Title

Recent advances of quantitative modelling to support invasive species eradication on islands

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ABSTRACT

The eradication of invasive species from islands is an important part of managing these ecologically unique and at-risk regions. Island eradications are complex projects and mathematical models play an important role in supporting efficient and transparent decision-making. In this review we cover the past applications of modelling to island eradications, which range from large-scale prioritisations across groups of islands, to project-level decision-making tools. While quantitative models have been formulated and parameterised for a range of important problems, there are also critical research gaps. Many applications of quantitative modelling lack uncertainty analyses, and are therefore over-confident. Forecasting the ecosystem-wide impacts of species eradications is still extremely challenging, despite recent progress in the field. Overall, the field of quantitative modelling is well-developed for island eradication planning. Multiple practical modelling tools are available for, and are being applied to, a diverse suite of important decisions, and quantitative modelling is well-placed to address pressing issues in the field.

INTRODUCTION

Despite their small landmass, islands support a large proportion of global biodiversity and an even greater proportion of threatened biodiversity (Mittermeier et al. 2004). Through a combination of environmental uniqueness, isolation, and their sheer number (there are hundreds of thousands of recognised islands (Sayre et al. 2019)), islands have evolved into hotspots of endemism: approximately 15% of the world's vertebrate species and 20% of the world's vascular plants are endemic to islands (Millennium Ecosystem Assessment 2005). In the Anthropocene, high human population densities, along with the acceleration of existing invasion processes, and the creation of new ones, have made them hotspots of species extinction and threat. Almost half of all recorded animal extinctions have been species that were endemic to islands (Duncan et al. 2013; Tershy et al. 2015).

Islands are not only biologically unique, they present unique conservation challenges. Their remote location creates logistical challenges that drive up the costs of management and risks of failure (Holmes et al. 2015). However, this same spatial isolation can be beneficial, as it may make it easier to quarantine the island from future human impacts – although invasive species are currently more prevalent on more isolated islands

(Moser et al. 2018). Their small spatial scale makes intensive management feasible (e.g., invasive species eradications), but it also means that their ecosystems are small and vulnerable, both to environmental and demographic stochasticity. Small ecosystems are more prone to instability, which can exaggerate natural population dynamics into threatening cycles (Gerlach 2001).

Invasive species are a major driver of island extinctions, and effectively managing invasive populations can deliver enormous benefits to island species and ecosystems (Veitch & Clout 2002; Jones et al. 2016). Consistent, long-term control of invasive populations can be effective, but eradication is often the goal of conservation organisations, since it has several benefits (Simberloff 2014). Firstly, a successful eradication project has a finite timespan, and securing funding for short-term projects with specific outcomes can be easier than asking for indefinite funding for ongoing control (Bomford & O'Brien 1995). Eradication completely removes a threat from the ecosystem, which can have significant benefits compared to keeping a species at low density: single individuals of invasive predators can cause huge damage and the mere presence of a species can cause behaviour change in others (Lima 2002). Eradication of invasive species from islands has already delivered enormous benefits to global conservation (Simberloff et al. 2018), including species conservation benefits to 236 species (Jones et al. 2016).

Island eradications are complex projects, affected by diverse factors. Quantitative modelling and optimisation has an important role to play in supporting island eradication decisions. A mathematical formulation helps to make explicit our assumptions and understanding of complex system dynamics, predict the efficacy of management alternatives, and forecast novel environmental changes. It should take the form of equations that can clearly compare the relative performance of any two potential conservation actions. In conjunction with modelling, optimisation methods can support conservation decision-making by pinpointing efficient and effective management strategies (García-Díaz et al. 2019).

There is an important distinction between a mathematical model and decision-support tools, and both are important when discussion modelling to support decisions on islands. Models are primarily for predicting or estimating aspects of the system. For example, to estimate the current population density of a species, or to predict how many years it would take to eradicate an invasive species, for a certain management strategy. In contrast, decision-support tools typically use the results of a mathematical model to help determine the effectiveness of different management strategies. For example, to determine how to split resources between baiting and trapping to achieve eradication quickly.

