



Short communication

Requirements, design and implementation of a general model of biological invasion

David Savage^{a,b}, Michael Renton^{a,b,c,*}^a School of Plant Biology, University of Western Australia, 35 Stirling Hwy, Crawley, WA 6009, Australia^b Cooperative Research Centre for National Plant Biosecurity, Level 2, Building 22, Innovation Centre, University Drive, University of Canberra, Bruce, ACT 2617, Australia^c CSIRO Sustainable Ecosystems, Floreat, WA 6014, Australia

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ABSTRACT

The speed at which a response to a novel biological invasion can be developed and implemented plays a crucial role in the ability of biosecurity practitioners to successfully contain or eradicate the invading organism. In developing a response to a novel invasion, computational models of biological spread can play a key role, allowing practitioners to rapidly evaluate a range of invasion scenarios and the likely distribution of the invading population over time. This in turn can allow practitioners to compare different response plans and select those that will be most cost-effective and most likely to succeed. Unfortunately, the development of models that are capable of providing a realistic description of invasive spread is a costly and time consuming exercise and developing models specifically tailored to each of the vast array of potentially invasive organisms is infeasible. Therefore, we have developed a general model of biological invasion (GMBI) that is capable of simulating the invasive spread of a diverse range of organisms across heterogeneous landscapes, and can be used to represent particular invasion scenarios. The GMBI includes a small, highly biologically meaningful parameter set that can be relatively easily estimated using expert knowledge, and can therefore be quickly setup to simulate the spread of organisms which have not previously been well characterised. In this paper we discuss the desirability of a GMBI and elucidate the characteristics that are required. We then describe the formulation of a model that meets these requirements and demonstrate how it meets these requirements by parameterising the model to simulate the spread of two very different types of invasive organisms, namely a fungal pathogen and a pest beetle. These simulations demonstrate the flexibility of our GMBI, and the ease with which the model can be parameterised using parameter values found in the literature or obtained through expert elicitation.

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1. Introduction

Biological invasions can be extremely costly, and may have significant impacts on both natural and agricultural ecosystems (Beale et al., 2008; Nairn et al., 1996; Perrings et al., 2005). In developing a response to biological invasions, simulation models can allow biosecurity practitioners to use available information to estimate the current distribution of an invading organism, to predict its future distribution and to assess any environmental or economic impacts that may follow. Simulation models can also allow practitioners to quickly evaluate the feasibility and effectiveness of particular strategies for eradication, control or management (Hastings et al., 2005; Kot et al., 1996). Unfortunately, the

development of detailed predictive models is a costly undertaking and, as a result, model development tends to focus on those organisms that pose the greatest risk (e.g. BenDor et al., 2006; Isard et al., 2007; Pitt et al., 2011). For biosecurity practitioners, this means that there is a relatively small library of detailed, specific models that they can draw on for information regarding the more infamous invasive organisms, but a much larger number of organisms for which no reliable models exist. Therefore, to complement this library of models a single, more general model of invasive spread would be beneficial. A general model of biological invasion (GMBI) could be used by biosecurity practitioners to simulate a far wider range of organisms that could potentially have significant impacts on agriculture or native ecosystems, but do not warrant the substantial investment required to build more detailed, specific models.

For a GMBI to be useful, it needs to strike a balance between the use of high level abstraction, which enables the required generality, and biological realism, which allows practitioners to parameterise

* Corresponding author at: School of Plant Biology, University of Western Australia, 35 Stirling Hwy, Crawley, WA 6009, Australia. Tel.: +61 8488 1959.

E-mail address: david.savage@mac.com (D. Savage).

the model based on their knowledge of particular invasive organisms. The level of detail included in the model should be coarse enough that the required parameter set is manageable by experts, but fine enough that the model can be used to obtain meaningful information about actual invasion events. In studying the theoretical nature of invasive spread a number of models have been presented that could be regarded as GMBIs (e.g. [Kot et al., 1996](#); [Lewis and Pacala, 2000](#); [Skellam, 1951](#)), however these models are highly abstracted and consist of parameter sets that have little biological meaning and would therefore be extremely difficult to quantify for a particular species and invasion scenario. We propose that a more useful GMBI would include enough detail to capture the unique aspects of each organism that are significant in determining its pattern of invasive spread. Therefore, a GMBI should include process representations and a parameter set comprehensive enough to simulate the essential components of invasive spread for a wide range of organisms, but remain simple enough that the model can be relatively easily parameterised using expert knowledge of the particular organism's biological characteristics, and the landscape under invasion. This will enable the model to be used to estimate the invasive spread of organisms for which extensive data is not readily available when a new invasion occurs.

