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Cyclic epidemics, population crashes, and irregular eruptions in simulated populations of the mountain pine beetle, *Dendroctonus ponderosae*

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ABSTRACT

The native Mountain Pine Beetle infests numerous native pine species in North America and can cause extensive mortality when populations enter an epidemic state. We used an agent based cellular model of coupled beetle and host tree populations to investigate the effects on long-term population dynamics of modifying three model components, representing factors that land managers have varying degrees of control over: number of host trees, health of host trees, and number of surviving beetle offspring. Within the parameter space, various behavior types emerged in the simulations: population crashes, regular endemic/epidemic cycles, and sporadic cycles. The largest, recurring epidemics occurred in simulations with dense populations of mostly vigorous trees and moderately high beetle offspring production. The fewest epidemics occurred with low beetle reproduction, and low tree population density. With all other factors held constant, reducing the tree population below a threshold reduced the proportion of cells experiencing beetle population epidemics. These results are consistent with field observations of reduced tree losses to beetle epidemics in thinned forest stands. The long-term simulations used in this study provide novel insights not captured by single-epidemic simulations, such as the fact that it was very difficult to maintain endemic populations for long periods, and that epidemics tended to be more erratic at higher tree densities.

1. Introduction

Native bark beetles with eruptive population dynamics, alternating between low-density endemic populations and large, high-density epidemic populations, are among the major disturbance types in temperate conifer forests (Bebi et al., 2003; Raffa et al., 2008; Veblen et al., 1994). Although population eruptions of these native insects may be viewed as part of the natural disturbance regime of forests, large scale epidemics generate intense public concern because of the potential for lost timber revenue (Dhar et al., 2016), impaired aesthetic and recreational value (Rosenberger et al., 2013), increased atmospheric carbon (Kurz et al., 2008; Logan and Powell, 2001), declining water quality (Mikkelson et al., 2013), and a perceived risk of large forest fires (Hart et al., 2015). In addition, higher than average winter temperatures in recent decades have increased overwinter survival, leading to unprecedented outbreaks of several *Dendroctonus* species, exacerbating concerns regarding the impacts of native insect disturbances. For example, synchronized population eruptions of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hereafter MPB) in western North America have killed millions of hectares of several species of pine trees in the United States and Canada since the most recent outbreaks began around in the mid-1990s (Raffa et al., 2008; Safranyik and Wilson, 2006).

Population eruptions that involve the transition from endemic to epidemic states often follow other disturbances, such as drought, fire, or storms, which can weaken trees and enhance the beetles' ability to attack host trees (Elkin and Reid, 2004; Marini et al., 2013; Raffa et al., 2008). In northern European forests, for example, after severe windstorms that cause large-scale tree death from windthrow, Norway Spruce bark beetle (*Ips typographicus*) populations take advantage of felled trees and transition into epidemics, resulting in the mortality of standing healthy trees (Wermelinger, 2004). In North American forests, epidemic outbreaks of bark beetles with similar cyclical population dynamics in the genera *Ips* and *Dendroctonus* can be facilitated by previous disturbances such as drought and fire (Perrakis et al., 2011; Raffa et al., 2008). Recent large epidemics in western North America

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may also be related to climate trends such as warmer winters (Chapman et al., 2012).

The timing of MPB lifecycle events is heavily influenced by climatic factors, principally temperature (Bentz et al., 1991). In much of the MPB species range, low winter temperatures are the most prominent constraint on MPB survival. In some areas of the MPB range, minimum winter temperatures below −40°C and unseasonably cold temperatures during critical periods in the fall and spring cause widespread MPB mortality (Bentz et al., 1991; Safranyik and Carroll, 2006; Safranyik et al., 1978). Unusually mild winters can result in greater survival and larger populations of emerging beetles. Since the success of a MPB mass attack of a vigorous tree depends on the confluence of large numbers of beetles in a small area, beetle overwinter survival rates are critical to the transition of endemic populations to epidemics.

At low population levels, MPBs show preference for vigor-impaired trees that do not have the resources to fend off attacking beetles. When enough impaired trees are present, beetles can reproduce and increase their population sufficiently so that they are able to employ successful mass attacks on larger, more vigorous trees. These trees provide them with higher quality food and overwinter shelter, and hence help to further increase population numbers. Thinning forests at opportune times can halt the increase in beetle numbers by removing highly susceptible, vigor-impaired trees (Gillette et al., 2014). Studies also suggest that thinning interferes with the pheromone communication system used by MPBs. As beetles send chemical pheromones to one another in order to attract additional beetles to a tree already under attack, thinning may enhance wind flow through a stand, thereby disrupting the effectiveness of pheromones as a form of communication (Bartos and Amman, 1989; Logan et al. 1998).

Temperature mediated changes to MPB population are beyond the direct control of land managers. The primary tool available for the management of MPBs is thinning, i.e. reducing the number of trees per hectare. It is an indirect method that can increase the resistance of a tree, as well as a stand, to attack (Mitchell et al. 1983; Waring and Pitman, 1985).