PURPOSE OF THE REVIEW

In this paper we review island invasive eradication challenges that have been productively addressed using quantitative modelling approaches and decision-support tools. Broadly, these modelling approaches belong to two categories. First, we review strategic problems, which decide which islands should be targeted for invasive species eradication (Figure 1A). These models support between-island decisions, and their choices are based on large databases, and statistical or expert-derived models of eradication cost and feasibility. Second, we review tactical problems, which focus on individual islands (Figure 1B). These models estimate quantities such as the probability of reinvasion, or the effectiveness of survey methods at detecting the presence of invasive species, and help managers to choose between the different options available to them. These within-island decisions generally offer a more diverse set of choices than the between-island models. For example: which species to target, what eradication methods to use, or for how long to apply those methods.

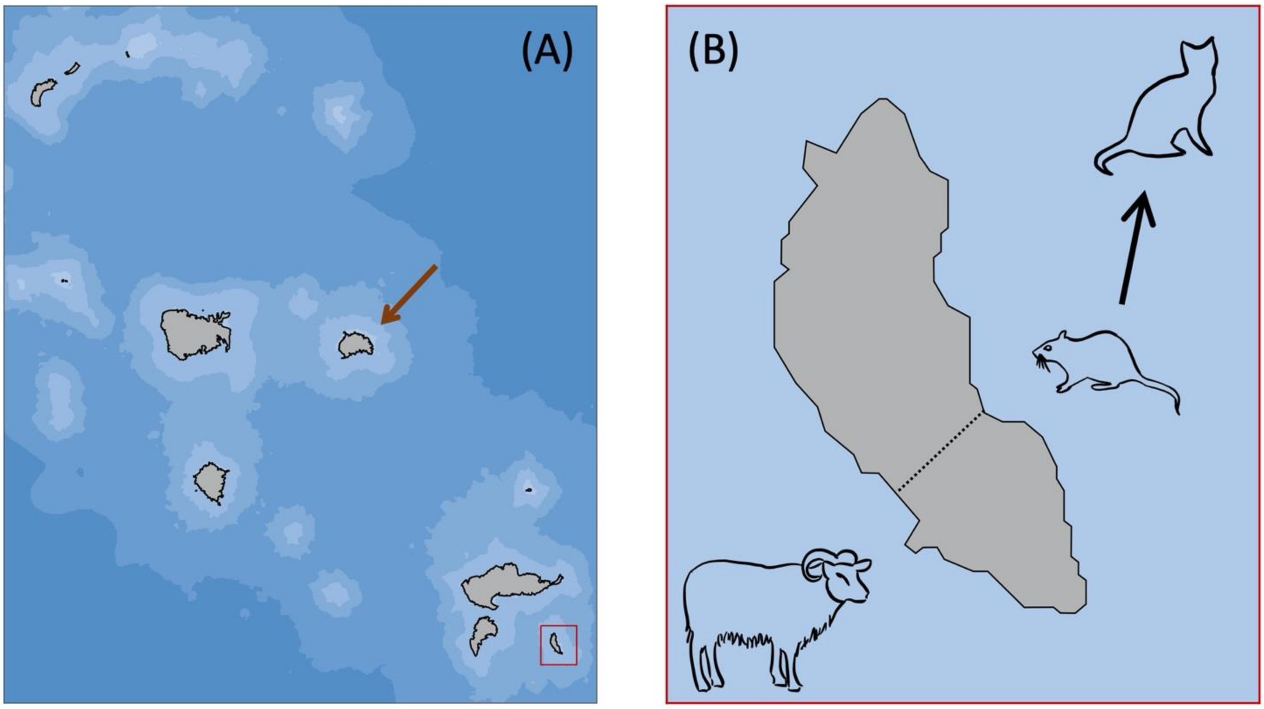

Figure 1: Panel (A) shows an example of a strategic, between-island eradication decision problem. The map shows the Marquesas Island group, in French Polynesia. Many of these islands contain invasive vertebrates, and differ in size, biogeography, threatened and invasive species, etc. Bathymetry, an important determinant of reinvasion risk, is shown by shaded contour lines. Invasive eradication projects have already occurred on Teuaua (indicated by the arrow) which were successful for Rattus exulans, but *unsuccessful for* R. rattus. *Projects are planned for 6 other islands in the group. Panel (B) focuses shows an example of tactical, within-island eradication decisions on Mohotani (indicated by the red box in panel A). Here, a planned eradication program will target rats* (Rattus rattus)*, cats* (Felis catus)*, and domestic sheep* (Ovis aries). *These three species require different eradication actions and have varied probabilities of success. In addition, cats and rats have a predator-prey relationship which will be disrupted by eradication actions. The dashed line suggests a potential internal fence, which may reduce both the cost of eradication, and the risk of failure, for some species.*

