



## Review

## Dynamic models in research and management of biological invasions



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## ABSTRACT

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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## 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,

we performed an extensive literature review to analyse the extent and the goals under which dynamic modelling has been applied for the analysis and management of biological invasions. We conducted a comprehensive review of published literature applying dynamic modelling approaches in the study of invasions and/or in the management of invasive species. Two major goals (G) were established, and four hypotheses (H) were tested:

**G1** – To examine the extent to which dynamic ecological modelling has been used to address biological invasions worldwide. To do so, we tested the following hypotheses:

**H1.1.** Dynamic modelling has been increasingly used for biological invasion studies; and

**H1.2.** Dynamic modelling has been increasingly used for studies on management of biological invasions.

**G2** – To understand how dynamic modelling has evolved through time regarding management strategies targeting biological invasions. To assess this goal, we tested the following hypotheses:

**H2.1.** The incidence of the research changed geographically and taxonomically over time; and

**H2.2.** The application of dynamic modelling in the assistance of invasive species management has transitioned over time, particularly from purely dynamic to static-dynamic hybrid models.

## 2. Analytical framework

### 2.1. Overview

We applied an analytical framework grounded on standard protocols for literature reviews (Higgins and Green, 2011), to trace a historical overview and identify current patterns of incidence of dynamic modelling in invasion literature. We gave particular focus to invasion management, for which dynamic models can be

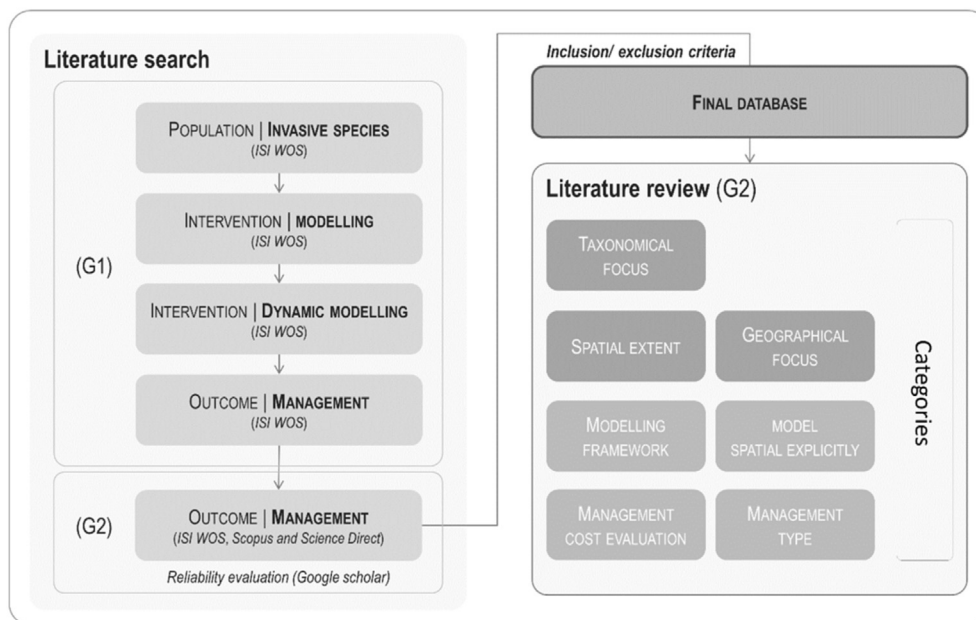
especially useful (Cuddington et al., 2013). The framework was organised around the aforementioned goals (G1, G2) and hypotheses (H1.1 and H1.2 for G1; H2.1 and H2.2 for G2; see Fig. 1, Table 1). Further details on the rationale for each hypothesis are provided in Appendix S1.

The analytical framework started with a literature search, which included the selection of keywords and search engines, an evaluation of the reliability of the search, and the application of exclusion and inclusion criteria. A literature review was then conducted to classify the records retrieved during the search, and to extract the relevant information for testing our hypotheses (Fig. 1).

### 2.2. Literature search

Literature searches are grounded on the use of keywords and specific search engines; therefore, a good selection of keywords is crucial for achieving a representative screening of pertinent publications (Higgins and Green, 2011). For this review, keyword selection followed a Population-Intervention-Comparison-Outcome (PICO) strategy, in which “invasive species” was defined as Population, “dynamic modelling” as Intervention, and “management” as Outcome. The selection was based on a review of previous keywords from a list of reference papers, and under a participatory approach with a team of researchers specialised in modelling and managing invasive species (Fig. 1). The final list of keywords included the most common and unambiguous words to reach the largest number of publications on the subject (see Appendix S2 for keyword selection and literature search protocol, and Appendix S3 for the final list of keywords).

The time span of the search was 1900–2014. Searches were carried out from October to November 2015, and were updated in March and April 2016. To address G1, ISI Web of Science (ISI WOS; <http://webofknowledge.com/>) was used, since it offers the widest coverage of published scientific literature through time (Falagas et al., 2008). To address G2, we additionally used the search



**Fig. 1.** The analytical workflow. The Literature search comprised hierarchical searches grounded on keywords expressing Invasive species (Population), Modelling (Intervention), and Management (Outcome) in ISI Web of Science (ISI WOS) for Goal 1 (G1); and in ISI WOS, Scopus and Science direct for Goal 2 (G2). The Reliability evaluation was the process by which the comprehensiveness of the search was assessed, through comparison with a search in Google Scholar. Records from the combined search (G2) were then submitted to inclusion/exclusion criteria (see Appendix S4), in which irrelevant records were removed from the database. The Literature review focused on records from the final database which were individually reviewed and classified according to seven categories, related to the sub-hypotheses under Goal 2 (see also Table 1).

