

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

**Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals**

**This is the author's manuscript**

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1737199> since 2020-04-27T19:34:47Z

*Published version:*

DOI:10.1111/mam.12185

*Terms of use:*

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

Bertolino, S., Sciandra, C., Bosso, L., Russo, D., Lurz, P. W., & Di Febbraro, M. (2020). Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals. *Mammal Review*, 50(2), 187-199.

## Special Issue on Invasive Mammal Species

### Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals

Sandro BERTOLINO\* *Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino, Italy. Email: sandro.bertolino@unito.it*

Chiara SCIANDRA *Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino, Italy. Email: chiara.sciandra@gmail.com*

Luciano BOSSO *Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Via Università 100, 80055, Portici (Na), Italy. Email: luciano.bosso@unina.it*

Danilo RUSSO *Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Via Università 100, 80055, Portici (Na), Italy and School of Biological Sciences, University of Bristol, Bristol Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK. Email: danrusso@unina.it*

Peter W.W. LURZ *Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush Campus, Roslin, Midlothian, EH25 9RG, UK. Email: peter.lurz@ed.ac.uk*

Mirko DI FEBBRARO *Dipartimento di Bioscienze e Territorio, Università del Molise, Contrada Fonte Lappone, 86090, Pesche (Isernia), Italy. Email: mirko.difebbraro@unimol.it*

\* Correspondence author

## ABSTRACT

1. Invasive alien species are major drivers of global change that can have severe impacts on biodiversity and human well-being. Management strategies implemented to mitigate these impacts are based on a hierarchical approach, from prevention of invasion, via early warning and rapid response, to invasive species management.
2. We evaluated how different classes of spatially explicit models have been used as predictive tools to improve the effectiveness of management strategies. A review of literature published between 2000 and 2019 was undertaken to retrieve studies addressing alien mammal species through these models.
3. We collected 62 studies, dealing with 70 (26.8%) of the 261 mammal species that are considered to be introduced worldwide. Most of the studies dealt with species from the orders Rodentia (34%) and Artiodactyla and Carnivora (both 24%); the most commonly studied families were Sciuridae (13%) and Muridae (12%).
4. Most of the studies (73%) provided spatial predictions of potential species spread, while only ca. 15% of the studies included evaluations of management options. About 29% of the studies were considered useful in risk assessment procedures, but only because they presented climatic suitability predictions worldwide, while studies modelling suitability before a species was introduced locally are still lacking for mammals. With some exceptions, spatially explicit population models are still little used, probably because of the perceived need for detailed information on life history parameters.
5. Spatially explicit models have been used in relatively few studies dealing with invasive mammals, and most of them covered a restricted pool of species. Most of the studies used climate matching to evaluate the suitability of geographic areas worldwide or the possibility of species that were

already established spreading further. Modelling procedures could be a useful tool to assess the risk of establishment for species not yet present in an area but likely to arrive; however, such studies are lacking for mammals.

**Keywords:** biological invasions, conservation, global, invasive mammals, management, non-native species, spatially explicit population models

## INTRODUCTION

Non-native species are leading drivers of global change, causing severe impacts on biodiversity, ecosystem functionality, economy and human well-being (Kumschick et al. 2015, Stoett et al. 2019). The rate of species introduction continues to increase (Seebens et al. 2017). Only for fish and mammals, the rate of new introductions seems to have declined in recent years, indicating an increasing awareness of the problems related to biological invasions and a possibility of reversing the general trend. For instance, the most frequent pathways for mammal introductions were intentional releases of animals from captivity, escapes from fur farms and zoos, and introductions for hunting (Genovesi et al. 2009). The application of security systems to captive animals and efforts to discourage hunters from releasing alien mammals have reduced the importance of these sources of introductions in recent years, while the release or escape of animals from the pet trade increases (Genovesi et al. 2009).

The invasion process can be divided into a series of stages that range from transport and introduction to a new area, to establishment and spread (Blackburn et al. 2011). At each stage, barriers need to be overcome by individuals in order for them to pass on to the next stage. In the recipient area, individuals escape from any containment or are deliberately introduced (e.g. escaping or being released from gardens, pet cages, zoos, introductions for hunting or angling) to reach the new environment, where they can reproduce and establish themselves if they are able to adapt to the local climatic conditions (Mori et al. 2018). Species can then remain localised or spread over large areas, leading to impacts on ecosystems and human activities (Kumschick et al. 2015).

It is now recognised that to mitigate the impacts of non-native species it is necessary to adopt an integrated and hierarchical management strategy that may act on the different stages of the invasion process. This strategy should be based on prevention and should include the management of pathways and the screening of species that are likely to enter recipient areas, development of early warning and rapid response systems to react quickly to new invasions, and eradication or control of populations already established (Genovesi & Shine 2004). All these steps are for example included in European Union regulations that co-ordinate actions of member states against non-native species (Regulation EU 1143/2014, Tollington et al. 2017).

The successful prevention, early warning and management of non-native species are based on screening procedures and estimated likelihoods of the ability of species to adapt and spread in target areas. Spatially explicit models are important tools used in each of these steps. A growing number of modelling approaches are being used to estimate current and future distributions, abundance and population dynamics of non-native species (Lohr et al. 2017). These models link observed species' distributions to environmental variables and/or species-specific biological and behavioural features such as dispersal, adaptation, competition and other processes (Austin 2002). As the integration of all these variables in a single model is typically challenging, analyses take advantage of integrated models combining different techniques and approaches (Holcombe 2007). Several important modelling advancements have been developed in the last sixty years (Robinson et al. 2017). For example, our understanding of the spread process has advanced significantly from the early, purely theoretical models towards more sophisticated approaches, including empirical information on species' behaviour and responses to local environmental conditions (White et al. 2008). These models

have the power to provide more refined and robust predictions about establishment risks and likely patterns of spread, and can be directly applied for conservation and management purposes.

Modelling the distribution and effects of non-native species in a new area can be complex and needs to be supported by sound ecological information on the target species and its habitat requirements (Lohr et al. 2017). In fact, when species are introduced to a non-native area, they interact with other species directly or indirectly and this may generate unexpected effects (Cerri et al. 2017, Iacolina et al. 2019). An important approach to prevention is based on predicting the potential outcome of introductions according to ecological requirements of potential invaders and factors influencing the likelihood of establishment (Di Febbraro et al. 2013). Data on the native range of a species can be used to model its ecological niche and project the niche at the global scale to locate potential areas with increased establishment likelihood. Including future scenarios of global change, either climatic or land-use, allows the evaluation of future risk of expansion, thus informing management strategies (Hof et al. 2011, Di Febbraro et al. 2019). Available biotic and abiotic information at the global scale, together with recent developments in spatial modelling, have shed light on individual behavioural processes underlying population dynamics (Thuiller et al. 2005).

