outbreak effectively once it becomes large-scale (Kulakowski, 2016). Factors that make sanitation felling less effective include the late detection of infestations by visual signs, the lack of technical and human resources, the high costs of debarking, or the rugged terrain conditions (Wermelinger, 2004). Due to these factors, sanitation felling intensities in practice is unlikely to reach 100 %, and even 75 % may not be feasible on larger scales (Dobor et al., 2020). However, removing or debarking infested trees on time is still the most effective measure to prevent bark beetles from spreading (Jönsson et al., 2012; Stadelmann et al., 2013; Wermelinger, 2004). While several other modeling studies on *Ips typographus* and *Picea abies* such as Fahse and Heurich (2011); Seidl et al. (2012); Kautz et al. (2014, 2016); Potterf and Bone (2017) already exist, the study presented here is the first to scale a spatially explicit and fully individual-based model with individual traits, interactions and sensing from the plot level to the landscape level and from a single year to several decades by applying a metamodel approach. Despite this design and approach differences, it supports the findings of other studies regarding climate change-induced increase in beetle activity on infestation disturbance severity (Seidl et al., 2008; Dobor et al., 2020) and of management effectiveness against the infestation risk and dispersal (Fahse and Heurich, 2011; Dobor et al., 2020).

6.2 Methods evaluation

The results presented in Chapters 2 to 4 of this dissertation should be interpreted with some caution. In the following section, some criticisms are raised, relating primarily to the assumptions of the developed simulation models and the systematic literature review in Chapter 3 of this dissertation. It should be noted that this criticism is incomplete here. The outlook section afterward will mention more points in the form of a description of how these problems, which are related to the methodology used and have already been discussed or not, can be solved in possible further studies. In the following paragraphs, a discussion of the chosen methodology divided by the thesis chapters will be given, enhancing the remarks during the discussion of the respective studies.

Despite being a mechanistic precise, spatially explicit, and individual-based model, the IPS-SPREADS model presented in Chapter 2 still makes several assumptions, possibly oversimplifying essential processes in the *Ips typographus* and *Picea abies* system. Such examples include that wind speed and direction do not vary during a simulation run. No detailed information on speed and direction was available throughout the year and in the area. Therefore, the wind was implemented to depict a general and global scenario in the model to limit computational costs. As the study results presented in Chapter 2 revealed, even with this general implementation of wind speed and direction, the agreement between model prediction and real-world observations of infestation patterns during a mass outbreak increased substantially. Another caveat regarding simplifying essential processes in the IPS-SPREADS model is the calculation of spruce vitality based on the predisposition assessment systems - PAS (Netherer and Nopp-Mayr, 2005): While the PAS model accounts for different properties of the given forest stands like tree age, canopy closure or tree height as well as of the respective forest site like soil productivity, water retention capability or exposition, it was calculated only once for the simulation study as the forest inventory data inside the national park was several years old. With this, essential factors on tree vitality, such as water deficit through drought stress (Netherer et al., 2019; Netherer, 2022) that vary throughout the season or the years, were not considered. Furthermore, other essential disturbances were not taken into account, such as wind-felling of spruce trees (Potterf and Bone, 2017; Nardi et al., 2022) that facilitate or promote bark beetle infestations. The main reason for this simplification and others mentioned before was the vast computational cost of the IPS-SPREADS model, which limited its analysis and application to one year with three beetle generations at maximum even under the usage of the high-performance cluster (HPC) of the TU Dresden. Nevertheless, thanks to thorough code optimization, the model performs well if it is applied for initial infestations or the development of early outbreak stages.

One main point of criticism for the study described in Chapter 3 of this thesis can be seen in the selection process of studies to be evaluated: For each of the reviewed databases and combination of keywords, only the first 50 entries sorted by relevance were investigated and selected, if they described a metamodel application in an agent-based modeling context. With this limitation of search results, the candidate may have missed important literature during his systematic review. However, on the other side, this limitation allowed for a reasonable scope of work and a higher reproducibility of the search procedure. Another point of criticism must be mentioned regarding the scope and content of the developed and applied rating of the investigated metamodel applications: To keep the rating process uniform and precise, only three criteria each for metamodel quality and implementation effort were chosen. Further criteria could have changed the rating process's outcome and improved the rating results' information quality. In addition, the metamodel quality rating was primarily based on the assessment of the authors of the corresponding study to be rated, which may be based on a subjective evaluation and influence the assessment of metamodel quality by the reviewers. In order to limit the rating effort and to assess the difficulties in executing the metamodels in a widely applied and openly accessible statistical software, the rating of metamodel implementation effort was primarily based on the coverage and availability in R (RCoreTeam, 2020) and no other programming language or statistical tool was considered. Nevertheless, the chosen criteria represent a variety of modeling aspects that were important to several Ph.D. students and postdoctoral researchers and provide a valuable baseline for choosing a suitable metamodel type for the application purpose.