These categories reveal two key limitations to our review. First, a whole section of eradication planning problems fall outside the scope of these models. For example, the jurisdiction, governance, and regulation of islands is often unusual, and will influence conservation decisions. Stakeholder value systems are also important to consider, as different people and organisations prioritise species and ecosystems differently. On inhabited islands, issues of community consultation (Myers et al. 2000; Blackburn et al. 2010; Oppel et al.

2011) and social dynamics (Glen et al. 2013; Russell & Taylor 2017; Crandall et al. 2018; Russell et al. 2018; Aley et al. 2020) will also affect which actions will be feasible or successful. On these and many other questions, quantitative decision-support tools currently have relatively little to say (as does our personal expertise). Second, our two categories have an implicit sequence: we first decide where to act, and we then decide what to do when we arrive there. In truth the two decisions are interdependent: between-island decisions will depend on what within-island actions we will take. Most decision-support tools place an artificial hierarchy on this process, but some methods have tried to weave these scales together (Helmstedt et al. 2016; Lohr et al. 2017b). Finally, throughout this review, we focus on methods relevant to the eradication of invasive mammals, both because they are the major island invaders (Bellard et al. 2017), but also because they are the focus of most of the literature. We include references to other vertebrates, invertebrates, and plants where these are available. We also call upon modelling in non-insular problems, provided that the mathematical concepts are useful to island projects.

An overview of island eradication modelling offers an opportunity to review the contributions made by quantitative methods to island conservation, but also highlights scope for improved modelling, and emerging challenges. We therefore finish our review by asking: what is the future role of modelling in island invasive species eradication?

Table 1: Glossary of important terms for modelling and decision-making in conservation, with references for further detail on their meaning and implementation.

Key term	Meaning	References
Adaptive management	A method that formalises 'learning by doing' within a decision-making and mathematical framework.	McCarthy and Possingham (2007)
Decision-support tool	A piece of software that can assist in decision-making, which communicates estimates of impact of different interventions	Schwartz et al. (2018)

Multi-objective decision analysis	A framework for making decisions when the objective includes multiple distinct aims, such as values on costs.	Williams & Kendall (2017)
Return on investment (RoI)	An estimate of the benefit conservation project (the return) compared to the cost required to do the project (the investment).	Murdoch et al. (2007)
Quantitative model	A mathematical encoding of our understanding of a system. These underly decision-support tools.	García-Díaz et al. (2019)
Uncertainty	A description of how confident we are in an estimate of something. It is important for both parameter estimates and for model predictions.	Milner-Gulland & Shea (2017)
Value of information (VoI)	A method for estimating how important new data is for improving a decision, and it is useful for questions including 'should we act now or wait and collect more data?'	Canessa et al. (2015)

BETWEEN-ISLAND PRIORITISATION: WHERE DO WE ACT?

Why prioritise?

A substantial proportion of the world's islands contain one or more invasive species (Sax et al. 2002; Blackburn et al. 2004). Any island with human inhabitants is likely to have invasive species, since humans bring organisms both purposefully (e.g., domesticated animals, agricultural plants) and accidentally (e.g., ship rats), and because even a single human visit can be enough to deliver non-native species (although multiple invasion events may be more common; Cristescu, M. E. (2015)). Governmental and non-governmental conservation actors are therefore faced with a set of options that vastly exceeds their resources; they must choose a subset to target for eradication. A jurisdiction that exemplifies this issue is Western Australia, where the state government Department of Parks and Wildlife has authority over 3,424 offshore islands, supporting 104 known endemic taxa (Ward 2009; Morris 2012). A large number also support populations of invasive species. 13 exotic mammal species have been recorded on 121 different islands, including 9 with rats (mostly *Rattus rattus*), 16 with house mice (*Mus musculus*), 4 with cats (*Felis catus*) and 11 with foxes (*Vulpes vulpes*). Many Western Australian islands are therefore suitable candidates for eradication programs (and the state has undertaken at least 74 successful eradications since the 1970s), but the budget for island conservation is only sufficient to manage a handful each year. While this is just one department, similar issues are faced broadly by management agencies (Gregory et al. 2014).