**Table 1**

Goals of the study, hypotheses and sub-hypotheses with related categories and classes used in the literature review, and their respective motivations.

Hypotheses	Sub-hypotheses	Categories	Classes	Motivations
<b>Goal 1. To examine the extent to which dynamic ecological modelling has been used to address biological invasions worldwide</b>				
H 1.1: Dynamic modelling has been increasingly used for biological invasion studies	–	–	–	To assess how dynamic modelling has been applied in invasion research and in invasion management
H 1.2: Dynamic modelling has been increasingly used for studies on management of biological invasions	–	–	–	
<b>Goal 2. To understand how dynamic modelling has evolved through time regarding management strategies targeting biological invasions</b>				
H 2.1: The incidence of the research changed geographically and taxonomically over time	<p><b>H 2.1.1:</b> From taxonomic groups with well-known impacts to a more general species selection</p> <p><b>H 2.1.2:</b> From continents with a longer history of research in invasion biology to more general areas</p> <p><b>H 2.1.3:</b> From local and regional extent to global studies</p>	<p><b>Taxonomical focus:</b> What is the taxonomical group of focus?</p> <p><b>Geographical focus:</b> What is the targeted study area?</p> <p><b>Spatial extent:</b> What is the spatial scale of the study?</p>	<p>Plant, Invertebrate, Vertebrate, Other, Not specified</p> <p>Global, Europe, South America, North America, Africa, Asia, Oceania, Antarctica, No reference</p> <p>Global (multiple continents), Regional (within one continent but in multiple countries), Local (within one country), No reference</p>	To assess how dynamic modelling has been targeting invasibility (considering where the invasion is taking place) and invasiveness (considering the taxonomical group that is invading)
H 2.2: The application of dynamic modelling in the assistance of invasive species management has transitioned over time	<p><b>H 2.2.1:</b> From a uniquely dynamic model to application of hybrid models, combined with static species modelling</p> <p><b>H 2.2.2:</b> From a no cost evaluation to a cost evaluation of management options</p> <p><b>H 2.2.3:</b> Between the chosen types of management options</p> <p><b>H 2.2.4:</b> From not spatially explicit to spatially explicit modelling approaches</p>	<p><b>Modelling framework:</b> Is the modelling approach a combination of dynamic approach with a species static model?</p> <p><b>Model spatially explicit:</b> Is the modelling approach spatially explicit?</p> <p><b>Management type:</b> What management options and type, if passive (P) or active (A), were considered? (Passive management referred to preventive actions, and active management indicated direct or indirect actions applied to invasive species post establishment.)</p> <p><b>Cost evaluation:</b> Was a management cost evaluation done?</p>	<p>Not combined with a species static model, Combined with a species static model</p> <p>Yes, No</p> <p>Risk assessment (P), Preventing (P), Monitoring (P), Control (A), Biological control (A), Eradication (A), Containment (A), Mitigation (A), Restoration (A), Other, No reference</p> <p>Yes, No</p>	To assess the main characteristics of dynamic modelling applied in the management of invasive species

engines Scopus (<https://www.scopus.com/>) and Science Direct (<http://www.sciencedirect.com/>), besides ISI WOS, to obtain a broader coverage of currently published literature (Higgins and Green, 2011). Records retrieved for G2 were combined after eliminating duplicates (total number of records,  $n = 1849$ ), using EndNote  $\times 7.4$  (Thomson Reuters, 2013).

To evaluate the reliability of the search, the first 50 records retrieved by Google Scholar (using the main keywords “invasive species” AND “model” AND “dynamic” AND “management”) were compared to the combined database (Fig. 1; following Higgins and Green, 2011). Records on the topic from Google Scholar that were absent from the combined database (corresponding to 3 out of 22 relevant retrieved records) were added to the database (total  $n = 1852$  records; Fig. 1). This former set of records was then subjected to exclusion/inclusion criteria to maintain suitable records and eliminate unsuitable ones from the final database (e.g. records on topics such as aliens/invasers from outer space; see Appendix S4 for details). Inclusion/exclusion criteria were applied by individually examining first the title, keywords and abstract of each record, and then the full text of the record (Fig. 1). Two reviewers applied the inclusion/exclusion criteria. The consistency of classification results was assessed through kappa statistics on 10% of randomly chosen records, resulting in a good consistency (kappa = 0.8; see Higgins and Green, 2011 for details).

### 2.3. Literature review and statistical analyses

The full text of each individual record from the final database ( $n = 369$ ) was reviewed to classify each record according to the categories (and classes) shown in Table 1. To test our goals and hypotheses, we performed descriptive and multivariate analyses. Descriptive statistics were used to assess the temporal trends of published records. For the outcomes of the Literature search (Fig. 1, G1), the total number of published records per year for each step of the literature search was represented using area plots. The proportion of records of each step in relation to the total number of published records per year was also plotted as smoothing curves showing averages for 2-year time periods, between 1904 (first record retrieved by our search) and 2014 (see section 3 “An historical perspective of published invasion research”). For the outcomes of the Literature review (Fig. 1, G2), the total number of records per year for each classification was represented through line plots with smoothing curves (averages for 2-year periods), for the time frame between 1987 (first record retrieved by our search) and 2014 (see sections 4.1 “Taxonomic and geographic focus” and 4.2 “Modelling approaches in invasive species management”). The proportion of records of each classification in relation to the total number of published records per year was represented as column plots. For ease of readability, records classified as “no reference” or “not

specified” (see Table 1) were not exhibited.