A point of criticism for the study presented in Chapter 4 of this thesis lies in the application of the carrying capacity extension despite it not improving the fit between metamodel prediction and observed infestation patterns. Following the principle of Ockham's razor in a modeling context (e.g. Bargagli-Stoffi et al., 2022) that suggests that the simplest explanation is likely to be correct, it should have been preferred to discard the capacity extension of the metamodel for the sake of simplicity and also less computational cost. However, as there was no information on areas with 100 % spruce mortality in the baseline data of the national park, grid cells where most spruce trees had died were still categorized as having the highest level of infestation. Therefore, the carrying capacity extension could not improve the agreement between model prediction and observations. Furthermore, to accurately represent and evaluate the danger of infestation in nearby forests, both extensions were required to determine the percentage of dead spruce trees in each grid cell and the percentage of grid cells with entirely dead spruces. Another point of criticism for the presented study lies within the overall low scores during model validation. The spread of beetles to neighboring grid cells with an edge length of 250 m may not adequately capture the spread of infestation during mass outbreak conditions as most new infestations occur within a range of 100 m (Kautz et al., 2011; Wichmann and Ravn, 2001) to 500 m (Kautz et al., 2011; Stadelmann et al., 2013). In addition, one of the two years used for validation was one of the region's hottest and driest ever recorded, with three whole beetle generations and two sister broods (Institute of Forest Entomology and protection, 2022). This drought event could result in an underestimation of real-world infestation development. Although the fit between the model's predictions and observations could be more substantial, the metric is crucial for comprehending the rationale behind selecting the metamodel type (combination of extensions) and highlighting the significance and impact of such extensions on the metamodel's usability. Cipriotti et al. (2016) made similar extensions to their metamodel in their original upscaling study, enhancing the validity of their outputs.

6.3 Outlook

This section addresses some of the criticisms raised and suggests several avenues for future research. Some of these have already been explored through preliminary analysis during this doctoral thesis or are in preparation through master theses under the direct or indirect supervision of the candidate of this thesis.

Mixed stands and their impact on infestation risks In the future, mixed forest stands are expected to become more common in forest conversion efforts due to their many advantages over pure stands. These advantages include increased stability against disturbances and calamities for individual trees and the entire stand due to increased structural and species richness (Bravo-Oviedo et al., 2014; Knoke et al., 2008). Conifers in mixed stands have been found to produce more resin than those in pure stands, which helps defend against bark beetle attacks (Baier et al., 2002; Wermelinger, 2004). Mixed forests also have greater resilience and ability to recover after damage events (Bravo-Oviedo et al., 2014; Knoke et al., 2008). In mixed and richly structured stands, the mortality risk for individual tree species is generally lower, and they are less prone to mass insect reproduction. This is due to a broader distribution of host tree species, the presence of alternative hosts, and an increase in the abundance and diversity of antagonists (Hlásny et al., 2021; Knoke et al., 2008). Mixed stands are often more productive and provide broader ecosystem services. By spreading risk across multiple tree species, the risk of economic losses is reduced (Bravo-Oviedo et al., 2014; Forrester, 2014; Knoke et al., 2008).

In order to investigate the effects of different spatial configurations of mixed forests with the IPS-SPREADS model, it would be necessary to remove the GIS-data-based creation of the simulation world and implement the creation of artificial forest structures. Examples of spatial configurations of deciduous and spruce trees inside the model world could be randomly distributed, grouped by tree species, or in stripes. It is also possible to independently vary species' height or age distribution. These adjustments could then be used to analyze thresholds for infestation and mass outbreak risks of *Ips typographus* and to derive recommendations for optimal stand management regarding climate change and forest conversion.

Open access GIS data for tree vitality, beetle source trees, and beetle development Open access GIS data has several advantages that make it a valuable resource in modeling bark beetle infestation spread: One of the main benefits is its openly accessible and widespread availability, allowing easy data access. Open access GIS data can also help circumvent data limitations that may arise due to long intervals between forest inventory sampling. Using data from the European Union's earth observation program 'Copernicus' can also increase the applicability of the IPS-SPREADS model for all of Europe. Furthermore, open-access GIS data allows for more information and higher temporal resolution of data, providing more detailed and accurate insights. Specific examples regarding the IPS-SPREADS model include the calculation of tree vitality, the amount and location of beetle source trees, or the beetle development throughout the year.

