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Stochastic spread models: A comparison between an individual-based and a lattice-based model for assessing the expansion of invasive termites over a landscape

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ABSTRACT

Spatially-explicit simulation models can help state and local regulatory agencies to predict both the rate and direction of the spread of an invasive species from a set of surveyed locations. Such models can be used to develop successful early detection, quarantine, or eradication plans based on the predicted areas of infestation. Individual-based models (IBMs) are often used to replicate the dynamics of complex systems and are both able to incorporate individual differences and local interactions among organisms, as well as spatial details. In this work, we introduce a new stochastic lattice-based model for simulating the spread of invasive termites over a landscape and compare it to a recently published stochastic individual-based approach, based on the same ecological parameters, with the goal of improving its computational efficiency. The two modeling frameworks were tested over a homogeneous landscape with randomly located sources of infestation. Further, the setting of a case-study of an invasive termite, *Nasutitermes corniger* (Motschulsky), was used to simulate the spread of the species in Dania Beach, Florida, U.S.A., and the results of the proposed model were compared with an earlier application of the IBM over the same area. The results show that the extent of the infested areas predicted by the new lattice-based model is similar, thus comparable, to the individual-based model while improving the computation time significantly. The simulation presented in this work could be used by the regulatory authorities to draw one or more areas of intervention instead of wasting resources by randomly surveying unknown perimeters.

1. Introduction

Termites are serious pests of the urban environment and are responsible for severe damage to structural lumber (Rust and Su, 2012). It has been estimated that every year, in the continental United States alone, termites cause property damage up to billions of dollars (Edwards and Mill, 1986). Although human-assisted (also called anthropogenic) dispersal can play a significant role in the rate of expansion of an established exotic species, its nature is complex and unpredictable. Termites are not "hitchhiking" insect pests, i.e. they cannot easily be transported aboard commercial vehicles such as cars or boats. More specifically, the nesting core of a termite colony must be moved intact and both a water and food source must be available to the core throughout the movement (Hochmair and Scheffrahn, 2010). The natural spread of termites is expected to proceed fairly slowly for two main reasons: (i) they are weak fliers and their reproductives (winged individuals) can fly only a few hundred meters from the parent colony on average each year (Nutting, 1969); and (ii) a termite colony takes at least 4 years to mature and release the first reproductives from the nest (Evans, 2011). Given the unpredictability of human-assisted movements, it will be more useful here to restrict our study on termite dispersal by natural means and attempt to anticipate the rate and direction of termite spread.

The recent integration of Geographical Information Systems (GIS) with simulation models, coupled with advances in computing power, has allowed the development of spatially-explicit and dynamic simulation models, such as individual-based models (IBMs, hereafter), and lattice-based models, such as cellular automata (CA, hereafter) (Brown et al., 2005). Both types of models have been introduced in ecological modeling to capture the inherent complexity of various real-world problems (Steyaert, 1993) as alternative approaches to solving mathematical sets of equations such as partial differential equations (PDEs) (Alexanderian et al., 2011; Holmes et al., 1994). Moreover, the intricacy of a physical environment limits the applicability of mathematical models for modeling realistic dispersal of invasive species (Pitt, 2008). GIS allows for spatial complexity and simulation modeling takes GIS visualizations into the domain of temporal dynamics. Early examples of GIS-based simulation models include land-use change based on the Markov process (Burnham, 1973), and discrete state models of

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flow and transport (e.g. transport of pollutants) (Maidment, 1996). Other more recent computer-intensive approaches have been able to incorporate ecological information at a population level with landscape complexity (Wiegand et al., 2004).

While IBMs incorporate rules to describe the interactions between individual units, such as organisms, in which each individual can have a different set of behavioral, physiological, and other properties (Huston et al., 1988), in CA modeling the basic units of the simulation are discrete spatial cells, which can transition among different states (e.g. empty, infested, quantified occupation). CAs are the most basic form of lattice-based model and are able to model complex dynamics from biological, social, or physical processes by using simple rules (Toffoli and Margolus, 1987). Several improvements have been made to basic CAs in the past decade to include underlying landscape differences, more complex rules for changes of state, and stochastic parameters. Some examples of lattice-based models include wildfire spread models (Clarke et al., 1994), spread models of invasive ants (Pitt, 2009), spatial dynamics of urban and regional systems (Clarke and Gaydos, 1998), and epidemic propagation (Mikler et al., 2005; Morley and Chang, 2004). In the past years, different computer simulation approaches have been either compared (Ajelli et al., 2010; Lett et al., 1999) or integrated (Sudshira, 2010).