Numerous disturbances affecting the transition between endemic and epidemic states in MPB populations, including temperature increase and drought resulting from climate change, attack from other beetles, and wildfire, have been studied via field observations, lab experiments, and modeling (Bentz and Jönsson, 2015; Bone and Altaweel, 2014; Perez and Dragicevic, 2012; Powell and Raffa, 2011; Trappe et al., 2009). While such studies provide insight into the drivers of MPB outbreaks, the majority of studies focus efforts on beetles in the epidemic state, and those that examine state transitions have only focused on the transition from endemic to epidemic populations. Although Louis et al (Louis et al. 2016) emphasize that understanding the dynamics of endemic populations that exist between outbreaks is equally important for understanding the entire system, few papers have examined the long-term cyclical nature of MPB.

The goal of this study is to characterize how stand-level tree and beetle population dynamics potentially respond to changes in forest conditions, some of which can be influenced by management practices, others of which are climatically controlled. Specifically, we investigate how the interactions among the number of surviving beetle offspring produced in vigor-impaired trees, the maximum number of host trees per hectare, and the ratio of vigorous to vigor-impaired trees, could affect the overall beetle and tree demographic patterns within a forest stand. We build upon previous MPB simulation work, which has mostly focused on single eruptions, by investigating temporal patterns of eruption dynamics over long time intervals. To accomplish this goal, we developed an agent-based model (ABM) of coupled MPB and host pine population to investigate regions of parameter space in which global model behaviors, such as regular or irregular beetle population eruption cycles, emerge from the interactions between MPBs and host trees.

2. Methods

2.1. The model

The following is a brief description of the components of the ABM developed for this study, which focuses the submodels that are most relevant to the objectives. For complete descriptions of all submodels and parameters, see the supplemental model description following the format of the Overview, Design concepts, and Details protocol (ODD) as specified in (Grimm et al., 2010), and the supplemental list of model parameters. The model was implemented in Java (version 1.8) using Repast Simphony libraries (North et al., 2013) that were used to stage individual simulation runs on a computing cluster. All analyses and graphics were created using R (R Core Team, 2016). The equations needed for all of the model algorithms and calculations are included in the supplemental ODD protocol.

The model consists of a grid of cells, each of which represents a 1-hectare square forest patch with coupled populations of pine trees and MPBs. The counts of beetles and host pines in each cell are state variables that change in response to model processes. Tree populations are immobile and do not interact directly with neighboring cells. Beetles, on the other hand, disperse to neighboring cells, thus mediating all among-cell interactions.

The beetle populations exist in two phases: (1) a mobile emerging/dispersing phase and (2) a stationary attacking/reproducing phase. In the first phase beetles that survived the winter emerge from their host trees and disperse in search of new hosts. In the second phase beetles attack potential hosts in the cells to which they dispersed and produce offspring that will emerge at the beginning of the following season (Fig. 1).

Tree populations are subdivided into mature and immature trees, and a mature tree is then classified as vigorous (VT) or vigor-impaired (IT). Each year of the simulation, the cells' counts of VTs and ITs may be reduced by attacking beetles, reduced by age-related mortality, or increased by immature trees transitioning to a mature state. Beetles do not interact with the immature trees.

When mature trees are killed, they are replaced by a group of immature trees in a growth queue. Each group of immature trees spends 80 years in the queue after which they mature and are added to their cell's counts of VTs and ITs mature trees (ODD Fig. 1). The sum of all mature and immature tree on a cell is a constant set by a model parameter, which was varied between 200 and 2000 trees per hectare as described in the parameter sweep description below.

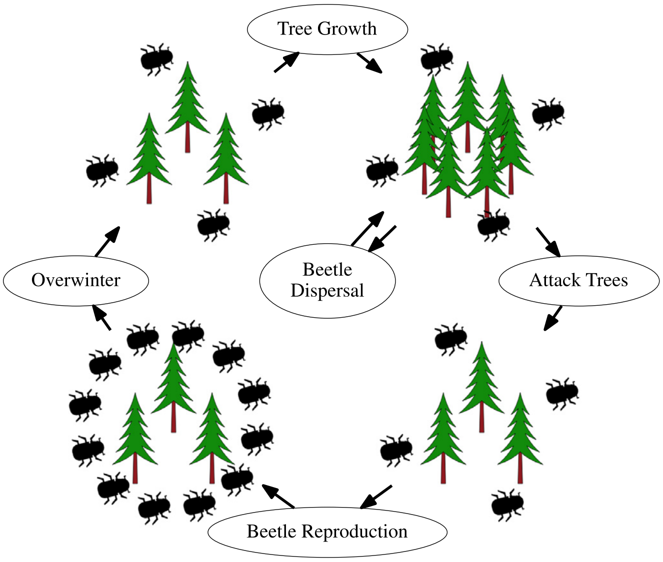

Fig. 1. Conceptual diagram of major components of the beetle/host system.