Island eradication therefore begins with a between-island prioritisation exercise – which islands should be targeted, given our limited resources? In mathematics, this type of combinatorial optimisation is called a “knapsack problem” (Hajkowicz et al. 2007); in spatial conservation prioritisation it’s often known as the Noah’s Ark problem : we need to choose a set of objects (islands) that maximise our conservation benefits (usually threatened species persistence), while still fitting into our knapsack (our eradication budget). In the past three decades, multiple prioritisation tools have been proposed to solve this problem for island eradications. All of them can be classified as variants of the knapsack problem, differing in their definition of the conservation goal, the set of islands they consider, the invasive species they focus on, and the system model.

An overview of island prioritisations

The first published island eradication prioritisation tool was written by Brooke and colleagues (Brooke et al. 2007), and it offers an appropriate type specimen of the decision-support tool. The goal of their proposed island eradication program was to benefit the conservation status of 130 globally-threatened bird species that are found on islands. Their objective function assumed that a bird species’ conservation status would improve if a larger proportion of its island range was invasive-free. They placed greater importance on species that belonged to higher threat categories and on species that were more severely impacted by invasive species. This benefit function clearly represents only a subset of the total biodiversity that might benefit or be harmed by the removal of invasive species from these islands, but it does represent a clear, tractable goal that could be pursued by a funding organisation (e.g., an international bird conservation organisation).

To maximise this benefit, the authors selected the 20 highest-priority islands from the set of 367 islands that are smaller than 1,000 km^2, have globally-threatened birds, and have at least one known invasive vertebrate. Their conservation action was to eradicate species of invasive vertebrate, which they categorised as either ungulate, carnivore, rodent, or bird. Their model of the system dynamics was particularly simple – they assumed that when an island was targeted for eradication, all invasive species were removed; eradication was guaranteed to be successful; and reinvasion would not occur. However, they did consider the effects of removing a range of invasive species, and they further considered how the cost of eradication (and therefore the number of projects that could be pursued with a fixed budget) depends on the size of the island, its location, and the species present. Brooke and colleagues' primary result is also typical of island eradication prioritisation analyses – they decided on their list of 20 islands by applying a greedy optimisation algorithm to the dataset.

Brooke and colleagues undertook a sophisticated between-islands prioritisation exercise, particularly given its publication date, but they did omit several important factors, including the likelihood of reinvasion, the possibility of eradicating only a subset of the species on each island (e.g., cats, but not rats), and uncertainty in their various parameter sets. In the years that followed, new prioritisation methods would engage with these various factors.

Proliferation of prioritisations

There are now a very large number of published articles that describe island eradication prioritisation methods – all variants on this original theme. Some define alternate conservation benefit functions, using either a broader set of species (Dawson et al. 2015 p. 201), or a more narrow set (e.g., 3 species of petrel; Ratcliffe et al. 2009).

Like Brooke et al. (2007), many of these analyses choose high-priority islands from across the whole world (Dawson et al. 2015; Spatz et al. 2017; Holmes et al. 2019). However, others restrict their attention to particular jurisdictions, such as the islands of northern Western Australia (Lohr et al. 2015), British Columbia (Donlan et al. 2015), western Mexico (Latofski-Robles et al. 2015), or the United Kingdom (Ratcliffe et al. 2009). More spatially-restricted analyses lack the scope and impact provided by a global map, but they offer a better match to the crucial scales of budgets and governance. Most island eradication programs are funded and regulated at national or subnational scales; these governance constraints are as real as the challenges presented by remote location or large size.

Different island eradication prioritisations target different sets of invasive species for eradication. Nogales et al. (2013), for example, focus on the eradication of cats, a critical threat to seabirds on the world's islands. Capizzi et al. (2010), Ratcliffe et al. (2009), and Harris et al. (2011) all focus on the eradication of rodents, the most widely distributed invasive vertebrate, while Lohr et al. (2015) prioritised the eradication of invasive weeds. Finally, a few of these articles assume that the process of eradication is more complicated than complete and guaranteed eradication of all invasives, as modelled by Brooke et al. (2007). For example, Helmstedt et al. (2016) offer the option of eradicating only the most important invasive species on each island, rather than every last one. Other methods take into account the very real risk of re-invasion (Harris et al. 2011), project failure (Dawson et al. 2015), or community opposition (Holmes et al. 2019).

