Journal of Environmental Management 196 (2017) 594–606

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Review

# Dynamic models in research and management of biological invasions

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A R T I C L E I N F O

*Article history:*
Received 29 June 2016
Received in revised form
10 March 2017
Accepted 19 March 2017

*Keywords:*
Hybrid models
Management
Non-native species
Scientometrics
Spatial-temporal dynamics
Static models

A B S T R A C T

Invasive species are increasing in number, extent and impact worldwide. Effective invasion management has thus become a core socio-ecological challenge. To tackle this challenge, integrating spatial-temporal dynamics of invasion processes with modelling approaches is a promising approach. The inclusion of dynamic processes in such modelling frameworks (i.e. dynamic or hybrid models, here defined as models that integrate both dynamic and static approaches) adds an explicit temporal dimension to the study and management of invasions, enabling the prediction of invasions and optimisation of multi-scale management and governance. However, the extent to which dynamic approaches have been used for that purpose is under-investigated. Based on a literature review, we examined the extent to which dynamic modelling has been used to address invasions worldwide. We then evaluated how the use of dynamic modelling has evolved through time in the scope of invasive species management. The results suggest that modelling, in particular dynamic modelling, has been increasingly applied to biological invasions, especially to support management decisions at local scales. Also, the combination of dynamic and static modelling approaches (hybrid models with a spatially explicit output) can be especially effective, not only to support management at early invasion stages (from prevention to early detection), but also to improve the monitoring of invasion processes and impact assessment. Further development and testing of such hybrid models may well be regarded as a priority for future research aiming to improve the management of invasions across scales.



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http://dx.doi.org/10.1016/j.jenvman.2017.03.060
0301-4797/

## 1. Introduction

Invasive non-native species (hereafter "invasive species") are increasing in number and extent worldwide (Pyšek and Richardson, 2010), constituting a phenomenon that may implicate important ecological, economic and social impacts (Fei et al., 2014; Pyšek and Richardson, 2010; Simberloff et al., 2013; Tassin and Kull, 2015). Invasive species can alter the structure and functioning of ecosystems (Gaertner et al., 2014; Pyšek and Richardson, 2010), with consequences for native biodiversity and for ecosystem services (Gaertner et al., 2014; Theoharides and Dukes, 2007; Vaz et al., 2017a). The need to tackle invasions and their impacts has fostered an increasing commitment of researchers and practitioners in the management of invaded ecosystems (Estevez et al., 2015; Rotherham and Lambert, 2012). The development of predictive tools to enable knowledge-based decision-making has become fundamental for the effective management of invasive species (Ameden et al., 2009; Vicente et al., 2016, 2013). In recent years, ecological models have improved our understanding of the key drivers, processes and impacts of invasions (Neubert and Caswell, 2000; Vicente et al., 2010). These models have also allowed us to predict potential areas of invasive species distribution and to forecast possible impacts under different socio-ecological scenarios (Peterson et al., 2008; Vicente et al., 2016).

More broadly, ecological modelling has promoted advances in many socio-environmental issues, such as eutrophication and its mitigation (e.g. Alvera-Azcárate et al., 2003), climate change impacts (e.g. Vicente et al., 2013), pollution effects (e.g. Hinojosa et al., 2008), land management (e.g. Miller and Urban, 2000), or ecological monitoring (e.g. Amorim et al., 2014; Carvalho et al., 2016; Vicente et al., 2016). When properly designed, parametrised and calibrated, ecological models can effectively simulate conditions and processes that might be difficult or even impossible to understand otherwise (Jørgensen and Fath, 2011). Efforts to describe and accurately predict the behaviour of a wide range of (socio-) ecological systems have fostered the development of several modelling approaches suiting particular goals (Jørgensen and Bendoricchio, 2001). Among the many dichotomies used to classify modelling approaches (e.g. Reductionist/Holistic; Deterministic/Stochastic; Linear/Nonlinear), two major types of ecological models can be recognised, differing in their capacity to describe and analyse the nature of processes by which a phenomenon is created: static models and dynamic models (Hannon and Ruth, 2014).