Subsequently, multivariate analysis was employed to visualise the similarities between our variables: the classifications derived from our *Literature review* (G2 - H2.2, Table 1). Principal Component Analysis (PCA) was applied to the categories “cost evaluation”, “type of management”, “spatially explicit nature” and “modelling framework” (see Fig. 1). PCA is a statistical procedure that displays the pattern of similarity of observations and variables. The PCA extracted information from the classification matrix of our record database, described by our inter-correlated variables, converting it into linearly uncorrelated, orthogonal, variables called principal components. This method projects the distance between objects in a reduced space, by simplifying the description of our database, thereby expressing the maximum variance captured in the database, while enabling the visualization of patterns of similarity between variables as points in a map (see Abdi and Williams, 2010; Legendre and Legendre, 1998 for details on PCA). To obtain the PCA, the classification matrix was first created by classifying a record as 1, if verified, and 0, if not verified, for each variable. To illustrate, for the variable “No Cost”, a value of 1 was assigned to those records that did not evaluate the cost of management, whereas a value of 0 was assigned to those that evaluated the cost of management. Then, the statistical reduction of the classification matrix was obtained by computing the first two principal components of the PCA, as they covered most of the variance in the database (68%). Finally, a projection of variables in the PCA biplot was presented to illustrate similarities between variables. All statistical procedures were conducted using Statistica v13 (StatCorp, 2013).

### 3. An historical perspective of published dynamic invasion models

The number of records including keywords related to “invasive species” (see Appendix S3) retrieved by ISI WOS was 27,429 (Step 1; see Fig. 1). From these, 7248 records also included “modelling” related keywords; 2395 further included “dynamic modelling” keywords; and 1277 records also included keywords related to “management”.

Biological invasions are a relatively recent topic in science, only established as a discipline after the middle of the XX century, following the publication of *The Ecology of Invasions by Animals and Plants*, by Charles Elton (1958) (Richardson and Pysek, 2008; Simberloff, 2010). An increase in the number of records with invasive species keywords was observed, as expected, with a rapid increase occurring after 1990 (Fig. 2). We note, however, that this growth relies on the assumption that keywords directly reflect the subject of studies (from now on this assumption underlies our discussion). The growth of scientific focus on biological invasions since the early 1990s has already been suggested by several studies (Davis, 2006; Lockwood et al., 2013; Lowry et al., 2013; Macisaac et al., 2010; Ricciardi and MacIsaac, 2008; Simberloff, 2010; Vaz et al., 2017b). It has been associated with the 1982 SCOPE program (Davis, 2006; Simberloff, 2010), in which biological invasions became a key issue to academics and stakeholders focused on the conservation, environmental and socio-economic implications of invasions (Hobbs and Richardson, 2010; Humair et al., 2015; McNeely, 2001). Moreover, this rising concern resulted in a growing availability of invasion data, allowing for more quantitative analyses and for predictive modelling to become a hallmark in the field of invasions (Ricciardi and MacIsaac, 2008; Simberloff, 2010).

The increase in records focused on invasive species modelling was also mostly observed since the 1990s. Nevertheless, the application of modelling techniques to invasive species can be traced back to the early XX century, with Cooks’ research on

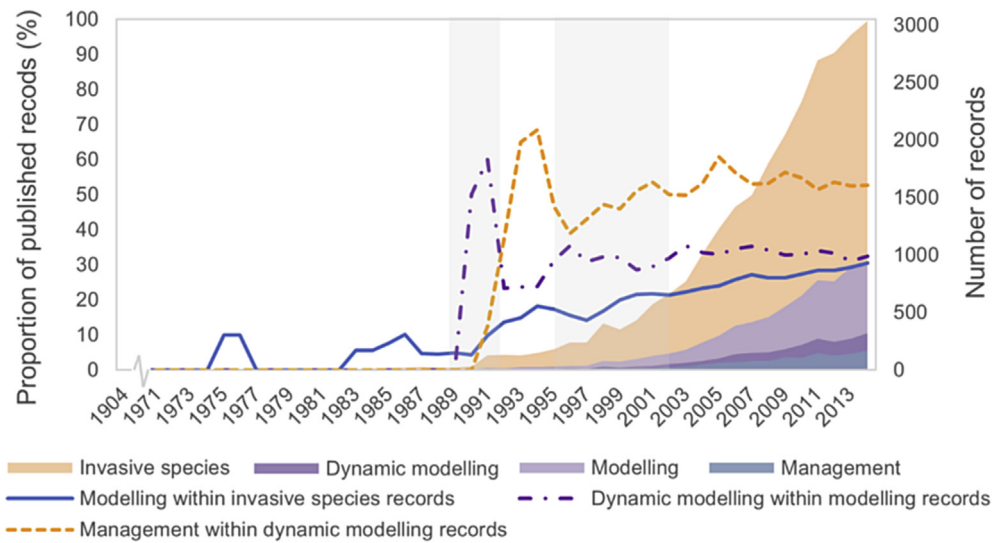
predicting habitat suitability (e.g. Cook, 1924; see Sutherst, 2014), or to the 1950s, with Skellam’s research on the application of dynamic modelling (Skellam, 1951). However, (dynamic) modelling of invasive species only became more frequent since the late 1990s (Fig. 2), in agreement with results from other assessments focused on modelling literature. For instance, Jørgensen (2008) showed that the number of modelling papers published from 2001 to 2006 was about nine times the number of papers published from 1975 to 1980. This increase in modelling literature over the last decades may be attributed to developments in computer technology and advances in the general knowledge about invasions, with the accumulation of relevant databases (Davis, 2006; Jørgensen and Fath, 2011; Simberloff, 2010).