Common prioritisation issues

An abundance of prioritisation analyses creates an abundance of high-priority lists. To some extent these lists of priority islands can coexist alongside each other, since they often focus on different locations, different invasive species, and different conservation goals. However, in cases where there is conflict between competing lists, it's important to identify which prioritisation will achieve superior conservation outcomes. Three flaws commonly occur in island prioritisation analyses. The first is about how outcomes are valued, the second concerns the expected project cost, and the third involves the treatment of uncertainty. As we discuss below, these are critical aspects of an effective prioritisation methodology.

Flawed methods

Some prioritisation analyses apply *ad hoc* methodologies known as "scoring schemes" to combine the different elements of the between-islands problem into a single metric that can be ranked. The shortcomings of scoring schemes are outlined at length in Game et al. (2013), but they can generally be identified by two factors. First, the absence of a clearly-defined, quantitative conservation objective (Game et al. 2013). A quantitative island conservation objective could be to maximise the number of invasive-predator free islands, given a fixed eradication budget. A quantitative conservation objective provides a transparent and explicit basis for choosing between better and worse actions. It's also critical when decisions depend on a combination of different elements (e.g., economic cost and social acceptability). Island priorities should be determined in a return-on-investment framework (Murdoch et al. 2007), or evaluated using multi-objective decision-making (Kennedy et al. 2008).

Absent costs

Some prioritisations do not consider how the costs of eradication vary between different locations, or between different invasive species. Instead, they recommend that islands be ranked by their biodiversity value, or by their urgency (Donlan & Wilcox 2007). This will not result in an cost-efficient prioritisation, a fact that has been recognised in conservation planning since the mid-1990s (Boyd et al. 2015). Cost is a crucial element of conservation prioritisation (Ando et al. 1998; Bode et al. 2008a; Brown et al. 2015), and is generally more heterogeneous (and therefore more important for determining priorities) than factors such as threat or species richness (Naidoo et al. 2006; Bode et al. 2008b). This is particularly true for island eradications, where logistics are critical and where resources are scarce, relative to the scale of the problem (Martins et al. 2006). Moreover, island biogeography theory tells us that larger islands contain more biodiversity (MacArthur & Wilson 2001), and this will tend to attract the attention of prioritisation analyses that do not consider cost. However, eradication costs scale rapidly with island size (Martins et al. 2006; Campbell et al. 2011; Bode et al. 2013), and so in many cases the benefits offered by larger islands are a mirage. This situation – where costs are positively correlated with benefits – is where the inclusion of costs is most critical (Boyd et al. 2015).

Some papers argue that costs are so hard to estimate that they should be ignored (Donlan & Wilcox 2007). We disagree: statistical estimators can explain a substantial proportion of cost variation in previous projects (Martins et al. 2006), and it is almost always better to include uncertain cost information than to ignore it (Naidoo et al. 2006; Brooke et al. 2007b). Although we do acknowledge that estimating costs can be challenging and that we should avoid using point estimates without uncertainty bounds. However, provided cost estimates incorporate our best knowledge of uncertainty, costs should be included in prioritisations.

Uncertainty

The rationale for ignoring costs is based on a kernel of truth: cost estimates for island eradications are indeed highly uncertain. Moreover, all of the key parameters that drive prioritisations are uncertain – the presence, abundance, and conservation status of the threatened species; the probability of eradication success; and the probability of reinvasion among them. Data with large uncertainties should not be ignored – and this includes estimates of eradication costs – but nor should it be treated as though it were accurate. Nevertheless, existing island prioritisations typically use parameter estimates without fully accounting for the effect of uncertainty. We return to the treatment of uncertainty in our final recommendations.