Among spatially explicit modelling approaches, species distribution models (SDMs) have been increasingly used to predict the spatial extent of invasions and identify areas at risk of invasion. However, modelling potential ranges of invasive organisms poses special challenges to ecological modellers, as extrapolated invasive species distribution models (iSDMs) may violate the assumption of the species being in equilibrium with environmental conditions, a fundamental working postulate for static iSDMs (Guisan & Thuiller 2005, Václavík & Meentemeyer 2009, but see also Chapman et al. 2019). Species are considered to be at equilibrium with their environment if they occur in all suitable locations and are absent from all unsuitable ones (Araujo & Pearson 2005). In fact, non-equilibrium is more likely under ecological scenarios that involve biotic interactions, metapopulation dynamics or slow colonisation after recent environmental changes. Non-equilibrium may significantly affect non-native species modelling, as departure from equilibrium is particularly likely in the earlier stages of invasion, due to colonisation time lag and dispersal limitations (Václavík & Meentemeyer 2009). The stage of invasion may influence iSDMs by affecting the extent to which occurrence observations do or do not match the species' environmental niche (Zimmermann et al. 2010). For example, if a species is at an early stage of invasion, sampling its emerging realised niche may capture only a small portion of the environmental conditions that are potentially characteristic of the organism, leading to an underestimated geographical range potentially colonized by the species. However, if a species is ecologically more specialised and exhibits strong habitat similarity between native and invaded areas (Rahbek et al. 2007), the environmental suitability of an area might be easier to predict. Thus, the relationship between sampling in a specific geographical area and approximation of a species' environmental niche is not straightforward.

Another approach is given by spatially explicit population dynamics models (SEPMs). These are mathematical models that combine accurate habitat information (e.g. land-cover data derived from remote sensing) with the simulation of life history processes such as reproduction, mortality and dispersal of a species, in order to predict its likely abundance and distribution. SEPMs can be employed to explore species' likely spread to inform policy-makers and managers on time scales and areas of expansion, as well as on the effort needed to take successful action (e.g. Bertolino et al. 2008).

The aim of this study is to review the use of spatially explicit models as tools to inform managers and scientists of the likelihood that a non-native mammal species (referred to as invasive alien species or IAS) may successfully overcome the different invasion stages. The structure of the review follows the composition of a hierarchical management strategy, i.e. it includes the steps prevention, early warning and rapid response, and management. Management includes eradication, spatial containment and population control.

## METHODS

We compiled a list of 261 mammal species introduced worldwide using the Global Invasive Species Database (GISD; ISSG 2015) and the Global Register of Introduced and Invasive Species (GRIIS; Pagad et al. 2018; Appendix S1).

To evaluate the role of spatially explicit modelling techniques in supporting risk assessment, early warning and rapid response, and management procedures for mammalian IAS, we performed a review of published studies using the Scopus search engine. Specifically, to set the search queries, we applied the following scheme: *model x IAS specific term x species*. In this scheme, *model* included: "species distribution models", "ecological niche models", "species distribution modelling" and "ecological niche modelling"; *IAS specific term* included: "invasive", "non-native", "alien", "introduced", "non-indigenous", "biological invasion"; and *species* included the 261 IAS. We restricted our literature search to studies published from 2000 to 2019. We also extended our search to appropriate titles included in the various reference lists.

The year 2000 cut-off was set so as to retrieve only those studies using spatially explicit models using the methods these tools assumed in recent years. This is particularly true about SDMs, where one of the first studies formalising theoretical principles and methodological steps as they are widely recognised today is Guisan and Zimmermann (2000). Although earlier studies using SDM-like approaches exist (e.g. Box 1981), current spatially explicit models have evolved considerably since those initial efforts.

We initially retrieved 2074 studies meeting the search criteria. After screening titles and abstracts, we removed those studies that addressed unrelated topics, retaining 62 studies (Appendix S2). Subsequently, we characterised the studies according to six Boolean categories: 1) "single- vs multi-species" (i.e. studies focused on one mammal IAS, vs. those including more than one IAS); 2) "worst100" (i.e. studies focused on a mammal listed in the "100 of the World's Worst Invasive Alien Species" [Lowe et al. 2004], vs. those focused on other mammal IAS); 3) "management" (i.e. studies that evaluated the effects of different management scenarios, vs. those which did not); 4) "spread" (i.e. studies focusing on mapping the expansion of the geographical range of one or more IAS, vs. those not mapping spread); 5) "future prediction" (i.e. studies providing predictions on future global change, i.e. climate and land-use, vs. those not providing such predictions); 6) "risk assessment and prevention" (i.e. studies carried out on IAS before their introduction in a given area, thus useful for risk assessment, vs. studies performed after IAS introduction and not useful for risk assessment). Each study was classified in each Boolean category according to its characteristics. Studies providing worldwide spatial predictions of invasion risk were considered useful for risk assessment. Lastly, we extracted the year of publication of each study. The list of 100 of the world's worst invasive species was produced by ISSG/IUCN experts with the aim to increase awareness of the risks and impacts of biological invasions amongst the general public and stakeholders; it contains 14 mammal species (Lowe et al. 2004). There have been several calls to extend this list (e.g. Nentwig et al. 2018, which is not the result of a ranking assessment, but it was based on expert opinion and representativeness of taxonomic and habitat diversity). However, we used the 'worst 100' list, because its widespread diffusion may have influenced the choice of species for researchers including spatial models.

Starting from the documents retrieved, we evaluated whether there was any temporal trend in the number of studies using models published on mammal IAS. We tested for the significance of this trend by fitting a generalised linear model with a Poisson error distribution (Poisson GLM), allowing for both linear and quadratic relationships. Subsequently, we quantified if there was any temporal trend in each of the Boolean categories. In this case too, we fitted a Poisson GLM for each Boolean category. Lastly, we fitted a log-linear model to test if there was a statistically significant difference among the frequencies of the studies belonging to each Boolean category.

## RESULTS

Of the 261 listed species, 26.8% occurred in published studies (Fig. 1). The mammalian orders Rodentia (34%), Artiodactyla and Carnivora (24% each) were the most represented. On the other hand, the orders Afrosoricida, Lipothyphla, Diprotodontia and Perissodactyla were the least represented, being the subject of only ca. 1% of the retrieved studies (Figure 2). Among families, Sciuridae and Muridae occurred in ca. 13% and 12% of the studies, and Bovidae and Cervidae each in ca. 9% (Fig. 2). Most of the studies were geographically concentrated in Oceania, western Europe, USA and south-western Asia. Some studies provided global (10) and continental-scale predictions (four for Europe and one for North America), while a few studies occurred in South Africa, Uruguay and Antarctica (Fig. 3). As for the six Boolean categories, most of the studies dealt with a single IAS (ca. 78%; Fig. 4), and about 59% of the studies were centred on mammal IAS listed among the ‘worst 100’. Furthermore, only ca. 15% of the studies dealt with IAS management topics, while almost 73% provided spatial predictions of potential IAS spread (Fig. 4). About 23% of the studies included spatial predictions of future global change scenarios. Only 29% of studies might be useful in a risk assessment procedure; the remaining 71% were carried out after IAS introduction events (Fig. 4). Most of the 29% studies were classified as useful in a risk assessment prevention context only because they provided worldwide predictions of invasion risk (Appendix S3). In fact, none of the studies used spatial models as a pure risk assessment tool for an IAS not yet found in a given study area.

SDMs are the most widely used model type for the management of IAS; in fact, they were used in about 80% of the studies (Appendix S3). More specifically, Maxent and Biomod2 were the most widely used software packages in the modelling studies of IAS; they were applied in about 49% and 33% of studies, respectively (Appendix S3).

The number of studies published between 2000 and 2019 on IAS increased significantly through time ( $R^2 = 0.55$ ), though the quadratic term of this relationship was not significant (Fig. 5). In addition, we found that all six Boolean categories except ‘management’ showed an increase in the percentage of the reference category, yet none of these trends was statistically significant (Appendix S4). Lastly, the log-linear model results showed significant differences among the frequencies of the studies falling into the six Boolean categories. Specifically, we found that studies providing predictions of potential spread were significantly overrepresented. In contrast, studies useful for risk assessment purposes, providing predictions on future global change, focusing on multiple IAS and dealing with management topics were significantly underrepresented (Fig. 6).