Similar trends were perceived for records dealing with dynamic modelling of invasions in general, and specifically with invasion management. These results support our hypotheses H1.1 (i.e. dynamic modelling has been increasingly used for biological invasion studies) and H1.2 (i.e. dynamic modelling has been increasingly used for studies on management of biological invasion; Fig. 2). Dynamic models represented roughly one third of the modelling records focused on invasive species, and about half of these were designed for management purposes (see Fig. 2).

More broadly, the application of dynamic modelling techniques prevailed in the early stages of ecological modelling. According to Jørgensen (2008), from 1975 to 1980, studies with dynamic models represented more than 90% of the publications in ecological modelling. From 2001 to 2006, studies on system dynamics modelling still comprised more than half of the modelling publications, with new approaches growing such as static biogeochemical and bioenergetics, individual based models, cellular automata, and spatially explicit models. During that period, static approaches represented no more than 15% of modelling studies (Jørgensen, 2008).

This focus on dynamic modelling for applications in invasion management may be explained by an increasing pressure to manage invasions and mitigate their impacts. This is demonstrated in several initiatives such as the European Environment Agency (1998) report on invasive species, the Clinton administration’s (1999) directives to prevent and control alien invasive species, the National Research Council (2002) report on the *Scientific basis for predicting the invasive potential of nonindigenous plant and plant pests*, in the USA, or the IUCN “Guidelines for the prevention of biodiversity loss caused by alien invasive species” (2000) (see Davis, 2006). Further, Shigesada and Kawasaki (1997) book on “*Biological invasions: theory and practice*” may be symptomatic of the increasing focus on dynamic modelling in invasive species management in the late 1990s (Davis, 2006). This book reviewed mathematical modelling applications in invasion ecology, resulting from an increased demand to understand and predict invasive species distributions.

The growing need to tackle invasions, and the many institutional incentives to do so, may have fostered further application of dynamic modelling in the management of invasions. The Millennium Ecosystem Assessment (2005) highlighted the threats posed by invasive species on biodiversity, ecosystem services and human well-being across biomes. The World Organization for Animal Health and the International Plant Protection Convention both stressed management priorities for non-native species (Keller et al., 2011), as did other institutions and initiatives (e.g. see Shine et al., 2010 for a review on former EU policy to combat invasive species). Throughout this process of growing awareness and knowledge production, the need to incorporate dynamic modelling to support decision-making for invasion management has been repeatedly emphasised (Cuddington et al., 2013; Gallien et al., 2010; Hulme, 2006).



**Fig. 2.** The number of records retrieved by the search (in ISI Web of Science) on invasive species modelling, dynamic modelling, and management, from 1904 to 2014 (smoothing curves showing averages for 2-year time periods; on the right y-axis). The figure also illustrates the proportions of modelling records within invasion studies, of dynamic modelling records within modelling invasive species studies, and of management records within dynamic modelling of invasive species (on the left y-axis). Time periods highlighted in light grey are discussed in more detail throughout the text. Gaps in the x-axis represent time periods for which no records were retrieved.

#### 4. Trends in the modelling of biological invasions for management

##### 4.1. Taxonomic and geographic focus

Invasive species comprise several taxonomic groups and occur in most regions of the world (Pyšek et al., 2008). From the total set of records considered in our literature search (Fig. 1;  $n = 1849$ ), 20% (369 records) were considered suitable for our literature review (Appendix S5). In the latter, plants were the most prevalent taxonomic group (44.27%), followed by invertebrates (32.80%) and vertebrates (18.15%), with other taxa representing the remaining 4.78% records. This focus on plants and invertebrates was observed in almost every year of the focal period (1997–2014; Fig. 3a). The earliest record on modelling for invasion management was from 1997 and focused on the plant *Acacia saligna* (wattle; Higgins et al., 1997). In 1998, several invertebrates and vertebrates were targeted for the first time in published management models. Examples from our dataset included studies on *Lymantria dispar* (gypsy moth; Sharov and Liebhold, 1998; Sharov et al., 1998), *Dreissena polymorpha* (zebra mussel; Schneider et al., 1998) and *Bufo marinus* (cane toad; Lampo and De Leo, 1998). Since the 2000s, further studies were published focusing on invasive arthropods, such as *Procambarus clarkii* (red swamp crayfish; Marchi et al., 2011), one of the most problematic invasive crustaceans worldwide. Other taxa were only mentioned from 2005 onwards, with an emphasis on phytoplankton modelling studies (Petrovskii et al., 2005).

Geographically, the set of reviewed records comprised studies conducted in different parts of the world (Fig. 3b), although North America was by far the most represented continent (46.57%), followed by Europe (19.86%), Oceania (19.49%), and finally by other continents (11.19%). Studies involving multiple continents were scarce, representing only 2.89% of all records. The earliest study found in the literature search was conducted in South Africa, in 1997 (Higgins et al., 1997). North America and Oceania were first mentioned in 1998 (e.g. Edwards et al., 1998; Lampo and De Leo, 1998), and Europe in 2000 (Wadsworth et al., 2000). The first study covering more than one continent was published in 2004 (Morrison et al., 2004), and since then more continents were