Data-based prioritisation decisions

A prerequisite for making between-island prioritisation decisions is that broadly comparable data for every island being considered is available. Generally speaking, these information requirements (i) are details on the native species on each island that are threatened by invasive species; (ii) the invasive species present on each island; (iii) the expected cost of eradicating each of those species, in isolation or conjunction; and (iv) the probability that such an eradication would be successful, if attempted (Island Conservation 2018). At its most primitive, this information can be a series of lists that can be combined in a cost-effectiveness equation (Murdoch et al. 2007; Joseph et al. 2009).

Datasets are available to parameterise the key components of between-island prioritisations, although their quality and completeness varies considerably. Alongside databases on island biogeography (e.g., size, location, environment, topography (Sayre et al. 2019)), lists of native and invasive species on islands are freely available, from national (e.g., (Department of the Environment and Energy 2016)) and international (Invasive

Species Specialist Group ISSG 2015 p. 1; Threatened Island Biodiversity Database Partners 2018) sources. These types of information can be gathered before an eradication is attempted. In contrast, data on the cost of eradication, on the probability that an eradication project will succeed, and on the probability of reinvasion, will not always exist for specific islands until eradication has been attempted or achieved. For these types of data, statistical estimators can be used to predict the values in advance. Large datasets exist that collate historical island eradication data – both for successful and unsuccessful projects (DIISE 2015). A subset of these projects have even recorded the costs incurred in the process (Howald et al. 2007; Campbell et al. 2011; Holmes et al. 2015). Statistical models have proven capable of explaining some of the variation in cost and probability of success, highlighting the role of island isolation, invasive species identity, and island size (Martins et al. 2006; Wenger et al. 2017; Jardine & Sanchirico 2018).

The demand for detailed data

As between-island prioritisations increase in complexity and scope, they demand more information, and more specific information. These prioritisations might require, for example, quantitative estimates of the abundance of threatened species on each island (e.g., Capizzi et al. 2010; Helmstedt et al. 2016; Lohr et al. 2017b). They might also ask for predictions about post-management scenarios. For example, Joseph and colleagues' prioritisation requires an estimate of how much feral cat eradication will decrease the extinction probability of the Chatham Island oystercatcher (Joseph et al. 2009). Helmstedt and colleagues (2016) methods not only requires abundance estimates for each threatened native species on each island, they require a prediction of what those abundances would be in the presence of different invasive species communities (e.g., when cats, rats, and mice are present; when rats and mice are present, when only mice are present, etc.). To estimate the range of potential benefits for their three island prioritisation, they were therefore required to estimate 204 abundance parameter values under multiple different invasive species communities. The Island Decision Support System outlined by Lohr and colleagues (Lohr et al. 2017b) is the most complex prioritisation scheme yet proposed: each of its insular ecosystems is modelled by a bespoke multispecies ecosystem model.

The role of experts

The information requirements of large-scale prioritisation models are complex, numerous, and hard to estimate statistically. Instead, these analyses generally use expert elicitation to parameterise their models (eg Holmes et al. 2019), based on formal, semi-structured elicitation techniques (Speirs-Bridge et al. 2010). Expert judgement can rapidly estimate many prioritisation parameters, but the results are of uncertain accuracy. Expert ecologists are vulnerable to the same cognitive frailties as the rest of the population, and their estimates of quantitative model parameters can be both uncertain and poorly calibrated (i.e., over-confident (Burgman et al. 2011; Sutherland & Burgman 2015)). These facts make a formal analysis of uncertainty even more important for complex, expert-based prioritisations.

WITHIN-ISLAND PRIORITISATION: WHAT DO WE DO?

If we hold to our strictly hierarchical decision framework, then once the between-islands decision has been made, we thereafter need to determine precisely what to do on those high-priority islands. For example, which invasive species should we target first and how should we reduce their abundance? The most straightforward way in which quantitative models can support decision-making is for them to forecast how candidate actions will affect the future state of an island ecosystem. How these models manifest depends greatly on their intended use and the target system. Nevertheless, underpinning all of the work we discuss in this section are models that forecast how management actions will perform if implemented.

Should we act?

Before we proceed with any eradication, there are case-specific issues that must be considered that will not be captured by between-island prioritisation modelling. Two questions can determine whether the project should proceed. First, how likely is it that the species can be removed and prevented from reinvading? Second, how certain are we that removing the candidate species will improve the island’s conservation value?