## DISCUSSION

### Prevention

Prevention is the most cost-effective action for a biosecurity policy aimed at reducing the impact of IASs. A strategy based on prevention should manage pathways of entry and prioritise species that may arrive in a recipient area and then impact biodiversity and human well-being.

Prioritisation requires developing lists of species that may reach a geographical area and evaluating their likelihood of entry, establishment, and spread, and the associated risk of impacts. Horizon scanning and risk assessment are two procedures increasingly used to screen species that may invade new areas. Applied to IAS management, horizon scanning is a technique that allows for rapid screening of a large number of species through expert opinion and consensus methods, with the aim of ranking the species to highlight potential future invaders before they arrive (Roy et al. 2014). Risk assessment is a more in-depth process of evaluating ecological and biological evidence to determine the level of invasion risk associated with a single species already present in an area, or one that has not arrived yet (Essl et al. 2011).

Modelling approaches for broad-scale screening procedures aim to predict which species have the characteristics to maintain viable populations and spread in a given area if they reach it. This

prediction is related to the concept of ecological niche, i.e. the range of ecological conditions within which a species can maintain viable populations (Hutchinson 1978). Most screening studies use SDMs including climate variables, as climate is often seen as the main driver at large spatial scales (Thuiller 2004), and layers with climatic data are readily available. Land-use and topographic variables may be more important at finer scales and are therefore used alone or in addition to climatic variables for local predictions (Pearson et al. 2004, Di Febbraro et al. 2019).

The application of SDMs to predict the possibility of a species' invasion before it arrives in a potential recipient area requires the fundamental assumption of so-called 'niche conservatism'. This assumes that the species' niche maintains its original features when the species reaches a new area (Peterson 2003). Under a niche conservatism approach, researchers calibrate their models using the species' native range to extrapolate the described climatic niche into new areas (Richardson & Thuiller 2007). However, risk assessment based only on the climatic niche calibrated in the native range is likely to underestimate suitable areas, as the species' observed niche may be constrained by ecological interactions (e.g. by competitors, predation, parasitism), and species may have the ability to adapt to new climatic conditions (Hof et al. 2011, Di Febbraro et al. 2013). Mammals, in particular, can also respond to climatic constraints by adapting their habitat choice or behaviour (Wong & Candolin 2015).

Risk assessment procedures involving SDMs deal with another important factor that may affect suitability predictions, namely the ability of a model to yield reliable predictions into unsampled space, i.e. model transferability. Model transferability is difficult to assess since it may depend on the general research objectives, as well as the dataset used for calibration and the choice of modelling algorithm (Sequeira et al. 2018). Although new metrics to quantify model transferability have been proposed (e.g. Bell & Schlaepfer 2016), further investigations are needed to provide a general interpretation of their appropriateness and effectiveness.

There is an ever-growing number of modelling studies predicting the likelihood of invasion by species that have not yet arrived in a target area, but to our best knowledge, no such study has yet dealt with mammals. Gallardo and Aldridge (2013), for example, predicted the risk of the invasion of Great Britain and Ireland by 12 aquatic species (invertebrates, fish and plants), some of them not present in the study area. The studies we retrieved were considered useful for risk assessment mainly because they made predictions of climatic suitability worldwide, while studies on mammals at a local scale before a species is introduced are still lacking. However, considering the amount of data needed for many modelling approaches, species considered for predictive models should be selected for their high likelihood of arriving in a country, e.g. by being present in neighbouring countries or common in the pet trade. Horizon scanning may be used to prioritise those that are most likely to arrive (Roy et al. 2014).

### **Early warning and rapid response**

An early warning and rapid response system (EWRRS) is a framework designed to respond to biological invasions through a co-ordinated system of several activities such as surveillance and monitoring, diagnosis of invading species, risk assessments, dissemination of information including reporting to competent authorities, and enforcement of appropriate responses. An EWRRS is often considered the second line of defence after prevention, and is a critical component of any effective invasive species management program (Robinson et al. 2017). In fact, it is crucial to improve our ability to detect and promptly report on new incursions of IAS, so that timely and reliable risk assessments can be produced, and effective management responses can be enacted wherever needed. If the system is effective and widespread through geographical areas, most of the new species will be reported at the beginning of invasion, when only few individuals are present in the recipient area (Robinson et al. 2017). Clearly, a rapid response can be useful in limiting eradication costs and damage to local ecosystems, particularly at an early invasion phase. Furthermore, timely eradications involve the removal of fewer animals than later ones, and may be more easily accepted by citizens and local stakeholders (Shackleton et al. 2019).

SDMs and SEPMs are valuable approaches for monitoring IAS, particularly for early detection and rapid assessment. In fact, these modelling tools might help to inform how a population could be spatially distributed in a new area and how it could react in a different environment. Ecologists have therefore used these models to analyse the current and future ranges of IAS, in order to assess their invasion ability and distribution patterns. An efficient EWRRS program is based on obtaining relevant information in a timely manner. Too often, the necessary knowledge was obtained only many years after the first report of IAS in a new area (e.g. Mori et al. 2015, Di Febbraro et al. 2016). A delayed use of models to help EWRRS is probably due to modellers' belief that a model needs to be well-parameterised and validated to be empirically useful. Model development and validation is a time-consuming process, which is problematic when an early response is vital to counteract the invasion and the spread of IAS. Even a preliminary model can be useful for identifying potential knowledge gaps to be filled and providing guidelines for initial risk assessments.

IAS of many taxa have been analysed using SDMs and SEPMs (e.g. Gallardo & Aldridge 2013). However, invasive alien mammals appear to be an exception, particularly when it comes to early detection and rapid assessment of their potential spread. The majority of models used to predict mammalian IAS distributions in EWRRS are ecological models which result in IAS prediction maps, and, less commonly, spatial-temporal models (Bertolino et al. 2008). These maps are particularly useful to managers that are responsible for monitoring the spread of IAS and conducting associated early response actions. Modelling studies have successfully been carried out for some alien mammal species, such as the Northern raccoon *Procyon lotor*, squirrel species (family Sciuridae), coypu *Myocastor coypus*, brushtail possum *Trichosurus vulpecula* (see Appendix S3).

Currently, SDMs are the modelling method most commonly applied to the management of IAS at an early stage of invasion (Appendix S3). SDMs and SEPMs have mainly been used to: 1) predict current and future potential distribution of IAS; 2) detect IAS dispersal corridors and hot spots for their invasion; and 3) know the rate of expansion of IAS since the estimated date of their introduction. The results of these modelling approaches have been used to assess the potential impacts of IAS expansion on the conservation of local biodiversity and environment. Often the expansion of a species is linked to the presence of another, and a recent modelling approach incorporates species co-occurrence data into an SDM to create a joint species distribution model (Pollock et al. 2014). However, a test of this approach to see how well joint species distribution models can detect species interactions from co-occurrence data suggests that they work for mutualism and competition but fail to detect predator-prey interactions (Zurell et al. 2018).

Despite the potential advantages offered for IAS control, spatially explicit models have not been incorporated into systematic management planning due to, for example, computational challenges (Cattarino et al. 2016). Yet, the efficiency of these tools in predicting invasions is of primary importance for preventive invasion planning, as the eradication of IAS after their establishment is expensive and often unsuccessful. Accurate modelling approaches may produce alternative scenarios to evaluate the risk of spread of new species, which may be useful for the application of EWRRS.