Static models can be defined as models that represent a phenomenon at a given point in time or that compare the phenomenon at different points in time (i.e. comparative static models; Hannon and Ruth, 2014). A widely applied type of static models is habitat suitability models (HSMs), which are statistical-based phenomenological screening tools (Gallien et al., 2010) that associate a given response variable (e.g. the occurrence of a species) with environmental variables or predictors (e.g. temperature, precipitation; Franklin, 2010; Guisan and Thuiller, 2005). These models have been commonly used in invasion ecology, for example to predict current and future potential distributions of invasive species (e.g. Peterson et al., 2003; Vicente et al., 2010, 2013). However, static models are limited by the lack of information on local dynamics, processes and interactions that characterize invasion processes as complex phenomena (Gallien et al., 2010). In fact, predicting future range dynamics can be particularly challenging, as invasive species are usually recent arrivals whose distribution is still not in equilibrium with the new environmental conditions (Rouget et al., 2004).

Dynamic models are based on ecological processes (e.g. process-based models), and differ from static models by explicitly incorporating time-dependent changes in the state of a system (Hannon and Ruth, 2014). These models include, among others, biogeochemical dynamics models (e.g. Soetaert et al., 2000), population dynamics models (e.g. Kriticos et al., 2003), individual-based models (IBMs; e.g. Nehrbass and Winkler, 2007), and cellular automata systems (e.g. Crespo-Perez et al., 2011). Examples of dynamic modelling approaches can be traced back to the classical Lotka-Volterra models in the 1920s, to models of population dynamics in the 1950s, and to eutrophication models during the 1960s. More recently, spatially explicit IBMs and cellular automata have seen their growth in the late 2000s and 2010s (Chen et al., 2011; Jørgensen, 1994, 2008; Jørgensen and Fath, 2011).

Dynamic models can overcome several limitations of static models, since they can extrapolate beyond known conditions and be implemented under multifactorial management scenarios (Cuddington et al., 2013). In fact, the utility of dynamic models for conservation planning and management has been profusely highlighted (e.g. Cuddington et al., 2013; Franklin, 2010; Richardson and Whittaker, 2010; Thuiller et al., 2008). They have also been recognised as the most appropriate type of models to guide management decisions (Cuddington et al., 2013). Nevertheless, the application of dynamic modelling in the scope of invasions requires a deep understanding of the spatial-temporal dynamics of invasion processes (Gallien et al., 2010). Detailed information is required on the characteristics of invasive species (i.e. invasiveness traits; Gallien et al., 2010; Guisan and Zimmermann, 2000), on the features of areas under invasion (i.e. their invasibility; Gallien et al., 2010) and on the socio-environmental variables that may influence a given invasion process (Gallien et al., 2010).

In this context, there has been an increasing interest in hybrid models, specifically frameworks coupling dynamic and static models (e.g. Brook et al., 2009; Richardson et al., 2010; Santos and Cabral, 2004; Zurell et al., 2016). Hybrid models combine the predictive accuracy and low data requirements of static models with the ability of dynamic models to describe underlying processes (Franklin, 2010; Gallien et al., 2010). A hybrid approach can be illustrated by the integration of HSMs and process-based models for the management of invasive species. For instance, Meier et al. (2014) coupled HSMs and population spread models to analyse the effectiveness of invasive species control actions under alternative cost scenarios and different management goals. Richardson et al. (2010) defined regions of high risk of invasion by coupling a cellular automata model with HSMs.

Albeit the former examples, the extent to which dynamic and hybrid models have been applied in the study and management of biological invasions is still under-investigated. A detailed analysis of the contexts and motivations under which those models have been applied, as well as of the insights obtained from their application, could pave the way for further development and testing. Therefore,