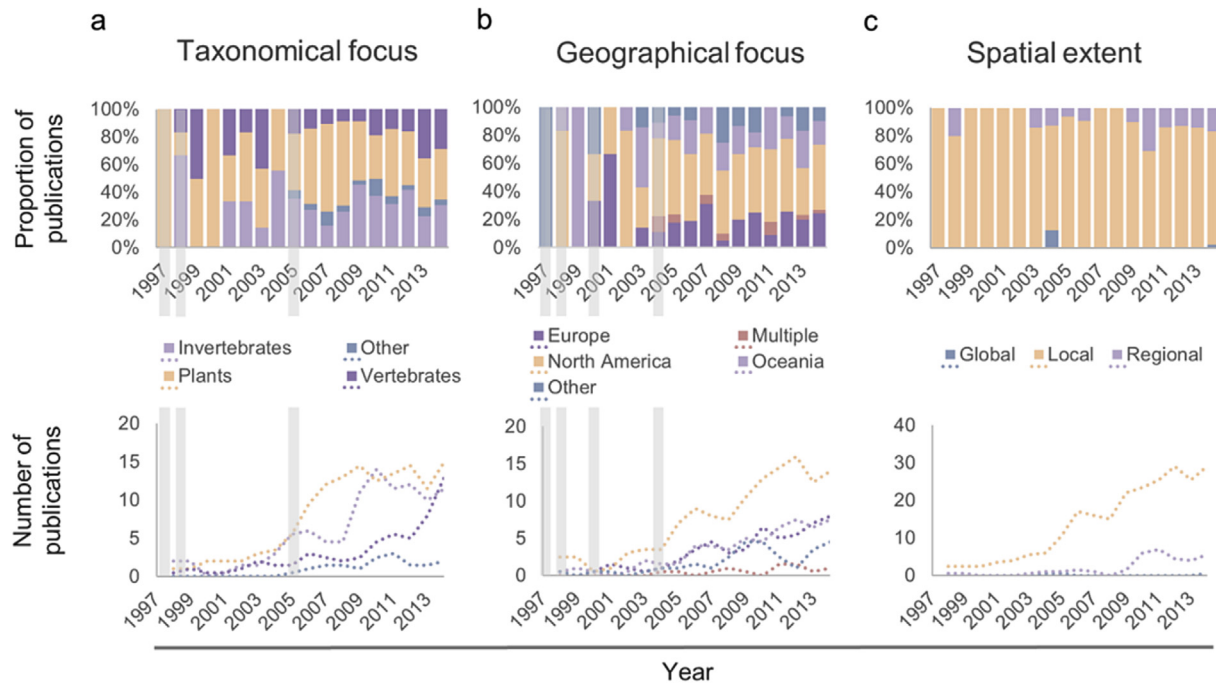
simultaneously targeted by modelling studies (Fig. 3b). Regarding the spatial extent, our set of records was clearly dominated by local studies (86.6%), whereas the regional (12.7%) and global (0.7%) scales represented only a small fraction of the records (Fig. 3c). These results support our hypothesis H2.1, that the geographical and taxonomical focus of the dynamic modelling studies changed through time.

Most records were centred on plants and insects, and were conducted in developed regions (Fig. 3). This is consistent with previous studies that showed a biased focus on invasion ecology and more broadly in ecological research (Dana et al., 2014; Kueffer et al., 2013; Martin et al., 2012; Pyšek et al., 2008; Ruiz et al., 2000; Wilson et al., 2007). Pyšek et al. (2008) had already suggested that plants and insects were the most represented taxa in invasion research (together accounting for almost two-thirds of the studied taxa), and that more than half of invasion studies were conducted in North America. Martin et al. (2012) highlighted that countries with the highest Gross National Income (GNI) were over-represented in their analysis of the global distribution and environmental context of terrestrial field studies.

One of the main issues driving the selection of target organisms in invasion research has been the magnitude of the ecological impacts and the level of invasiveness of each species (Pyšek et al., 2008). Weeds and pests tended to be more targeted by invasion studies mostly due to their economic impacts in agriculture and forestry (Wilson et al., 2007). In addition, a bias in the target geographic areas could be associated with research intensity inequality, since research investment is more strongly determined by economic priorities and practical limitations than by geographical and socio-political barriers (Pyšek et al., 2008; Wilson et al., 2007). Moreover, developed regions with large trade volumes will necessarily have the by-product of receiving more potentially invasive species (Pyšek et al., 2008). We are nevertheless aware that the geographic pattern of invasion literature captured in our search could be biased, as we exclusively focused on English keywords.