This paper describes a GMBI that meets the requirements outlined above, and demonstrates its ability to simulate the invasive spread of very different organism types. We first present the modelling challenge, by discussing in greater details the requirements that guided and motivated the construction of our GMBI based on the current understanding of invasion ecology reported in the literature and the desired applicability of such a model; this can be seen as a list of requirements that a model would need to possess in order to be useful as a GMBI (Section 2). We next provide a solution to this modelling challenge by describing the design and the implementation of a model that satisfies these requirements (Section 3). We then present two case studies, where we parameterise the GMBI to simulate the invasive spread of a fungal pathogen and a beetle as examples of the model's capabilities (Section 4). These example simulations show that the presented model meets the specified requirements for a GMBI and demonstrate the model's ability to represent very different types of organisms, with differing life-cycles and modes of dispersal, simply through re-parameterisation rather than modification of the model code. These examples also show that the GMBI can be parameterised relatively easily using expert knowledge and demonstrate that the GMBI can be used to consider and contrast various scenarios for invasive spread.

2. Requirements for a general model of biological invasion

In responding to a biological incursion the speed at which strategies for eradication or control are implemented can play a critical role in their success ([Croft and Braithwaite, 2008](#)). Therefore, the main purpose of our GMBI is to allow biosecurity practitioners to rapidly simulate the spread of an invasive species, and to quickly plan an appropriate response to novel incursions based on the results of this simulation. During the early stages of an incursion, there is likely to be limited data on how the specific invasive organism behaves in its new environment. Given this need for a rapid response, field or laboratory experiments that attempt to quantify important traits will generally be unfeasible and parameter values will therefore need to be estimated using expert knowledge of the organism in question. For this reason, the GMBI should not rely on large data sets for the empirical estimation of parameters. Instead, processes should be represented in a relatively mechanistic manner, so that parameters to be estimated have a clear biological meaning that can be relatively easily interpreted by, or

communicated to, biologists with expertise in the particular organism of interest.

In developing a GMBI, we followed closely the ideas on invasion ecology set out in [Catford et al. \(2009\)](#), [Colautti et al. \(2006\)](#), [Colautti and MacIsaac \(2004\)](#) and also in [Coutts et al. \(2011\)](#). While the discussion in [Catford et al.](#) and [Coutts et al.](#) is largely concerned with invasive plants, we believe that the ideas presented have a broader applicability.

[Catford et al. \(2009\)](#) identified six stages that comprise a biological invasion; (i) transport, (ii) introduction, (iii) colonisation, (iv) naturalisation, (v) spread and (vi) impacts. An invasion begins when individuals move from a donor population to a previously unoccupied location (i). If these individuals are able to survive in their new environment (ii), they form a new colony of mature adults (iii), which is able to reproduce, resulting in the establishment of a self-sustaining population (iv). As this population grows, it begins to spread at a regional scale (v), leading to ecological, economic and cultural impacts (vi). In each of these six stages, successful progression to the next stage is determined by three driving factors; propagule pressure, which describes the intensity of introductions into a given location, and both biotic and abiotic factors, which determine the likelihood that an individual will survive.

While the six stages of an invasion identified by [Catford et al. \(2009\)](#) were originally formulated to describe invasions at a regional scale, we can also consider them to apply at a more local scale across a heterogeneous landscape. If we consider the individual patches of habitat within a larger landscape area, then each patch may at some time experience initial propagule pressure, and as a result of local biotic and abiotic factors, may become occupied by an initial colony. If this colony is able to establish itself and go on to successfully reproduce, this will result in further propagule pressure being applied to neighbouring patches, leading to further infestation and the progression of individual habitat patches through each of the six stages. In developing our GMBI, we have considered the requirements that stem from this conceptual model, and have attempted to identify the major components of the main factors that drive invasions, and select those that have the greatest influence to be included in the model.

2.1. Propagule pressure and dispersal

Propagule pressure describes the number of propagules that are introduced into a given location over a given period of time ([Catford et al., 2009](#)). Note that for the purposes of this paper, we assume that the term propagule refers to any migrating individual regardless of their age, and their current physical form. Where the spatial nature of biological invasion is considered, propagule pressure is determined by the size and distribution of the invading population, and the invading organism's reproductive rate and dispersal capabilities. Dispersal capabilities are thought to be particularly important in driving biological invasions, and have been shown to be the primary driver of spread for invading weeds ([Coutts et al., 2011](#)). Long-distance dispersal, where small numbers of individuals disperse over distances far greater than the average dispersal distance, can be critical in sparking an invasion and in allowing populations to thrive in highly fragmented, dynamic landscapes ([Bohrer et al., 2005](#); [Johst et al., 2002](#); [Travis et al., 2010](#)), and can rapidly lead to multiple loci of heavy infestation ([Diggle et al., 2002](#); [Nathan and Katul, 2005](#)).

Dispersal may be deemed active or passive depending on the organism's ability to navigate over the course of its journey ([Nathan et al., 2010](#)). Passive dispersal occurs through a wide range of vectors including wind, water, rain-splash, and being carried inside or on other organisms. Active dispersal usually depends on active movement of the dispersing organism itself, possibly in combination with some other vector. Therefore, in order to simulate the

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