Tree vitality can be calculated through transpiration deficits, which refers to the difference between trees' actual and potential transpiration (Matthews et al., 2018). Acute transpiration deficits can reduce a tree's defenses against bark-beetle infestations due to higher terpene emissions from the trees and the restricted cooling effect of transpiration (Matthews et al., 2018). Transpiration deficits from June to August of the previous and current year are considered proxies for beetle attack (Netherer et al., 2019; Netherer, 2022) and could be used to more accurately assess the susceptibility of spruces to bark beetle attacks in the IPS-SPREADS model. The Sentinel-2 and Sentinel-3 satellite constellation contains the most spatial, temporal, and spectral characteristics required for accurate, field-scale evapotranspiration estimation (Guzinski et al., 2020). The one remaining major challenge is the spatial scale mismatch between the thermal-infrared observations acquired by the Sentinel-3 satellites at around 1 km resolution and the multi-spectral shortwave observations acquired by the Sentinel-2 satellite at around 20 m resolution (Guzinski et al., 2020). Guzinski et al. (2020) evaluated several approaches for bridging this gap by improving the spatial resolution of the thermal images.

Retrieving the amount and location of infested trees as possible beetle sources is a crucial prerequisite for the IPS-SPREADS model and the subsequent metamodel. The Copernicus program provides data from its Sentinel satellites that can be used to detect trees infested by bark beetles: For example, Fernandez-Carrillo et al. (2020) used Sentinel-2 images as the primary input for developing models to map bark beetle damage and severity. The study developed two models based on a change detection approach and Sentinel-2 images. The first model was based on bi-temporal regression in spruce areas to estimate forest vitality and bark beetle damage. The second model considered all forest areas but excluded clear-cuts and completely dead areas to map only changes in stands dominated by live trees. The study found that the models could detect bark beetle attacks at the last phases with high accuracy and produced maps that achieved an overall accuracy above 0.80.

Beetle development can be calculated using daily temperature data and topographical information such as exposition, inclination, or altitude (Baier et al., 2007; Netherer et al., 2019). By calculating degree days above certain thresholds, the timing of emergence in spring, host tree infestation, the beginning of possible sister broods, and the emergence of juvenile beetles during summer can be accurately represented (Baier et al., 2007). Sister broods or re-emergence is a phenomenon common to the spruce bark beetle (*Ips typographus*) and several other species of the Scolytinae subfamily. Re-emergence means that females finish oviposition, re-emerge and replenish their energy reserves by so-called regeneration feeding (Davídková and Doležal, 2017; Doležal and Sehnal, 2007). It is hypothesized that sister broods are essential in regions where *I. typographus* is monovoltine but has only moderate significance where this species has more than one generation per season (Wermelinger and Seifert, 1999). Precise simulation of beetle development, sister broods, and host colonization timing is essential for depicting accurate beetle densities and timing of detection and management actions throughout the year within the IPS-SPREADS model.

Additional management measures While the presented work focused solely on sanitation felling once after each beetle generation as a management measure to investigate effectiveness against infestation spread, several other management options could be investigated with the proposed model framework. Examples include designating a buffer zone around the national park, implementing detection and removal of infestations over time, or applying anti-attractants on susceptible trees. These examples will be highlighted in the following paragraphs, and a possible way to integrate the measure into the model framework will be given.

A buffer zone at the border of the national park used as an outbreak contention measure is a common practice in other national parks in Germany, such as Black Forest national park (Sonnemann et al., 2017) or the Bavarian Forest national park (Lobinger, 2015). Such a buffer zone with a width between 100 m (Niemeyer et al., 1995a) and 1500 m (Heurich, 2001) could be enough to substantially reduce the spread of infestations from protected to adjacent forest areas (Wermelinger, 2004). A possible way to implement and investigate its effectiveness against infestation spread in the presented model framework would be to assign all grid cells of the metamodel that intersect with the national park border as a buffer zone and to apply a different sanitation felling intensity or management regime there.

Recent studies highlight the importance and opportunities that detection and removal of infested trees over time due to visual clues or dogs smelling pheromones possess (Kautz et al., 2022; Vošvrdová et al., 2023). It is suggested that terrestrial detection accuracy and timeliness may be high enough to sufficiently suppress *Ips typographus* outbreak propagation when combined with subsequent sanitation felling (Kautz et al., 2022): For example, bordust led to 82 % correctly detected infestations during spring, while crown discoloration and defoliation made detection easier in late summer and autumn. The findings also suggest that hibernation trees should ideally be detected in late summer, and sanitation felling should be done before November. To further increase the detection of infested trees during spring, dogs smelling pheromones emitted by infesting beetles are a promising addition (Vošvrdová et al., 2023). In conclusion, the different terrestrial-based detection methods could be implemented in IPS-SPREADS to more accurately depict management measures against *Ips typographus* and investigate the impact of detection accuracy and timeliness on the effectiveness of subsequent sanitation felling against the spread of infestations. A possible approach to implement these detection measures would be to incorporate detection probabilities for infested trees in dependence on beetle development, host tree reaction, and time in general based on the findings of Kautz et al. (2022).

