Contents lists available at ScienceDirect

Ecological Modelling

Network spread of invasive species and infectious diseases

Christopher Strickland [a,*], Gerhard Dangelmayr [a], Patrick D. Shipman [a], Sunil Kumar [b], Thomas J. Stohlgren [b]

[a] Department of Mathematics, Colorado State University, Fort Collins, CO 80523-1874, United States
[b] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499, United States

ARTICLE INFO

ABSTRACT

Landscape heterogeneity, non-local spreading mechanisms, and long-distance transportation connections can affect the spread of an invasive species or infectious disease. In this paper, we introduce a mathematical model that combines a vector-based transportation network with models for continuous invasive spread. Given a strongly connected, directed graph of transportation rates, we assume that carriers can transport a biological invader to distant sites. Following a possible latent stage, the invader then possibly establishes in the new location and spreads outwards in the continuous domain. Numerical results are shown for the invasion of *Bromus tectorum* in Rocky Mountain National Park based on the presence probability model of Strickland et al. (2013) and compare favorably with data. Analysis of the network component of the model reveals a unique, stable steady-state solution of the infected vectors.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

The invasion of non-native plants, animals and pathogens has escalated dramatically over the last few decades with the increase of trade, transportation and other elements of globalization (Mack et al., 2000; Evangelista and Kumar, 2011; Stohlgren et al., 2013). Invasive species pose threats to global ecosystems, and they are a major environmental threat of the 21st Century (Mack et al., 2000; Stohlgren and Schnase, 2006). Impacts include loss of native species and habitat, economic suppression, reduced food and water security, and direct threats to human health. For example, the impact of emerald ash borer (*Agrilus planipennis*) on community residents in Ohio is estimated to be between 1.8 and 7.6 billion for tree loss, removal and replacement (Sydnor et al., 2007); the real estate value

of Montana's ranches has been reduced by 40% due to invasive spotted knapweed (*Centaurea maculosa*; Sheley et al. (1998)); the glassy winged sharpshooter (*Homalodisca vitripennis*, an invasive insect which carries a deadly plant bacterium to California grape, raisin, and wine industries and related tourism) is estimated to have an annual cost of approximately $35 billion (United States Department of Agriculture (USDA), 2010). Overall economic costs associated with invasive species in the United States are estimated to exceed $120 billion per year in terms of control costs, lost productivity, reduced water salvage, and reductions in rangeland quality and property values (Pimentel et al., 2000, 2005). The global economic costs of invasive species are estimated at $1.4 trillion annually, representing five percent of the global economy (Keller et al., 2007; Yemshanov et al., 2009). The economic costs of delaying active control and management efforts would be much greater and probably immeasurable (Eiswerth et al., 2008).

Since control costs rise exponentially with population size, early detection and ecological forecasting of invasive species are urgently needed for rapid response and remain a high priority for resource managers (Crowl et al., 2008). Ecological forecasting requires innovative and flexible mathematical models to map and predict harmful invasive plants, animals, and diseases in time and space (Stohlgren and Schnase, 2006). Consider the difficulty of

---

* Corresponding author. Current address: Statistical and Applied Mathematical Sciences Institute, 19 T.W. Alexander Drive, Research Triangle Park, NC 27709-4006, United States. Tel.: +1 919 685 9350x9308; fax: +1 919 685 9360.
 E-mail addresses: cstrickland@samsi.info (C. Strickland), gerhard@math.colostate.edu (G. Dangelmayr), shipman@math.colostate.edu (P.D. Shipman), Sunil.Kumar@colostate.edu (S. Kumar), Thomas.Stohlgren@colostate.edu (T.J. Stohlgren).

mapping an invasive species in a non-random environment varying in slope, aspect, elevation, vegetation type, and soil type. Now consider varying rates of spread dependent on optimal versus suboptimal conditions for reproduction and spread. How rapidly, and how far might the species spread in the short- or long-term? What might be the effects of nonlocal spread through a transportation network?

Ecological niche models (also called species distribution models, environmental matching models, and habitat suitability models) are increasingly being used to model and map invasive species distribution potential. Combining statistical algorithms with geographic information systems (GIS), ecological niche models attempt to predict probability of occurrence of a species by using presence-only or presence-absence data in combination with environmental variables to predict the species potential or actual distribution across a landscape (Franklin, 2009; Peterson et al., 2011). These models are based on Hutchinson's classical niche concept: the distributions of species are constrained by biotic interactions (e.g., competition and predation) and abiotic gradients (e.g., elevation, temperature and precipitation) (Hutchinson, 1957).