## **Management**

Eradication is a fundamental tool for protecting biodiversity from the negative effects of IAS (Howald et al. 2007, Robertson et al. 2017, Capizzi 2020). If removal actions do not obtain the expected result, the only option may be to move on to continuous control (Mill et al. 2020b). Therefore, careful planning is necessary to evaluate feasibility and effort needed for eradication, and field work should be adaptive (Martin & Lea 2020, Richardson et al. 2020). Modelling procedures have been used to evaluate the effectiveness of different management options and the effort needed for eradication (e.g. Tattoni et al. 2006). When eradication is considered impracticable, spatial containment or population control could be considered as the next logical option. Since these interventions are generally planned in the long term, a cost-benefit analysis is necessary to evaluate their sustainability.

Potential distribution maps derived from SDMs could support decision-making processes and management planning. Risk maps may be used to direct monitoring in a cost-effective way (see Lioy



et al. 2019 for an example with an invasive hornet), and to plan and evaluate control activities. Regression modelling was applied in a review of 15 large-scale removals of IAS in northern Europe in order to learn from these efforts (Robertson et al. 2017). This synthesis recommended a rapid response to new introductions as best practice to limit impacts to the environment as well as financial and welfare costs resulting from large-scale removals. An SEPM was used by Rushton et al. (2002) to simulate the impact and costs of introduced Eastern grey squirrels *Sciurus carolinensis* control operations on native Eurasian red squirrels *Sciurus vulgaris* in the UK. The model investigated both the removal of grey squirrels and the potential effect of proposed immunocontraception method (see Mill et al. 2020a for an application on goats). However, the model outcomes on grey squirrel control were not validated and findings remain speculative.

Spatially explicit models are particularly useful when the competitive effects of an IAS on native species are mediated by a third factor, such as a disease. The outcomes in this system are potentially complex and heterogeneous in both space and time. A classic example of disease-mediated competition is the case of Eastern grey squirrels in the UK where the species carries a squirrelpox virus lethal to the native Eurasian red squirrel (e.g. Lawton et al. 2010). SEPMs have been employed to evaluate to what extent the virus carried by grey squirrels is responsible for red squirrel decline in the northwest of England (Rushton et al. 2006). Whilst in the case of tree squirrels their link to forest cover is easily mapped and their ecology in Europe is well understood, a criticism of SEPM approaches has been their complexity, data needs, and attempts to model processes that are sometimes poorly understood.

A more recent and more transparent mathematical modelling approach for the red-grey-squirrel-pox system was taken by White et al. (2014), who also simulated the impacts of control and disease. The authors developed a framework that falls between deterministic and rule-based approaches, and represents the stochastic nature of successful IAS spread. The intricate interplay between an IAS, disease and landscape characteristics favouring dispersal and thus disease spread was also explored by White et al. (2017) with a spatially explicit version of the model.

Most modelling studies included in this review pertain to a few species, e.g. squirrels, coypu, brushtail possum, wild boar *Sus scrofa*. The success in modelling tree squirrels in the above-mentioned studies may be related to their close link to forest cover, a feature that is easily mapped, as well as the availability of good ecological data. Their appeal to the general public and the related interest may also have favoured availability of research funding and modelling exercises. In the same way, coypu modelling was facilitated by the close link of this semiaquatic rodent with easily mapped water bodies, while possum and wild boar are two species with relevant impacts on biodiversity, crops (wild boar) and livestock (as the brushtail possum is a vector of bovine tuberculosis).

Among the limitations of our review, we acknowledge that we might have underestimated the number of studies using spatially explicit models on IAS, as a large portion of them is likely to be confined to the grey literature. Furthermore, we did not cover the entire range of modelling techniques that have been used to investigate IAS, such as e.g. pathway modelling, metapopulation and population viability models, connectivity models, individual-based models, network analysis, etc. Lastly, we might have missed some relevant old studies due to our decision to limit research scanning to the last ca. 20 years. While acknowledging these overall drawbacks, we are confident that we describe rather comprehensively the general trends in mainstream research papers and modelling tools that have focused on mammal IAS phenomenon in recent years.

The process of diffusion of emerging infectious diseases is similar to the process of IAS invasions, as disease vectors are technically IAS themselves (e.g. Crawl et al. 2008). However, a detailed search and review of this topic went beyond the scope of this study.

## CONCLUSION

Human-mediated movement of species around the world is one of the main drivers of ecosystem change and biodiversity loss (Kumschick et al. 2015). SDMs and SEPMS are useful tools that can inform screening procedures and decision-making processes related to IAS management. These models have been used to inform researchers and managers acting at every stage of the invasion process, from prevention to establishment and spread, as well as for evaluating impacts. Modelling procedures are particularly useful in planning and evaluating management actions, since they can be used to explore, compare and assess the implications of different scenarios in terms of likely success, cost and effort needed. Maxent and Biomod2 are currently the software packages most commonly used to study these fields, perhaps because they are free and have accurate prediction ability. However, there has been little or no research into whether SDMs are actually reliable predictors of potential establishment and spread of introduced species. The validation of model simulations with field data should be investigated in the future.

Our review evaluated the use of SDMs and SEPMS in published studies. However, many other examples may have been reported in the grey literature, especially in risk-assessment evaluations and management plans. Most of the studies we reviewed used climate matching to evaluate the suitability of geographic areas worldwide. At the local scale, published studies mainly explored the risk of species that were already established expanding their range. This was also investigated in relation to different future global change scenarios. Whilst SDMs could easily be used to evaluate the suitability of recipient areas before species are introduced, this kind of assessment has not been reported yet in the mammal literature, though examples may occur in unpublished reports.

SEPMS link simulation of population dynamics with predictions of species' distribution. Therefore, they could be used to evaluate population changes over time linked to accurate landscape descriptions (land cover data, forest cover maps etc.). These models are therefore particularly useful for comparing different management scenarios.

The effectiveness of SDMs and SEPMS is based on the availability of distribution data. Large open databases, such as GBIF ([www.gbif.org](http://www.gbif.org)) and iNaturalist ([www.inaturalist.org](http://www.inaturalist.org)), and the availability of many regional sources of records now make species distribution data easily available. Moreover, many information systems and online databases have been created specifically for reporting biological invasions at different spatial scales, and are connected with citizen science projects (see Katsanevakis & Roy 2015 and references therein).

Overall, SDMs and SEPMS have proven to be important tools for implementing effective management strategies for invasive alien mammals, but published papers on this application are still limited, and most modelling evaluation probably remains confined to the grey literature. We hope that this review will stimulate researchers to make more extensive use of these models during IAS management, and to publish their results in order to share their experiences and make them available to researchers working on other projects.

