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Original Research Article

Simulating bark beetle population dynamics in response to windthrow events

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ABSTRACT

The relationship between windthrow disturbance and outbreaks of European spruce bark beetle *Ips typographus* L. in European Norway spruce forests has been the focus of recent studies. However, the nature in which the spatial characteristics of windthrow events influence bark beetle population dynamics is rarely examined. This represents a significant gap in the literature, as our understanding of how spatial windthrow patterns influence bark beetles can be useful for management efforts to help mitigate large-scale bark beetle disturbance. The objective of this study is to simulate how windthrow events facilitate bark beetle population state transitions from endemic and epidemic levels using a spatially explicit agent-based model. We examined how the spatial extent of windthrow events and the size of tree clusters impacted by windthrow influence this state transition. The results show that the beetle population transition slows with increasing spatial extent of a windthrow event and with larger clusters of windthrown trees, while scattered patterns of windthrown 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. Moreover, it provides a basis for further research to discover the impact of potential forest management applications aiming to mitigate the risk of bark beetle outbreaks.

1. Introduction

Wind disturbance plays a significant role in shaping Norway spruce *Picea abies* (L.) Karst. forest ecosystems in central and northern Europe (Kuuluvainen et al., 2014; Panayotov et al., 2011). Severe wind events lead to tree mortality, resulting in gaps in the forest canopy that encourage the growth of younger unaffected trees. At the same time, wind events can change the composition of the forest by facilitating large-scale outbreaks of bark beetles, such as the European spruce bark beetle (ESB) *Ips typographus* L. (Christiansen and Bakke, 1988; Marini et al., 2013; Økland and Berryman, 2004).

Native to spruce forests in Europe and Asia (Wood and Bright, 1992), the ESB typically occurs in low (endemic) population numbers where it attacks unhealthy trees in order to reproduce. The low number of compromised trees constrains beetle population numbers; however, after a windstorm, beetles have a greater number of available compromised trees to infest (Göthlin et al., 2000; Schroeder and Lindelöw,2002). In the year following a windstorm, beetles almost exclusively infest windthrown trees (Göthlin et al., 2000). This leads to higher reproductive success and increased population numbers, but at the same time depletes available hosts (Økland and Bjørnstad, 2006). The combination of increased population numbers and depletion of breeding materials can force beetles to attack healthy, living trees (Bouget and Duelli, 2004; Schlyter and Anderbrant, 1989), typically starting in the second year after a wind disturbance event (Göthlin et al., 2000; Kärvemo et al., 2014; Schroeder and Lindelöw,2002). At this point, beetle populations transition to an epidemic state in which widespread tree mortality ensues (Christiansen and Bakke, 1988).

The nature in which windthrow events lead to a state transition between endemic and epidemic beetle populations is a complex process guided by multi-scale interactions between insects and host trees, leading to landscape-level patterns of forest cover change. Until recently, the spatial scalar divide in methods for examining spruce beetles and windthrow has challenged our ability to investigate the complexity of the relationship between these two disturbance agents. On the one hand, there is a depth of micro-scale research related to beetle physiology, including life cycle development (Sauvard, 2004), timing of beetle emergence from host trees and subsequent dispersal behaviour (Botterweg,

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1982; Byers and Lofqvist, 1989; Öhrn, 2012; Zumr, 1992), reproduction (Wermelinger and Seifert, 1999), lifespan (Austara and Midtgaard, 1986), and chemical communication between beetles (Byers, 2004; Sun et al., 2006). On the other hand, there exists substantial landscape-scale research based on observations of windthrow severity and beetle-induced tree mortality (Kärvemo et al., 2014; Økland and Bjørnstad, 2006; Schroeder and Lindelöw, 2002; Wermelinger et al., 2002). Yet, minimal research exists that directly explores how individual beetle physiology and beetle-host interactions collectively influence the landscape-scale patterns of beetle-induced tree mortality resulting from windthrow events.

Agent-based modelling (ABM) provides an opportunity to explicitly represent spruce beetle physiology and how interactions between beetles and host trees lead to emergent patterns of tree mortality in post-windthrown landscapes. Beetles, either individuals or collections of beetles, can be represented as a single agent that interacts with trees, as represented by cells in a grid. ABM can simulate windthrow by specifying time steps at which tree resistance is diminished, subsequently decreasing the number of beetles required to infest a tree. The resulting increase in beetle population numbers acts as a catalyst for a state transition between endemic and epidemic populations. ABM can therefore serve as an approach to understanding how the characteristics of wind events facilitate epidemics.

