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Original Research Article

Epidemiological landscape models reproduce cyclic insect outbreaks

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ABSTRACT

Forest insect outbreaks can have large impacts on ecosystems and understanding the underlying ecological processes is critical for their management. Current process-based modeling approaches of insect outbreaks are often based on population processes operating at small spatial scales (i.e. within individual forest stands). As such, they are difficult to parameterize and offer limited applicability when modeling and predicting outbreaks at the landscape level where management actions take place. In this paper, we propose a new process-based landscape model of forest insect outbreaks that is based on stand defoliation, the Forest-Infected-Recovering-Forest (FIRF) model. We explore both spatially-implicit (mean field equations with global dispersal) and spatially-explicit (cellular automata with limited dispersal between neighboring stands) versions of this model to assess the role of dispersal in the landscape dynamics of outbreaks. We show that density-dependent dispersal is necessary to generate cyclic outbreaks in the spatially-implicit version of the model. The spatially-explicit FIRF model with local and stochastic dispersal displays cyclic outbreaks at the landscape scale and patchy outbreaks in space, even without density-dependence. Our simple, process-based FIRF model reproduces large scale outbreaks and can provide an innovative approach to model and manage forest pests at the landscape scale.

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1. Introduction

Many species undergo massive outbreaks, fluctuations in population densities that occur synchronously in multiple locations, sometimes with surprising regularity in time (Elton, 1924; Liebhold et al., 2004). Forest insects in particular have large recurrent population oscillations, such as spruce budworm, larch budmoth, gypsy moth, autumnal/winter moth (Bjørnstad et al., 2002; Ims et al., 2004; Johnson et al., 2006; Williams and Liebhold, 2000; Tenow et al., 2012). Landscape-wide outbreaks of forest insects produce large-scale defoliation and mortality of host tree species, some extending over millions of hectares. Insect outbreaks modify forest succession and composition, alter nutrient cycling, with profound consequences on ecosystem functions and services (Boyd et al., 2013; McCullough et al., 1998). These damages have led forest managers in affected territories to seek effective intervention strategies that dampen their negative consequences and impede their propagation over large expanses.

Numerous hypotheses to explain outbreaks of forest insects have been explored and/or implemented in what can be broadly divided into statistical and process-based models (Cuddington et al., 2013). Statistical (phenomenological, static, empirical) models describe and reproduce outbreaks from the characteristics of their distribution (e.g. outbreak location and duration, James et al., 2010). Because these models are derived from data sampled during past conditions, they may have limited ability to forecast the occurrence of outbreaks in changing management and weather conditions (Gustafson, 2013). On the other hand, process-based models (dynamic, mechanistic) are developed from ecological hypotheses about the plant-insect dynamics (Bjørnstad and Grenfell, 2001). Because they are based on ecological processes, these models are thought to be able to predict beyond sampled data (Cooke et al., 2007; Evans et al., 2012).

Most process-based models of insect outbreaks generally represent dynamics of population densities. The design, parameterization and validation of process-based models with local population-level dynamics presents two major difficulties: (1) it requires comprehensive knowledge of the many processes operating at the local population level, and (2) it requires estimates

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of insect densities. However, these requirements are difficult to meet because relationships between stand-scale processes and insect population dynamics are mostly studied in single locations (e.g. Royama, 1984). Moreover, if a phenomena is studied at the wrong scale, the resulting conclusions may be weak or unreliable (Meentemeyer et al., 2012; Peters et al., 2004). To circumvent this lack of data and avoid scale-mismatch, we investigate a landscape-scale model that is independent of small-scale within-stand population processes. The model represents forest stands with three possible states: *F*, a forest stand at endemic insect densities, *I*, an infested/infected stand at epidemic insect densities, and *R*, a recovering stand in which forest regenerates following defoliation. The model exploits the fact that stand densities of forest insects show extreme fluctuations between endemic and epidemic periods, corresponding to the forest or infected states (Royama, 1984) respectively. We refer to this model as a FIRF landscape model and explore its capacity to reproduce the macroscopic properties of insect outbreaks.