## REFERENCES

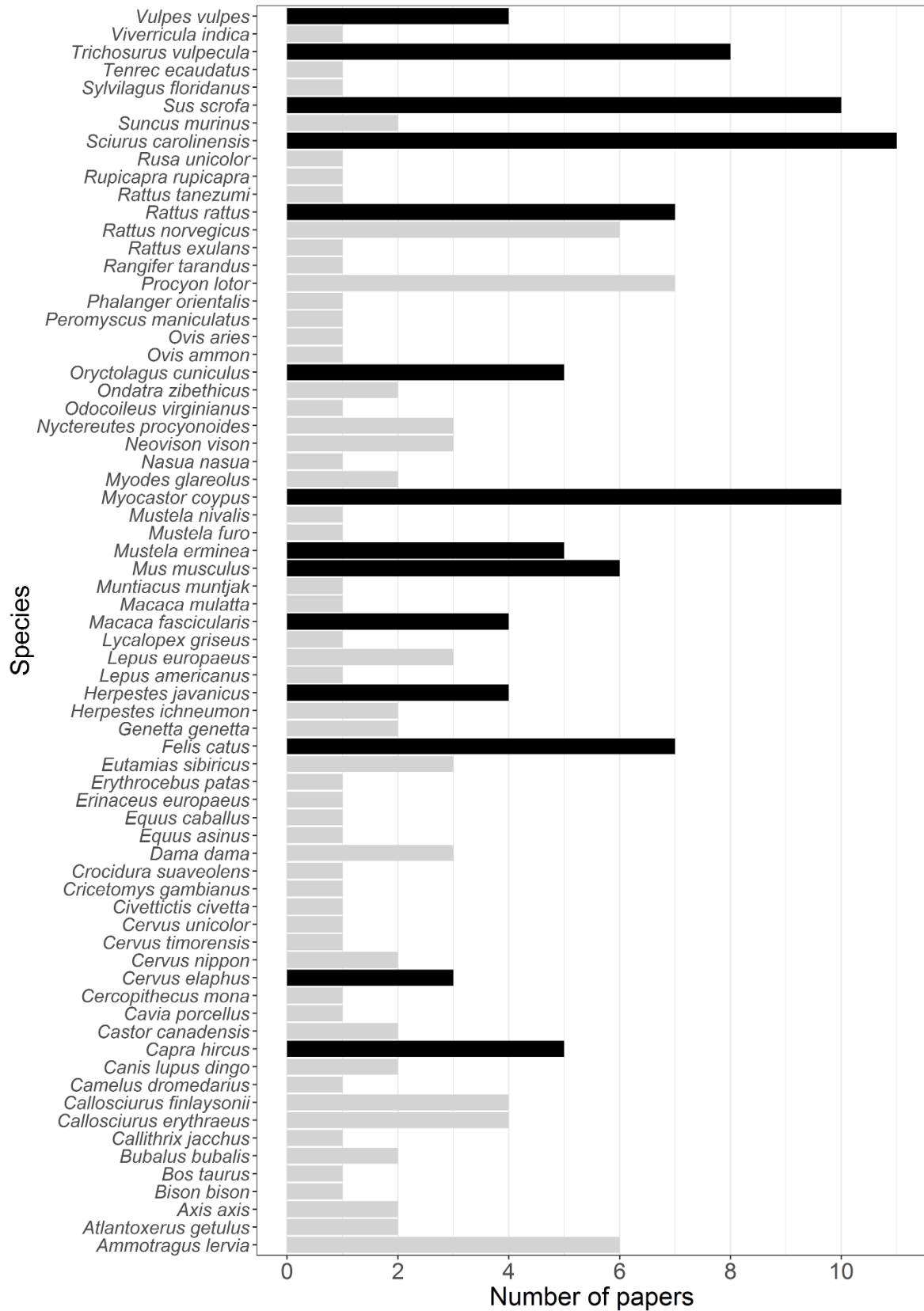
- Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography* 28: 693–695.
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101–118.
- Bell DM, Schlaepfer DR (2016) On the dangers of model complexity without ecological justification in species distribution modeling. *Ecological Modelling* 330: 50–59.
- Bertolino S, Lurz PWW, Sanderson R, Rushton S (2008) Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: a call for a co-ordinated European approach. *Biological Conservation* 141: 2564–2575.

- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339.
- Box EO (1981) Predicting physiognomic vegetation types with climate variables. *Vegetatio* 45: 127–139.
- Capizzi D (2020) A review of mammal eradications on Mediterranean islands. *Mammal Review* 50: in press.
- Cattarino L, Hermoso V, Bradford LW, Carwardine J, Wilson KA, Kennard MJ, Linke S (2016) Accounting for continuous species' response to management effort enhances cost-effectiveness of conservation decisions. *Biological Conservation* 197: 116–123.
- Cerri J, Ferretti M, Bertolino S (2017) Rabbits killing hares: an invasive mammal modifies native predator–prey dynamics. *Animal Conservation* 20: 511–519.
- Chapman D, Pescott OL, Roy HE, Tanner R (2019) Improving species distribution models for invasive non-native species with biologically informed pseudo-absence selection. *Journal of Biogeography* 46: 1029–1040.
- Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment* 6: 238–246.
- Di Febbraro M, Lurz PW, Genovesi P, Maiorano L, Girardello M, Bertolino S (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: a case with the American eastern grey squirrel. *PloS one* 8: e66559.
- Di Febbraro M, Martinoli A, Russo D, Preatoni D, Bertolino S (2016) Modelling the effects of climate change on the risk of invasion by alien squirrels. *Hystrix, the Italian Journal of Mammalogy* 27: 1–8.
- Di Febbraro M, Menchetti M, Russo D, Ancillotto L, Aloise G, Roscioni F et al. (2019) Integrating climate and land-use change scenarios in modelling the future spread of invasive squirrels in Italy. *Diversity and Distributions* 25: 644–659.
- Essl F, Nehring S, Klingenstein F, Milasowszky N, Nowack C, Rabitsch W (2011) Review of risk assessment systems of IAS in Europe and introducing the German-Austrian black list information system (GABLIS). *Journal for Nature Conservation* 19: 339–350.
- Gallardo B, Aldridge DC (2013) The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. *Journal of Applied Ecology* 50: 757–766.
- Genovesi P, Shine C (2004) European strategy on invasive alien species. *Nature and Environment* 161: 1–73.
- Genovesi P, Bacher S, Kobelt M, Pascal M, Scalera R (2009) Alien mammals of Europe. In: Hulme PE (ed) *Handbook of Alien Species in Europe*, 119–128. Springer, Dordrecht, the Netherlands.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.
- Hof C, Levinsky I, Araujo MB, Rahbek C (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology* 17: 2987–2990
- Holcombe T, Stohlgren TS, Jarnevich C (2007) Invasive species management and research using GIS. In: Witmer G, Pitt WC, Fagerstone KA, Clark CA (eds) *Managing Vertebrate Invasive Species: Proceedings of an International Symposium*, 108–114. USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, Colorado, USA.
- Howald G, Donlan CJ, Galvan JP, Russell JC, Parkes J, Samaniego A et al. (2007) Invasive rodent eradication on islands. *Conservation Biology* 21: 1258–1268.
- Hutchinson GE (1978) *An Introduction to Population Ecology*. Yale University Press, New Haven, Connecticut, USA.