##### 4.2. Modelling approaches in invasive species management

Although there has been a wide application of dynamic



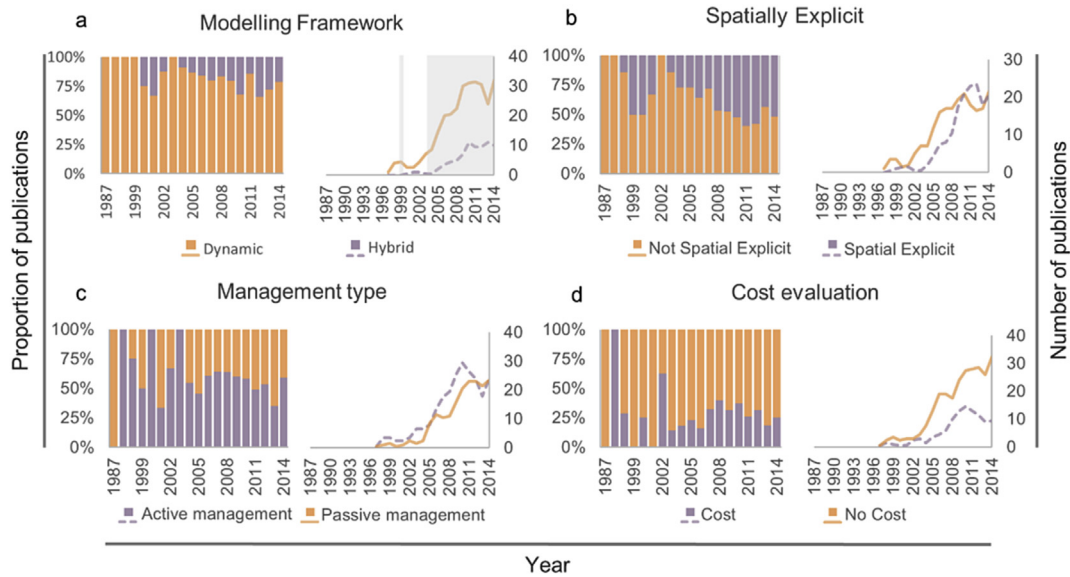
**Fig. 3.** Temporal trends by classification analysed under [Hypothesis 2.1](#): (a) Taxonomic focus, (b) Geographical Focus, and (c) Spatial extent. The upper row represents the proportion of records per year and the lower row represents absolute number of records per year (smoothing curves showing averages for 2-year time periods). Time periods highlighted in light grey are discussed in more detail in the text.

approaches in the field of ecological modelling ([Jørgensen, 2008](#)), our results show that dynamic modelling is still under-represented in invasion research (see [Fig. 2](#)). This could be due to the high data demand, complex model procedures and detailed parameterisation ([Gregr and Chan, 2015](#)) needed to understand, analyse, and forecast invasive species distribution and associated processes ([Gallien et al., 2010](#)). In our review, most studies using dynamic modelling approaches for invasion management focused on purely dynamic models (79.78%), whereas the remaining ones (20.22%) focused on hybrid models (i.e. combining static and dynamic approaches). Dynamic models were predominant until the beginning of the 2000s, with the first record in 1987 ([Crawley, 1987](#)). Since 2003, hybrid models began to be more frequently applied ([Fig. 4a](#)). This growth is consistent with the trend of general invasion modelling, which increasingly emphasises predictions of species distributions based on large-scale relationships, while simultaneously considering the most important dynamic processes ([Gallien et al., 2010](#)). Although a clear transition from purely dynamic to static-dynamic (i.e. hybrid) models was not observed, the results sustain our [H2.2](#) sub-hypothesis, showing a growing application of hybrid modelling approaches in the management of invasive species.

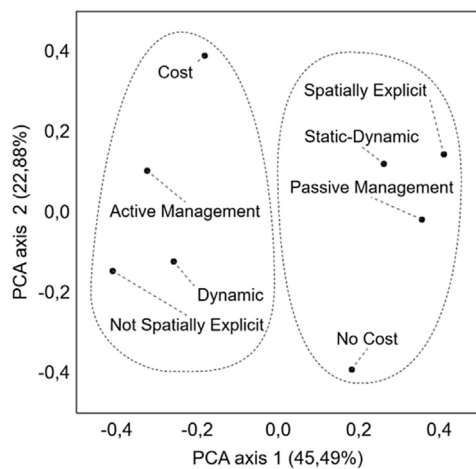
Modelling passive or active management options, and choosing to incorporate (or not) management costs, may result in the selection of different modelling approaches, which may be purely dynamic or hybrid models and may or may not have a spatially explicit dimension (following [Gallien et al., 2010](#)). From our results, we could see that non-spatially explicit models (57.68%) generally outnumbered those that included a spatial component (42.31%). Although both categories increased in number over the last years, a more recent increase in spatially explicit models was observed ([Fig. 4b](#)). Concerning the type of management, both preventive actions (i.e. passive management) and post-establishment actions (i.e. active management) increased through time, with an overall predominance of the latter (57.04%; [Fig. 4c](#)). Similar trends were observed for cost evaluation, with a growing number of records

published with and without cost evaluations ([Fig. 4d](#)), although only 27.76% of records presented an assessment of management costs. These results also support our [H2.2](#) hypothesis, whereby the application of dynamic modelling for the management of invasive species has evolved over time.

Two groups of model attributes linked to invasion management were discriminated along the first principal components axis (PCA axis 1, [Fig. 5](#)). The first group comprised spatially explicit, hybrid static-dynamic models supporting passive management options and, to a lesser extent, with no evaluation of management costs (right-hand side of [Fig. 5](#)). This confirms that combining static and dynamic models enables spatially explicit modelling, as opposed to classical dynamic models that may not be spatially explicit (e.g. population dynamics models; [Chen et al., 2011](#)). Also, the fact that static approaches (such as HSMs) are particularly effective in spatially predicting invasions, may justify the relation between hybrid models and passive management options, for which predicting invasions is of primary importance for preventive invasion management (e.g. [Vicente et al., 2016, 2013](#)). The association with “no cost evaluation” is consistent with the fact that passive management options may not rely on a budget (see [Dana et al., 2014](#) for similar results), as opposed to active management that entails costs. Studies in our database described hybrid models that coupled static HSMs with dynamic spread models (e.g. [Gallardo et al., 2012; Harris et al., 2011; Pitt et al., 2009; Potts et al., 2014; Smolik et al., 2010](#)). The dynamic component was generally a model able to represent spread dynamics, including interacting particle systems models (e.g. [Inglis et al., 2006; Roura-Pascual et al., 2009; Smolik et al., 2010](#)), cellular automata (e.g. [Lu et al., 2013](#)) or matrix models (e.g. [Sebert-Cuvillier et al., 2008](#)). HSMs may also be combined with models focused more broadly on population dynamics (namely growth, recruitment, reproduction), such as matrix models (e.g. [Brown et al., 2008](#)), density-dependent population models (e.g. [Potts et al., 2014](#)), cellular automata (e.g. [Johnston and Purkis, 2013](#)) or IBMs (e.g. [Lurz et al., 2001](#)).