A study by (Jakuš et al., 2022) showed the possibility of applying anti-attractants on susceptible trees to repel bark beetle infestations. The results suggest a redirecting effect of anti-attractants, causing fewer subsequent attacks in areas with treated trees than in control areas. These effects should already be visible when only one dispenser at a low position above the ground is installed, highlighting this approach's relatively low effort and possibility. Still, in conditions with severe drought and high beetle densities, applying such anti-attractants was ineffective regardless of the number of applied dispensers per susceptible tree (Jakuš et al., 2022). In order to investigate the effectiveness of the presented model framework, it would be possible to apply artificial dispensers within the IPS-SPREADS model to trees with high primary attractiveness. For calibrating the reduction of attractiveness facilitated by the dispenser, the data from Jakuš et al. (2022) could be used, as well as valuable information from parameterizing the aggregation pheromone dispensers used for the pheromone traps in the model from a previous work of the Ph.D. candidate.

6.4 Conclusions

This work builds on previous studies that investigated various aspects of the Norway spruce (*Picea abies*) and European spruce bark beetle (*Ips typographus*) system. These aspects include risk assessment, beetle development, dispersal, infestation patterns, the effectiveness of forest protection measures against the beetle spread, and the impact of bark beetle disturbance on the forest system and its interaction with other disturbances. A metamodel approach combines these simulation tools and applies them on different spatial and temporal scales in a novel and rigorous way. With this framework, it is shown, for the first time, that individual traits of bark beetles and host trees influence the distance, intensity, and patterns of infestations even during mass outbreaks and across spatial and temporal scales. In addition, the effectiveness of sanitation felling for mitigating further mass outbreak propagation and the effect of climate change-induced increases in bark beetle generation numbers on the outbreak development is assessed. Furthermore, application purposes and types of metamodels in an individual-based modeling context are reviewed and rated, showing that the most suited metamodel types vary regarding the chosen aim.

Regarding real-world forest protection and decision, following recommendations based on the presented results can be made:

1. Due to decreasing beetle energy levels under outbreak conditions, detection, and control measures should be applied closer to already infested trees as beetle flight and infestation distances are decreasing.

2. The importance of habitat connectivity during the metamodel application emphasizes the relevance of primarily targeting areas with groups of stressed trees as they can act as step-stones for further infestations around them or as a bridge between different forest areas.

3. When sanitation felling should effectively hinder further outbreak propagation, at least 80 % of the infested trees have to be removed or debarked in time.

4. As beetle drift by wind systematically altered emergent infestation patterns, detection and control measures of forest protection management should also

focus on forest edges as they act as the first landing zone of beetles drifted by the wind.

For further scientific studies on the topic investigating the dispersal and infestation of bark beetles through individual-based models, it is concluded that the application of a metamodel is highly recommended in order to get the best of both worlds: A mechanistic precise, and detailed model to robustly investigate the underlying processes of beetle dispersal, host detection, and colonization, and a fast and simplified model to apply these mechanics and the emergent results on broader spatial, temporal and population levels. It is also concluded, in order to improve the presented framework and to analyze management tools, there are several promising aspects to investigate, such as:

1. Facilitating open access and widely available GIS data such as from the Copernicus program of the European Union.
2. Integrating other management measures such as terrestrial detection based on visual clues, pheromone-smelling dogs, or anti-attractant application on possible host trees.
3. Implementing precise beetle development throughout the year and sister broods.
4. Extending the metamodel, for example, with a buffer zone around protected areas or weather data to realistically adjust tree vitality due to transpiration deficits throughout the year.

List of publications presented as thesis chapters

- **Pietzsch, B. W.**, Peter, F. J., & Berger, U. (2021). The Effect of Sanitation Felling on the Spread of the European Spruce Bark Beetle - An Individual-Based Modeling Approach. Frontiers in Forests and Global Change, 4, 1-15. `https://doi.org/10.3389/ffgc.2021.704930`

- **Pietzsch, B.**, Fiedler, S., Mertens, K. G., Richter, M., Scherer, C., Widyastuti, K., Wimmler, M.-C., Zakharova, L., & Berger, U. (2020). Metamodels for Evaluating, Calibrating and Applying Agent-Based Models: A Review. Journal of Artificial Societies and Social Simulation, 23(2). `https://doi.org/10.18564/jasss.4274`

- **Pietzsch, B. W.**, Wudel, C., & Berger, U. (2022). Nonparametric upscaling of bark beetle infestations and management from plot to landscape level by combining individual-based with Markov chain models. European Journal of Forest Research. `https://doi.org/10.1007/s10342-022-01512-1`

Publications apart the doctoral thesis

- **Pietzsch, B.**, Otto, L.-F., & Berger, U. (2018). Monitoring And Control Of The Spruce Bark Beetle (*Ips typographus* L. 1758) - A Simulation Study. Mitteilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie, 21, 99–104. `https://www.researchgate.net/publication/330185409`

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