- Iacolina L, Corlatti L, Buzan E, Safner T, Šprem N (2019) Hybridisation in European ungulates: an overview of the current status, causes, and consequences. *Mammal Review* 49: 45–59.
- Invasive Species Specialist Group ISSG 2015. The Global Invasive Species Database. Version 2015.1
- Katsanevakis S, Roy HE (2015) Alien species related information systems and information management. *Management of Biological Invasions* 6: 115–117.
- Kumschick S, Gaertner M, Vila M, Essl F, Jeschke JM, Pysek P et al. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* 65: 55–63.
- Lawton C, Cowan P, Bertolino S, Lurz PWW, Peters AR (2010) The consequences of introducing non-indigenous species: two case studies, the grey squirrel in Europe and the brushtail possum in New Zealand. *Scientific and Technical Review of the Office International des Epizooties* 29: 287–298.
- Lioy S, Manino A, Porporato M, Laurino D, Romano A, Capello M, Bertolino S (2019) Establishing surveillance areas for tackling the invasion of *Vespa velutina* in outbreaks and over the border of its expanding range. *NeoBiota* 46: 51–69.
- Lohr CA, Hone J, Bode M, Dickman CR, Wenger A, Pressey RL (2017) Modeling dynamics of native and invasive species to guide prioritization of management actions. *Ecosphere* 8: e01822.
- Lowe S, Browne M, Boudjelas S, De Poorter M (2004) 100 of the World's Worst Invasive Alien Species. A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) (Eds.), Auckland, New Zealand.
- Martin AR, Lea VJ (2020) A mink-free GB: perspectives on eradicating American mink *Neovison vison* from Great Britain and its islands. *Mammal Review* 50: in press.
- Mill A, Cowan D, van der Waal Z, Pidcock S, Gomm M, Stephens N, Brash M, White P, Mair L (2020a) Adaptive management of an iconic invasive goat *Capra hircus* population. *Mammal Review* 50: in press.
- Mill A, Crowley S, Lambin X, McKinney C, Maggs G, Robertson P, Robinson N, Ward A, Marzano M (2020b) The challenges of long-term invasive mammal management: lessons from the UK. *Mammal Review* 50: in press.
- Mori E, Mazza G, Menchetti M, Panzeri M, Gager Y, Bertolino S, Di Febbraro M (2015) The masked invader strikes again: the conquest of Italy by the Northern raccoon. *Hystrix, the Italian Journal of Mammalogy* 26: 47–51.
- Mori E, Zozzoli R, Menchetti M (2018) Global distribution and status of introduced Siberian chipmunks *Eutamias sibiricus*. *Mammal Review* 48: 139–152.
- Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilà M (2018) More than “100 worst” alien species in Europe. *Biological Invasions* 20: 1611–1621.
- Pagad S, Genovesi P, Carnevali L, Schigel D, McGeoch MA (2018) Introducing the Global Register of Introduced and Invasive Species. *Scientific Data* 5:170202.
- Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27: 285–298.
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78: 419–433.
- Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM et al. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5: 397–406.
- Rahbek C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFL, Graves GR (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B* 274: 165–174.
- Richardson DM, Thuiller W (2007) Home away from home – objective mapping of high-risk source areas for plant introductions. *Diversity and Distributions* 13: 299–312.
- Richardson S, Mill A, Davis D, Jam D, Ward A (2020) A systematic review of adaptive wildlife management for the control of invasive, non-native mammals and other human-wildlife conflicts. *Mammal Review* 50: in press.

- Robertson PA, Adriaens T, Lambin X, Mills A, Roy S, Shuttleworth CM, Sutton-Croft M (2017) The large-scale removal of mammalian invasive alien species in Northern Europe. *Pest Management Science* 73: 273–279.
- Robinson AP, Walshe T, Burgman MA, Nunn M (eds; 2017) *Invasive Species: Risk Assessment and Management*. Cambridge University Press, Cambridge, UK.
- Roy HE, Peyton J, Aldridge DC, Bantock T, Blackburn TM, Britton R et al. (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology* 20: 3859–3871
- Rushton SP, Gurnell J, Lurz PWW, Fuller RM (2002) Modeling impacts and costs of gray squirrel control regimes on the viability of red squirrel populations. *Journal of Wildlife Management* 66: 683–697.
- Rushton SP, Lurz PWW, Gurnell J, Nettleton P, Bruemmer C, Shirley MDF, Sainsbury AW (2006) Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology & Infection* 134: 521–533.
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke J et al. (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435.
- Sequeira AM, Bouchet PJ, Yates KL, Mengersen K, Caley MJ (2018) Transferring biodiversity models for conservation: opportunities and challenges. *Methods in Ecology and Evolution* 9: 1250–1264.
- Shackleton RT, Adriaens T, Brundu G, Dehnen-Schmutz K, Estévez RA, Fried J et al. (2019) Stakeholder engagement in the study and management of invasive alien species. *Journal of Environmental Management* 229: 88–101.
- Stoett P, Roy HE, Pauchard A (2019) Invasive alien species and planetary and global health policy. *The Lancet Planetary Health* 3: e400–e401.
- Tattoni C, Preatoni DG, Lurz PWW, Rushton SP, Tosi G, Martinoli A, Bertolino S, Wauters LA (2006) Modelling the expansion of grey squirrels (*Sciurus carolinensis*) in Lombardy, Northern Italy: implications for squirrel control. *Biological Invasions* 8: 1605–1619.
- Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10: 2020–2027.
- Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234–2250.
- Tollington S, Turbé A, Rabitsch W, Groombridge JJ, Scalera R, Essl F, Shwartz A (2017) Making the EU legislation on invasive species a conservation success. *Conservation Letters* 10: 112–120.
- Vaclavik T, Meentemeyer RK (2009) Invasive species distribution modeling (iSDM): are absence data and dispersal constraints needed to predict actual distributions?. *Ecological Modelling* 220: 3248–3258.
- White A, Bell SS, Lurz PWW, Boots M (2014) Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. *Journal of Applied Ecology* 51: 1631–1642.
- White A, Bell SS, Lurz PWW, Bryce J, Tonkin M, Ramoo K, Bamforth L, Jarrott A, Boots M (2017) Modelling disease spread in real landscapes: squirrelpox spread in Southern Scotland as a case study. *Hystrix, the Italian Journal of Mammalogy* 27: 1–8.
- White PC, Ford AE, Clout MN, Engeman RM, Roy S, Saunders G (2008) Alien invasive vertebrates in ecosystems: pattern, process and the social dimension. *Wildlife Research* 35: 171–179.
- Wong B, Candolin U (2015) Behavioral responses to changing environments. *Behavioral Ecology* 26: 665–673.
- Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning JC (2010) New trends in species distribution modelling. *Ecography* 33: 985–989.

Zurell D, Pollock LJ, Thuiller W (2018) Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments?. *Ecography* 41: 1812–1819.