The spread of species (including invasive species) has been the subject of numerous mathematical models (Higgins and Richardson, 1996, 1999; Higgins et al., 2003; Hastings et al., 2005; Gallien et al., 2010). Many of these models are based on a reaction–diffusion equation with Fickian diffusion and logistic growth (Skellam, 1951; Okubo and Levin, 2001; Maruvka and Shnerb, 2006). Models based on contact-birth processes as introduced by Mollison (1977) represent another approach, in which individuals have fixed spatial locations and the permanent location of each newly born individual is determined by a probability distribution. This approach is better suited to herbaceous invasive plant species that have permanent locations and therefore do not follow Fickian diffusion. In Strickland et al. (2013), we introduced a model, following Mollison's approach (Mollison, 1977), for the time-evolution of the occurrence probability of an invasive plant species. Since the quantity of interest is occurrence probability, not actual population size, data from ecological niche models could be used to determine initial conditions and spatially heterogeneous parameters. Other models combining suitability data with spread are models for the spread of invasive Argentinian ants (Roura-Pascual et al., 2009), and for the spread of invasive plants utilizing a cellular automaton model (Smolik et al., 2010).

Integro-differential equation models that incorporate information about dispersal distribution of plant seeds (Cain et al., 2000) can predict the propagation speed of an invasion front into a landscape (Kot et al., 1996; Strickland et al., 2013). All of these models, however, assume a continuous spatial domain and neglect the role of transportation networks in the spread of invasive species or diseases. Seed dispersal through transportation vectors such as humans (Benninger-Truax et al., 1992), birds (Carlo et al., 2013), or animals (Guiden, 2013) can significantly influence the spread of a species (Harsch et al., 2014), and long-distance jump dispersals have been documented in species such as ants as well (Suarez et al., 2001). Lookingbill et al. (2010) introduced a computational network model to study species spread through fragmented habitats. This approach is based on simulating the random walk of individuals through a landscape graph consisting of nodes representing habitat patches and connections (edges) between nodes. By observing the effect of removing edges, these authors identify bottlenecks in species dispersal. Ferrari et al. (2014) introduced a cellular automaton model for invasive species spread through a landscape graph, allowing the connections between nodes in the network to evolve over time. Simulations of this model point to prominent pathways of spread across a landscape.

In the context of epidemiology, multiple software packages exist to model long range network interactions between geographically distributed metapopulations. For example, GLEAMviz (Balcan et al., 2010) simulates infectious disease spread on a global scale, utilizing detailed airline data and information about local commuter patterns to connect separate metapopulations based on airport locations. The GLEAMviz environment allows the user to specify the exact infection model to be used, as well as transportation rules for each infected compartment (e.g., certain infected, symptomatic classes may not be allowed to travel outside their current occurrence). The Spatial and Temporal Epidemiological Modeling (STEM) (Ford et al., 2006) system is a similar software model, with a greater focus on being open source and modular in its approach. While the large spatial scale of these models makes a metapopulation approach ideal for modeling global or country-wide disease epidemics, it is not particularly adaptable to ecological invasions which are better approximated by a continuous, reaction-diffusion type paradigm on the local level.

The purpose of this paper is to develop a general dynamical systems model for the spread of invasive species or infectious diseases in a discrete (graph-based) network. We describe situations in which both transportation networks and an underlying continuous spread are at play, we then couple the graph-based model to a general model for continuous spread such as the Fisher-KPP equation or a model derived from a contact-birth process.

This paper is organized as follows: In Section 2, we introduce a graph-based population model in which individuals can become infected at nodes. The population of the graph is conserved, but every node acts like both a source and sink for individuals to leave and re-enter the graph uninfected. We then conduct analysis on this network model and show how it can be coupled to a spatially continuous infection model to obtain a more complete model of epidemic spread. In Section 3, we extend this model to the case of a herbaceous invader and show numerical results for cheatgrass (*Bromus tectorum*) spread in Rocky Mountain National Park. We conclude with a discussion of our results in Section 4.

2. Infectious disease epidemic model

2.1. Linear graph model

To begin modeling long-distance spread, we will first consider the general case of an epidemic with intermediary carrier vectors. These carrier vectors will not be infectious amongst themselves and remain on a transportation network with well defined nodes and directional rates of flow. At each node, carrier vectors can later interact with an underlying, spatially coupled model such as the one developed in Strickland et al. (2013). If the underlying model predicts invader presence at an assigned node location, network carrier vectors will become infected and possibly spread the epidemic to other nodes, which in turn infect the underlying model. The precise mechanics of this concept will be formalized in the following sections, including some immediately relevant analysis.

Consider an individual on a strongly connected,[1] directed graph, and let $X(t)$ be a stochastic variable which gives the node this individual occupies at time t. We assume that $X(t)$ satisfies the Markov property and represents a continuous-time Markov chain on the nodes of the graph. Let $g_{ij} \geq 0$ be the transition rate for the $j \to i$ node edge whenever $i \neq j$, and let

$$g_{jj} = -\sum_{i \neq j} g_{ij}. \tag{1}$$

---

[1] For every node, there exists a path through the graph to every other node. This is typical for transportation networks.