**Fig. 4.** Temporal trends, by classification, analysed under [Hypothesis 2.2](#): (a) Modelling framework, (b) Model spatially explicit, (c) Management type and (d) Cost evaluation. In each case, the plot on the right represents the absolute number of records per year (smoothing curves showing averages for 2-year time periods), while the plot on the left represents the proportion of records per year. Time periods discussed in more detail in the text are highlighted with a light grey shading.



**Fig. 5.** Principal Components Analysis (PCA) biplot, projecting the variables related to the categories of Cost evaluation, Type of management, Spatially explicit nature, and Modelling framework, onto the space defined by the two first principal components (PCA axis 1 and 2). Values in brackets refer to the amount of variance explained by PCA axis 1 and 2. The dashed lines enclose the two main groups of variables along PCA axis 1. For visualization purposes, variables were plotted as dots.

The second PCA group corresponds to non-spatially explicit, dynamic models applied to support active management and often associated with cost evaluation of management actions (left-hand side of [Fig. 5](#)). The ability of dynamic models to better mimic demographic processes, such as dispersal ([Hastings et al., 2005](#)) and growth ([Jongejans et al., 2008](#)), is of key importance for active control measures, since understanding population dynamics of invasive species is essential for undertaking a successful control program ([Grarock et al., 2013](#)). Studies in our database applied dynamic modelling to study population dynamics of invasive species, namely dispersal (e.g. [Calviño-Cancela and Rubido-Bará, 2013](#); [Havel et al., 2002](#)), growth (e.g. [Lindgren and Walker, 2012](#); [McArthur et al., 2013](#); [Nehrbass et al., 2006](#); [Osunkoya et al., 2013](#)) and recruitment (e.g. [Calviño-Cancela and Rubido-Bará, 2013](#); [Fordham et al., 2012](#); [Murphy et al., 2008](#)), as well as their

relation to Allee effects (e.g. [Boukal and Berec, 2009](#); [Chivers and Leung, 2012](#); [Drake and Lodge, 2006](#)). The latter has received much attention (see [Taylor and Hastings, 2005](#); [Tobin et al., 2011](#)) since non-native species are often subject to Allee dynamics. As such, efforts to reduce non-native populations below Allee thresholds can be an effective strategy to manage invasions ([Tobin et al., 2011](#)). Studies with dynamic modelling have also focused on species interactions, which is of high relevance e.g. to evaluate the effectiveness of biological control (e.g. [Kriticos et al., 2009](#); [Le Maitre et al., 2008](#); [Tonnang et al., 2009](#)).

Our review also highlighted that dynamic models allow the consideration of alternative cost and economic scenarios towards bioeconomics and the optimisation of management strategies (in line with [Fig. 5](#)). Several studies in our database applied stochastic dynamic modelling (e.g. [Bertolucci et al., 2013](#); [Eiswerth and Van Kooten, 2002](#); [Hyder et al., 2008](#)). This procedure allows the identification of optimal strategies by considering the possible changes in the states of a system over time ([Baxter and Possingham, 2011](#)). We also observed that while some studies considered cost-effectiveness of management strategies (e.g. [Blackwood et al., 2010](#); [Pichancourt et al., 2012](#)), others incorporated damage costs in general environmental evaluations or in agricultural yields (e.g. [Leung et al., 2002](#); [Mehta et al., 2007](#); [Wesseler and Fall 2010](#)).

## 5. Further enhancing invasion modelling for research and management

Invasion biology has long focused on understanding invasion processes, scrutinising what makes an invasive species thrive (invasiveness) or what makes a habitat prone to invasion (invasibility; [Hobbs and Richardson, 2010](#)). Still, claims have been made for a more practical invasion science that can work with multiple stakeholders and academics, based on interactive solutions ([Hobbs and Richardson, 2010](#); [Hulme, 2003](#); [Vaz et al., 2017a, 2017b](#)). The importance of effectively tackling invasions raises the need to devise, test and implement management actions, supporting decision-makers and managers with the best management options. Dynamic modelling has the ability to mimic invasion processes and to predict invasions, allowing clear assumptions and extrapolation



beyond known conditions while considering the effects of multiple management scenarios (Cuddington et al., 2013).

Dynamic models are usually applied at the scale that management actions take place (local or regional), but the success of invasion management can be influenced by regional and even global processes. Coupling a dynamic model with a static model in a hybrid framework allows the integration of multi-scale processes, including for e.g. biogeographic constraints (Cuddington et al., 2013). In addition, the integration of dynamic and static models offers the opportunity to include feedbacks by introducing multi-way interactions between sub-models, supporting better predictions of the impacts caused by biological invasions (Gallien et al., 2010). However, there are still challenges to be tackled in future research on hybrid approaches. For instance, the assumptions underlying dynamic models are often based on expert knowledge, and unequivocally would benefit from being supported by observations or experiments (Gallien et al., 2010). In addition, data driven models suggest reliability as they are based on “real data”, therefore, modelling such processes supports a mechanistic understanding (Dormann et al., 2012). Moreover, the adopted procedure in hybrid models must combine parameters compatible with both dynamic and static models, overcoming potential issues of circularity. For example, when HSMs implicitly and indirectly account for processes that are also explicitly considered in the dynamic model inducing the hybrid model to account for some processes twice (see Gallien et al., 2010). However, when properly developed and tested, they must be applied with insight and with regard to their underlying assumptions, enabling the understanding of whole-system processes such as resilience, resistance, persistence, regulation, and density dependence (Santos et al., 2013). This should also be applied at other scales, namely when individual or population properties are crucial to understand systemic phenomena (Santos et al., 2013), such as physiological traits of invaders (invasiveness) and effectiveness and costs of management actions (efficiency).