Previous studies have demonstrated the utility of ABM for simulating specific characteristics of ESB population dynamics. Examples include examining how variations in individual beetle traits impact subsequent tree mortality during a single generation (Kautz, 2016; Kautz et al., 2014), and estimating the level of forest management activities required to mitigate outbreaks (Fahse and Heurich, 2011). Additionally, Kausrud et al. (2011) have used ABM for modelling ESB population dynamics, while inspected the importance of beetle aggregation behaviour in beetle-killed forest patches. This relatively small yet compelling collection of existing research has set the groundwork for conceptualising ESB as agents in a simulation model, and has facilitated an opportunity to explore the role of windthrow events in driving ESB outbreaks.

The objective of this study is to evaluate the relationship between windthrow and ESB dynamics in causing emergent patterns of tree mortality using agent-based modelling. The model incorporates existing knowledge of beetle reproduction, mortality, host selection, and beetle–tree interaction in order to better understand how the spatial extent and size of clusters of windthrown trees influence the state transition between endemic and epidemic beetle populations.

2. Methods

2.1. Model description

The IPS-wind model developed in this study is an extension of the IPS model (*Infestation Pattern Simulation,* version 1.0) published by Kautz et al. (2014). The original IPS model simulates *I. typographus* L. dispersal and infestation patterns within a single generation, over a hypothetical forest stand. Our study modifies this existing model by simulating ESB dispersal and aggregation behaviour, and tree mortality over multiple generations. We

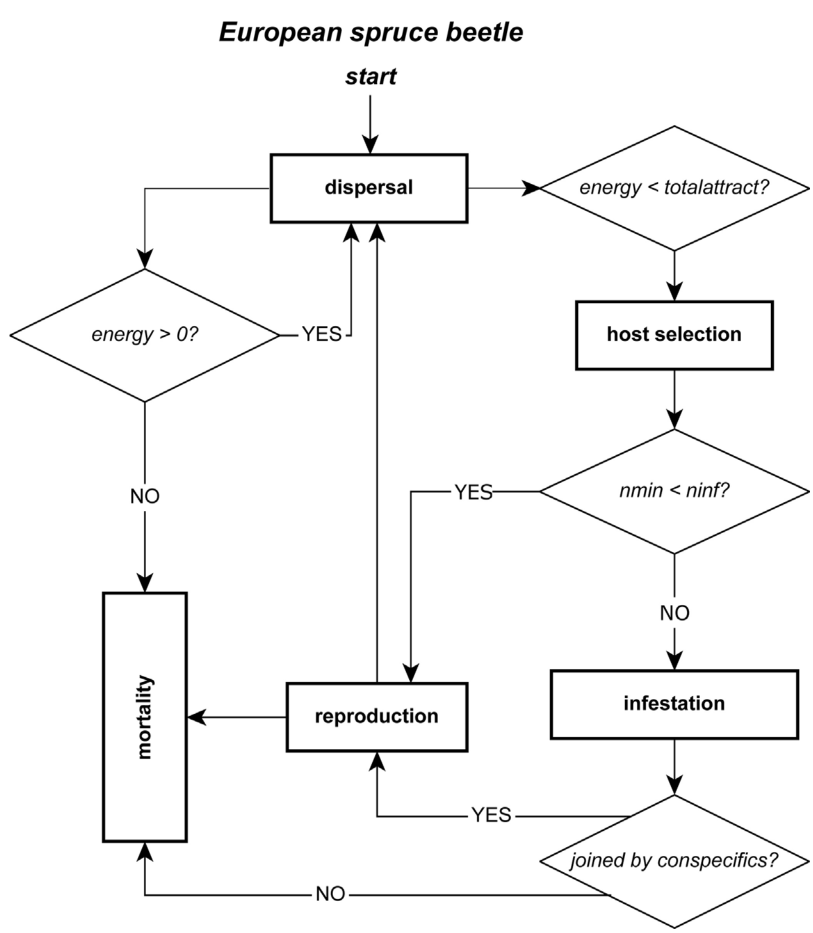

Fig. 1. Simplified model flow chart showing processes, decisions, resulting alternatives, and beetles' states.