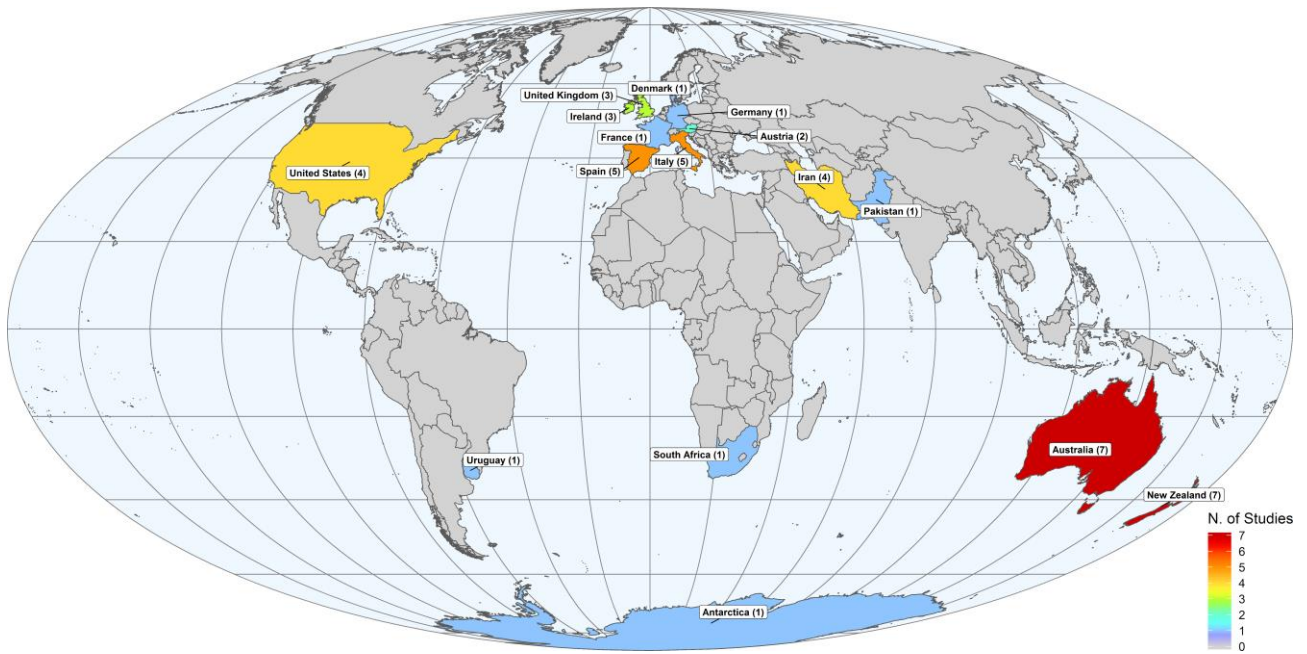


**Fig. 1.** Number of studies based on models retrieved for this review, for each mammal IAS. We excluded from the figure all species for which we did not find any published studies. Bars are shown in black for IAS listed among the “100 of the World's Worst Invasive Alien Species” (Lowe et al. 2004).

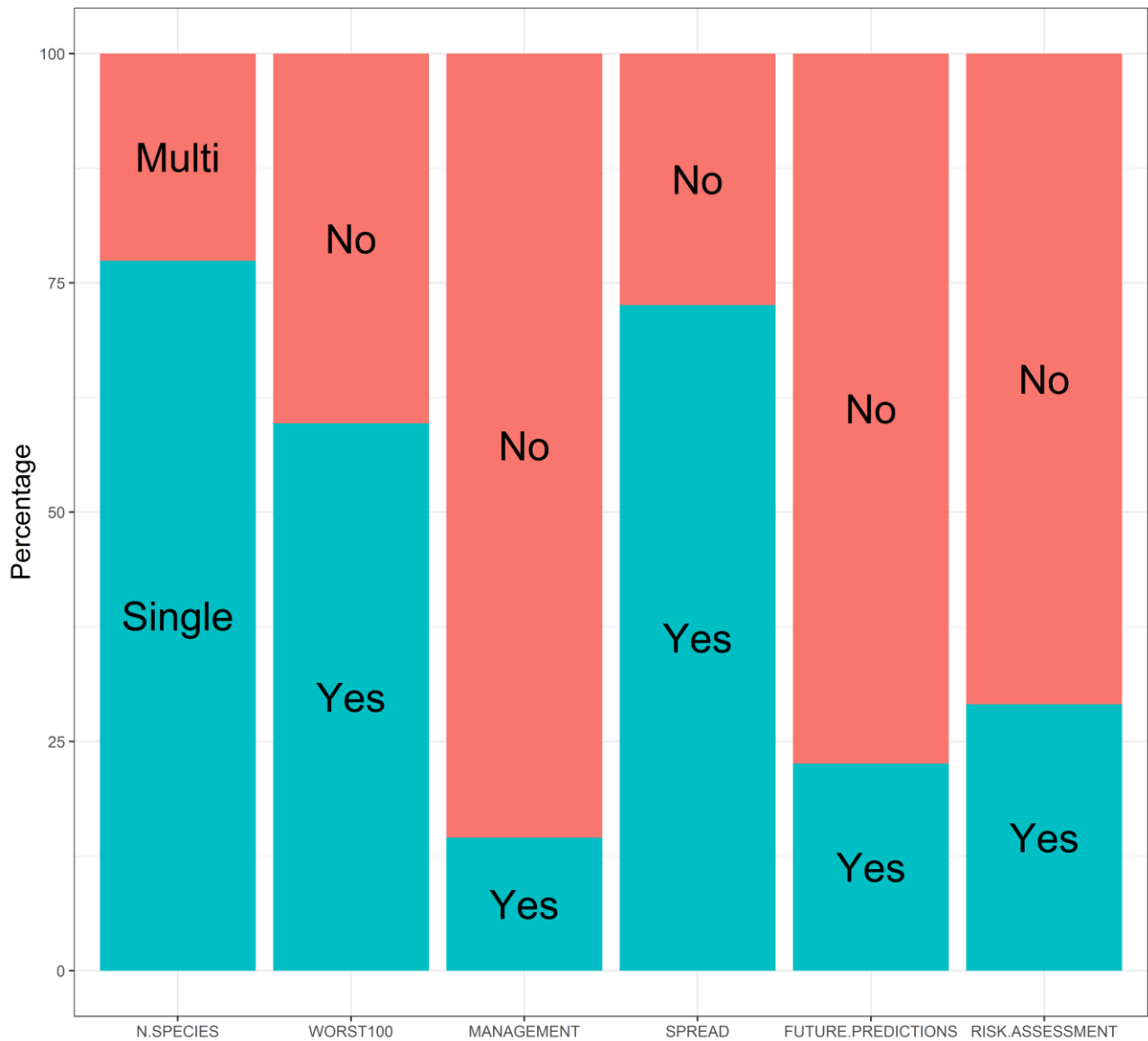


**Fig. 2.** The 62 studies on mammalian IAS included in the review, divided by mammalian orders (left) and families (right).