In this work, we develop a new stochastic lattice-based model in order to simulate the spatiotemporal spread of invasive termites. The model developed herein includes a set of relevant ecological parameters that can be modified according to the species of interest. Our model differs from more traditional CA approaches in that it is not based on rules for state transition depending on the state of the focal cell as well as the states of a defined set of neighboring cells. A recently published stochastic IBM for the spread of invasive termites (Tonini et al., 2013) was used as a benchmark for comparison with the new model in terms of predictions, computational runtime, and code efficiency. The main purpose of the new model is to improve computational speed over the IBM model, which is costly in terms of computational time. We believe that the model proposed herein represents a substantial improvement to the IBM and could give the regulatory agencies a better tool for targeting specific areas for survey, eradication, or quarantine effort.

The format of the paper is as follows. The new model, its framework and main parameters are described in Section 2. Results are presented in Section 3, while their interpretation is discussed in Section 4. Finally, conclusions on the advantages and limitations of the models tested herein are provided in Section 5.

2. Materials and methods

A side-by-side comparison between the proposed lattice-based model and the IBM by Tonini et al. (2013) was done by establishing a common ground in order to discount the unwanted effects due to their different frameworks. Both models were used in two different settings: (i) a homogeneous landscape, where different sets of N termite colonies were randomly located and considered as sources of invasion, and (ii) a case-study of an invasive termite, Nasutitermes corniger (Motschulsky), in Dania Beach, Florida, U.S.A. (Scheffrahn et al., 2002). The average area occupied at each time step was computed over all model replications (Monte Carlo estimation) and its value compared between the two modeling approaches. Moreover, the computational time was considered to assess the speed of the proposed model against the established IBM.

2.1. Model design

The lattice-based model proposed herein is spatially-explicit and stochastic with the purpose of simulating the spatiotemporal spread of a termite invasion by natural means over a realistic landscape (e.g. urban environment), starting from a set of initially surveyed colonies. The basic units of the model are the cells of a grid with a pre-defined spatial resolution. Each cell may assume one or more states expressed by the number of termite colonies contained in it. The temporal scale chosen for the simulations was discrete with one time step representing a year. In order to keep the model comparable to the IBM by Tonini et al. (2013), the resolution of the spatial grid was set to 100 × 100 m (= 1 ha).

The main ecological parameters, shown in Table 1, were kept identical to the IBM. A general description of each one of them follows here.

2.1.1. Colony age at first production of reproductives

The age at which a termite colony starts generating the first crop of winged reproductives (AFP, hereafter) contributes to the rate of spread of an invasion. The earlier the first reproductives are generated, the faster the invasion will proceed.

2.1.2. Pheromone attraction distance

Termite reproductives find potential mates of the opposite sex by sensing and responding to pheromones after concluding the dispersal flight (Bordereau and Pasteels, 2011). A new colony begins with a male–female (i.e. king and queen) couple of unwinged reproductives starting the nest in a proper substrate, such as soil or wood. The maximum pheromone attraction distance (PHR, hereafter) affects the chance that two heterosexual individuals find each other after the dispersal flight (see Fig. 1). The smaller this maximum distance is set, the smaller the number of new termite colonies will be.

2.1.3. Colony density

The maximum density of termite colonies over an area (DEN, hereafter) avoids overpopulation of grid cells in the simulation model. The higher this parameter is, the higher the chance for a nearby cell to become infested.

2.1.4. Survival rate

The overall survival rate of reproductives (SURV, hereafter) in a termite colony determines the number of reproductives that survive a dispersal flight and can thus potentially mate. Survival is expressed as an overall rate that considers both predation and injuries that typically occur as the reproductives start leaving the nest (i.e., preflight), volent predators in flight (capture by bats and birds), and nonvolent predators (e.g. ants and herps) as soon as they alight on the ground or on a tree (i.e., postflight) to search for a mate.

2.1.5. Male prevalence

The prevalence of male reproductives in a colony (MAR, hereafter) describes the percentage of males among the reproductives and affects the chance that a heterosexual pair unites within the pheromone attraction distance after the dispersal flight. That is, the chance decreases the further the value deviates from 50% of the males.

2.1.6. Amount of reproductives generated by a colony

The number of reproductives generated by a colony (SCR, hereafter) after reaching maturity (determined by the aforementioned AFP parameter) increases with age. Different scenarios representing the total number of reproductives by colony age can be chosen. A higher number of reproductives increases the chance of new colonies being formed.

2.1.7. Dispersal distance

The mean dispersal flight distance (DIST, hereafter) determines how far the termite reproductives are able to fly, on average, on their own. The higher this parameter value, the faster the termite spatial expansion will proceed.

The age of each colony is tracked along with the number of colonies within each grid cell. Depending on the number of colonies, their age, and the SURV parameter, each cell can be expressed as the total number of reproductives available to either stay within it or fly toward neighboring cells. The main process involved in the spread of termite colonies