Our review showed that the application of dynamic modelling in the management of invasive species has evolved in recent years. This has probably been due to technical improvements, the increased availability of data and knowledge on invasive species, and the growing appraisal of this type of modelling approaches due to their ability to describe global change phenomena (Gallien et al., 2010). Hybrid models may well be a future stepping-stone towards improved spatial representation of model simulations under alternative management options, notwithstanding that, such hybrid approaches may eventually be dropped in favour of more sophisticated dynamic modelling approaches (Bastos et al., 2012). Predictions from purely dynamic models may be difficult to spatialize (see Fig. 5), but new platforms combining different approaches to investigate large-scale holistic relationships (“top-down”), while considering the most important processes (“bottom-up”; e.g. Bastos et al., 2012; Santos et al., 2013; Soares-Filho et al., 2009), will foster spatially-explicit dynamic modelling in invasion biology (Santos et al., 2015). Likewise, the need to incorporate socio-economic dimensions to better optimise management strategies, describing cost and effectiveness of these strategies (Cuddington et al., 2013), will further empower dynamic approaches.

The pros and cons of dynamic modelling approaches in supporting management actions should be critically evaluated in future assessments. In fact, whether the modelling approaches reviewed here contribute to a better understanding and management of invasive species, compared to other conventional modelling types, is yet to be evaluated. Future research on invasion modelling and management should focus on understanding how uncertainties inherent to any modelling approach affect the success

of management actions. When evaluating modelling options and outputs, researchers and managers always need to consider the quality of the input data. Relying on appropriate data and evaluating how well the models are calibrated and validated is of key importance to better inform management actions (Gregg and Chan, 2015; Jørgensen and Fath, 2011). We thus suggest that future developments and assessments on the choice of modelling techniques (see e.g. Jørgensen, 2008; Jørgensen and Fath, 2011) to improve invasion management should prioritize questions such as: (1) How does uncertainty in model input and output translate into management advice? (2) To what extent, and in which stage, has dynamic modelling research been applied to invasive species management programmes? (3) How much has the nature and quality of the supporting dataset influenced the method applied? (4) How does the origin of spatially-explicit dynamic models in biological invasions influence their architecture? and finally (5) How do multi-model frameworks (such as hybrid approaches) influence model architecture and thus management options?

Considering invasive species impacts when developing models will also contribute to improve their usefulness for management. From these impact-driven models, efficient monitoring and management strategies can be designed to prevent new invasions or restore ecosystems that have been affected by biological invasions (Vicente et al., 2016). A strong emphasis should be given to those dynamic modelling approaches that simultaneously attempt to capture the structure and the composition of systems affected by long-term environmental disturbances (Jørgensen, 1994), such as those induced by invasions. Finally, the strategic role of models and their predictions to effectively communicate conservation and management outcomes to stakeholders (Guisan et al., 2013) should be emphasised in the scope of adaptive invasion management in the broader context of natural resource governance.

## 6. Conclusions

We performed an extensive literature review to analyse the extent and the motivations under which dynamic modelling has been applied in the study of biological invasions and in support of management actions. From our literature review and discussion, we highlight four main emergent patterns:

- Ecological modelling, and specifically dynamic modelling, has been increasingly used in invasion science, for both research and management. This relates to the growing awareness among academics and stakeholders of the potential impacts of invasions, and the need to understand and predict invasion processes.
- Dynamic modelling has shown important advantages for design and evaluation of management actions, particularly at local scales. The ability of dynamic models to capture crucial processes, such as those related to population dynamics, is of key importance to plan and implement management actions for invasive species.
- Most dynamic modelling applications in invasion management focus on plants and invertebrates, in developed regions of the world. The taxonomical focus may be linked to greater impact on economic sectors such as agriculture and forestry, whereas the emphasis on developed countries may be connected to the higher development of their science and education systems and larger trading volumes, resulting in higher incidence of potentially invasive species.
- Static and dynamic models are complementary approaches that allow the assessment of large-scale patterns, while simultaneously considering the most important underlying dynamic processes. Such hybrid combinations of dynamic and static

models have been increasingly used and may be particularly relevant to support the management of early invasion stages, therefore, their further development and testing should be considered a research priority.

Finally, while emphasising the need to acquire a better knowledge of the modelling-management repertoire, we further highlight the difficulties inherent to literature reviews. Researchers often struggle when selecting keywords for published papers (see e.g. Davis et al., 2001), since the use of search engines for literature reviews strongly relies on representative keywords grounded on standardized vocabularies. It is thus crucial that, in the future, denominations are standardized (e.g. in keywords and abstract writing) to facilitate bibliographic reviews. In spite of this, our review clearly showed that dynamic modelling has played (and will continue to play) an important role in support of decision-making for efficient invasion management. This key role is particularly grounded on its ability to mimic invasion processes, integrating species demography and dispersal patterns, while considering cost-effectiveness and optimisation scenarios towards better management options.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2017.03.060>.

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