The FIRF dynamic model of forest insect outbreaks follows the frameworks of metapopulation and epidemiological models. In metapopulation models, local populations can be present or absent, and regional persistence depends on dispersal (Levins, 1969; Hanski, 1998). This wide class of models are also called disturbance-recovery, state-transition, occupancy and patch-dynamic models and have been applied to various ecological situations, such as fires (Malamud et al., 1998; Staver and Levin, 2012; Keane et al., 2015), mussel bed colonization (Guichard et al., 2003) and semi-arid vegetation (Kéfi et al., 2007). Similarly, epidemiological models consider hosts (analogous to local populations in the metapopulation models) as infected or not, and do not track the density of infectious agents within each host. Epidemiology provides a tractable theory to understand epidemics and applies vaccines against human, animal and plant diseases (Kermack and McKendrick, 1927; Riley, 2007; Keeling and Rohani, 2008). Epidemiological models in which one patch represents one host have been used to represent the dynamics of theoretical (Rhodes et al., 1998; Fuentes et al., 1999; Filipe and Maule, 2004; Neri et al., 2011) and real epidemics (Kleczkowski et al., 1997; Eisinger and Thulke, 2008; Neri et al., 2011; Filipe et al., 2012). Metapopulation and epidemiological models are related because both deal with the absence or presence of a species in multiple locations, not local densities (Earn et al., 1998; Grenfell and Harwood, 1997; Rhodes et al., 1998). However, to our knowledge, epidemiological and metapopulation landscape models have rarely been applied to study cyclic forest insect landscape epidemics (Keane et al., 2015).

The goal of this paper is to build a simple, macroscopic and process-based epidemiological model to explore the consequences of dispersal on insect outbreaks. Metapopulation and epidemiological models easily map onto the landscape dynamics of forest insects and present certain advantages over population models. Focusing on forests instead of insects matches the type of large-scale data surveyed regarding the effects of outbreaks (tree defoliation), not the density of insects (Gray, 2008; Bouchard and Auger, 2014). Simplifying the model by using a lower modeling resolution is computationally efficient and requires fewer parameters. Just like epidemiological models do not model virus densities within infected individuals, modeling the number of insects is too fine-scale to be informative at a landscape-level. The desired output for forest management is the proportion of forest stands that are affected, and for that reason we model forests instead of insects. Using metapopulation and epidemiology theory would allow forest managers to use insights from those fields, for example that the strength and type of disease transmission are essential determinants of distribution and epidemics (Hanski, 1998; Riley, 2007; Keeling et al., 2003).

We study two versions of our model: a spatially-explicit version in which insects disperse among forest stands arranged on a grid, and a spatially-implicit version with global dispersal (between all forest stands regardless of location). We define outbreaks as sudden peaks in the proportion of infected stands at the regional scale. Comparing both versions reveals how limited dispersal distance of insects contributes to outbreak dynamics at the landscape scale. Our goal is to understand the conditions at which outbreaks occur, and to characterize the spatiotemporal signature of outbreaks emerging from between-stand insect dispersal. We first describe the rationale of the modeling approach, here inspired by the ecological dynamics of the spruce budworm, a major defoliator of North American forests. We then provide a detailed description of the spatially-implicit and spatially-explicit stochastic dispersal versions of the model. We explore the structural and parameter sensitivity of the model to understand the conditions required for outbreaks to occur. We specifically answer three questions; (1) Which dispersal parameters are required to produce outbreaks? (2) Which dispersal parameters determine cyclic outbreaks? (3) Which dispersal parameters determine the spatial distribution of outbreaks?

2. Methods

We develop a general model of defoliating insect dynamics at the landscape scale, whose implementation is largely inspired by the extensive literature on the spruce budworm *Choristoneura fumiferana*. Spruce budworm outbreaks have occurred with intervals of around 30 years during the last 500 years (Morin et al., 2007; Boulanger et al., 2012), and have profoundly structured the dynamics of North American forests (Fleming, 2000). Budworm outbreaks damage around 15% of the surface of Canadian forests during each outbreak (NFS, 2013), representing large revenue losses. We first provide a general overview of the model to lay out the underlying ecology, and then detail more specific information about its implementation.

2.1. FIRF model overview

The modeling unit is a forest stand and each stand can be in one of three possible states: *F* forest, *I* infected defoliated forest, and *R* recovering forest (Fig. 1). These stands are represented on a continuous lattice where each cell corresponds to a stand. We adapt the epidemiological Susceptible-Infected-Recovering-Susceptible model (SIRS, Hethcote, 1976; Anderson and May, 1979) to insect outbreaks that have a dispersing pest affecting a stationary regenerating resource. Note that in our model each stand can only take one value, in contrast to population-based lattice models that simulate the density of trees in different states in each stand. The *F*

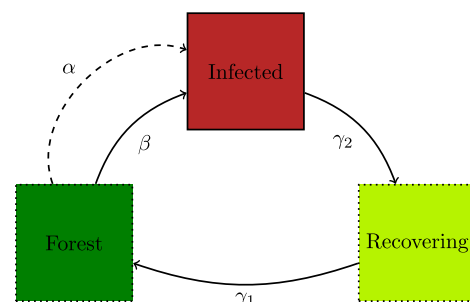


Fig. 1. Schema of the transitions between the three different states of the Forest-Infected-Recovering-Forest model of forest insect outbreaks. β is the probability of spontaneous infections, α is the probability of infection spread, γ_2 is the probability of infection dieback, γ_1 is the probability of forest recovery to mature, susceptible forest (also see Table S1).

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