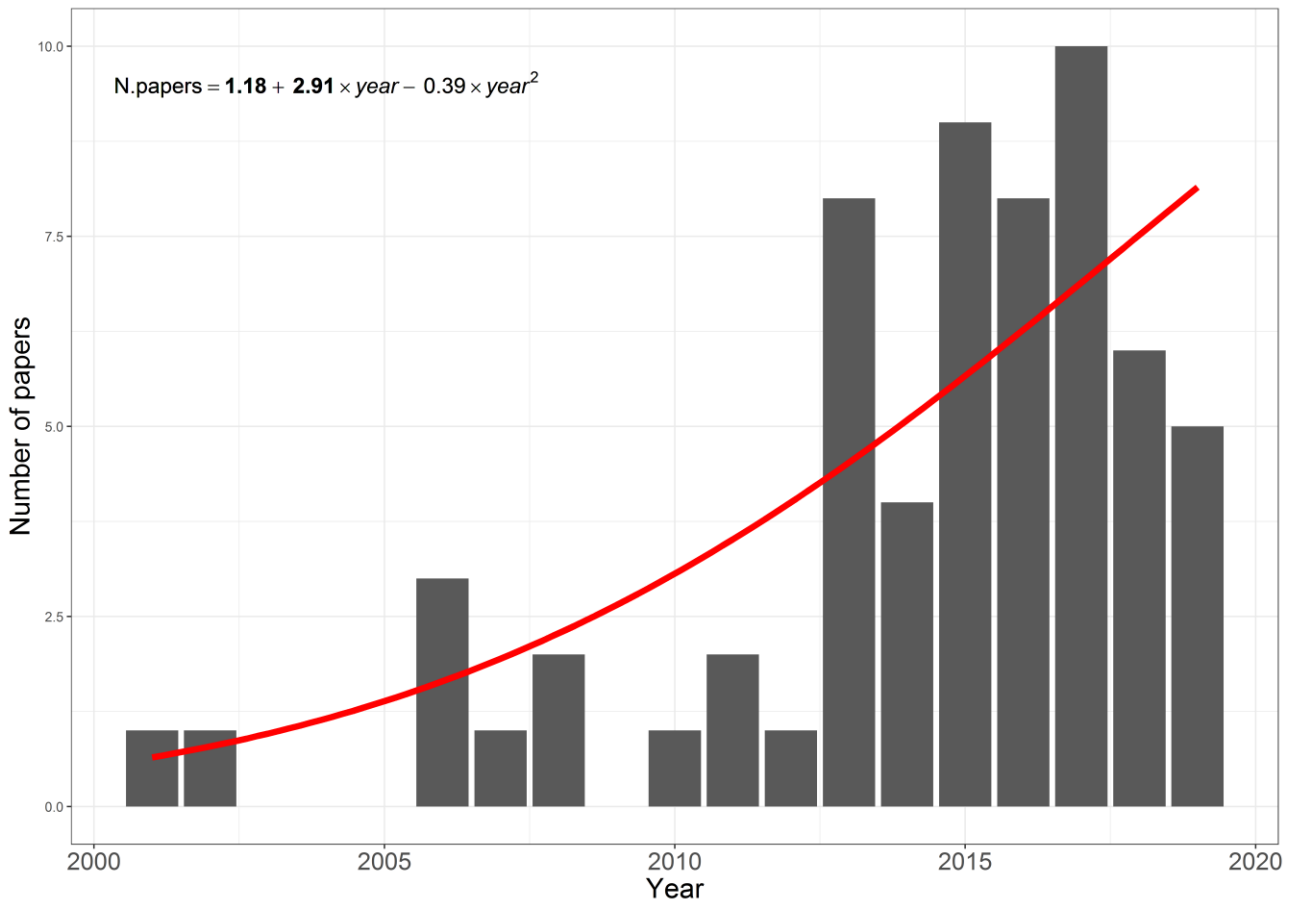




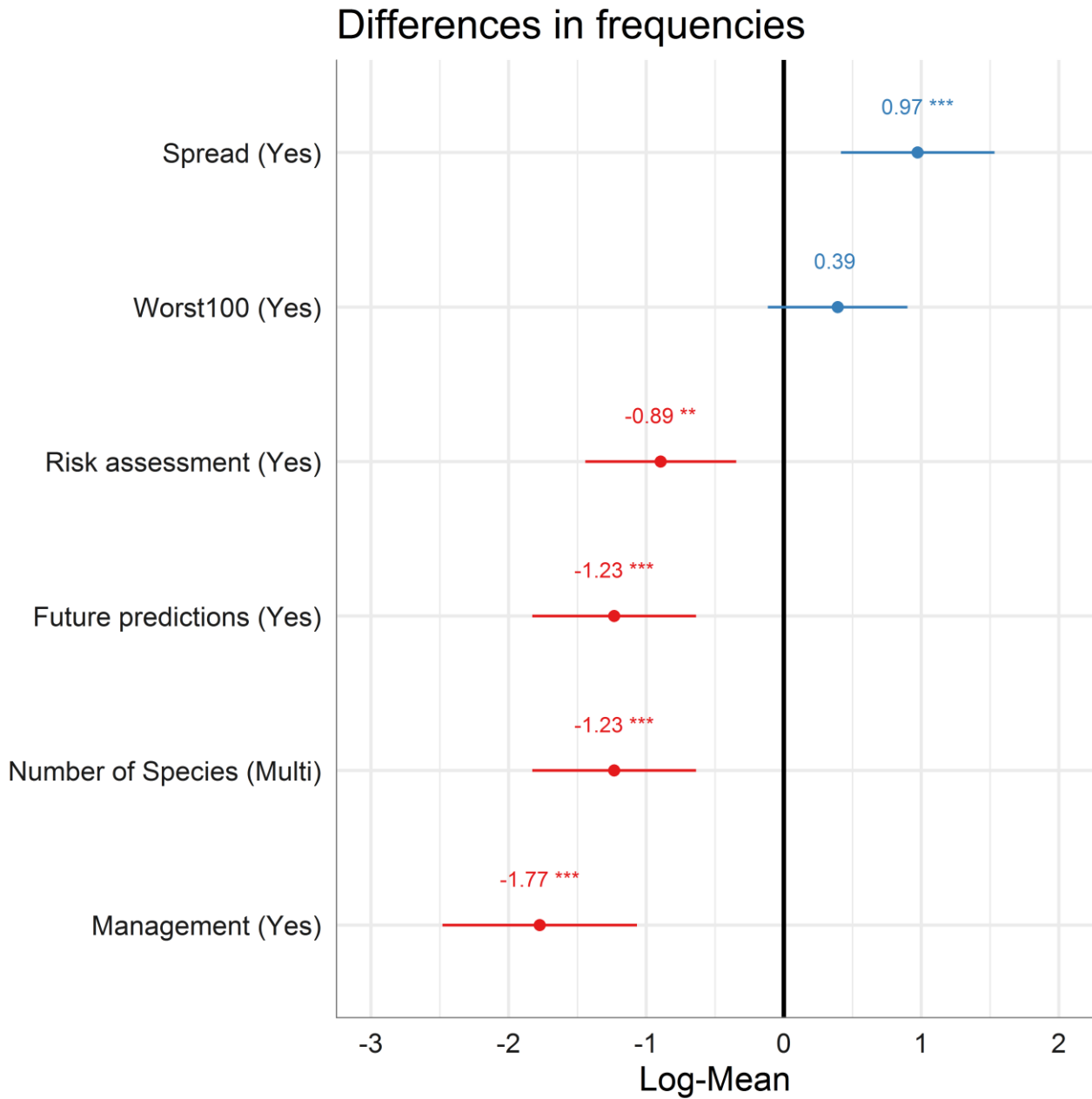
**Fig. 3.** Geographical distribution of the studies on mammalian IAS. The 14 global and continental-scale studies are not shown.



**Fig. 4.** Percentage of studies included in the review in each of the six Boolean categories: 1) “single- vs multi-species” (i.e. studies focused on one mammal IAS, vs. those including more than one IAS); 2) “worst100” (i.e. studies focused on a mammal listed in the “100 of the World's Worst Invasive Alien Species” [Lowe et al. 2004], vs. those focused on other mammal IAS); 3) “management” (i.e. studies that evaluated the effects of management scenarios, vs. those which did not ); 4) “spread” (i.e. studies focusing on mapping the expansion of the geographical range of one or more IAS, vs. those not mapping spread); 5) “future prediction” (i.e. studies providing predictions on future global change, i.e. climate and land-use, vs. those not providing such predictions); 6) “risk assessment and prevention” (i.e. studies carried out on IAS before their introduction in a given area, thus useful for risk assessment, vs. studies performed after IAS introduction and not useful for risk assessment).



**Fig. 5.** Number of studies retrieved that were published in each year between 2000 and 2019. The curve depicts the temporal trend modelled with the Poisson GLM. Model coefficients are shown in the equation in the upper-left corner. Values in bold indicate statistically significant coefficients.



**Fig. 6.** Difference in study frequency among the six Boolean categories. Dots depict coefficient estimates derived by the log-linear model, while the whiskers indicate the related standard error around each estimate (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ). In parentheses, we report the reference levels of each Boolean category used in frequency comparisons.

**Appendix S1.** List of mammal species that have been introduced worldwide.

**Appendix S2.** Compiled data from 62 publications found in the literature and included in this review.

**Appendix S3.** Location of research, model type, software package and reference for each species in the studies included in the review.

**Appendix S4.** Temporal trend of studies classified according to the six Boolean categories