Reinvasion probability

The isolation of insular ecosystems reduces the chances that the invasive species will reinvade following eradication (Carter et al. 2020). Nevertheless, island reinvasions are not uncommon, particularly within archipelagos, or to islands close to the mainland (Sposimo et al. 2012; Veale et al. 2013; Lohr et al. 2017a) (the probability of reinvasion must be nonzero, given that the invasive species already reached the island). If a species has a high chance of reinvasion, then this risk must be mitigated before eradication. If nearby invaded islands are the source of the threat, then eradicating across all of them may be the solution, with the optimal order determined by the connectivity between islands (Chades et al. 2011; Perry et al. 2017). If the risk of new arrivals can't be removed (e.g., human visitation is ongoing), then careful allocation between eradication, quarantine, and ongoing surveillance is required (Moore et al. 2010; Rout et al. 2011).

Reinvasion is caused by dispersal to an island, but it can also occur within each island, if the invasive populations are spatially and demographically independent. For example, Robertson & Gemmell (2004) showed that glacially-demarcated populations of rats on South Georgia Island did not exchange individuals, allowing them to be eradicated in sequence. On Dirk Hartog Island and the Channel Islands in contrast, independent populations were created by the construction of island-wide fences, which *post hoc* analyses suggest decreased both the costs of eradication and the risk of cost blow-outs (Bode et al. 2013).

Will eradication improve the ecosystem?

Removing an invasive species from an ecosystem can have drastic effects on other species (Courchamp et al. 1999; Rayner et al. 2007; Bull & Courchamp 2009; Ritchie & Johnson 2009; Lindenmayer et al. 2018), and it's important to carefully consider whether the net effect on the ecosystem will be positive. It may not even be clear that the remaining species can coexist, as the ecosystem may have changed substantially from its pre-invasion state. Ecosystem models can play an important risk-analysis role, as they can forecast how interventions in a system will evolve and impact multiple species. There are a range of methods used, including ecosystem ensemble modelling (Baker et al. 2017a, 2019a; Adams et al. 2020), fuzzy cognitive mapping (Dexter et al. 2012; Baker et al. 2018b) and qualitative modelling (Dambacher et al. 2003; Dambacher & Ramos-Jiliberto 2007; Raymond et al. 2011). Despite differences in mathematical approaches, each of these share the same core: a network of species interactions, and a large degree of uncertainty about the direct and indirect consequences of ecosystem interventions. The large uncertainty that accompanies these models is an ongoing challenge, and we address this in more detail in the *Species Interactions* section.

Project resource allocation

Individual eradication projects require careful planning, and modelling can provide insight to project-level issues, including how likely an eradication plan is to be successful; determining whether a species has been successfully eradicated or not; and how to divide limited resources between different actions, such as control and detection. In the following sections we discuss models and methods that relate to each of these topics.

Species detectability

Species detection is a fundamental part of modelling for island eradications. Good models of the detection process facilitates accurate models of the true population through time (Hespen et al. 2019) and to estimate the likelihood of a non-detection being a true absence or not. Inferring occupancy and population dynamics from observational data is a large area of research, with a wide range of methods available (Jarrad et al. 2015; MacKenzie 2018). However, one of the unique aspects of eradications is that populations are being actively managed, meaning that detection rates will be varying though time due to the change in population size (McCarthy et al. 2013), and this change in detectability provides information about how the population has changed. Additionally, removal data can be used to estimate population size though time (Davis et al. 2016), without the need for targeted methods, such as capture-mark-recapture (Pollock 2000). Bringing together different types of data to simultaneously estimate detection probabilities and population dynamics is a strength of integrated population modelling (Besbeas et al. 2002; Weegman et al. 2016; Riecke et al. 2019). In recent years, integrated population models have been used to infer population dynamics, species detection probability and the population eradication probability from removal data (Rout et al. 2014, 2018; Davis et al. 2019a p. 20).

Declaring eradication

As well as deciding when to start an eradication project, it’s crucial to know when to stop it. Control and surveillance actions must continue if the invasive species could still be present on the island, since a premature declaration of eradication could result in a rapid recovery of the invasive population. Eradication programs have failed in the past because of premature cessation (Solow et al. 2008). However, since detection is always an uncertain process, managers will never be 100% certain that an invasive has truly been eradicated.

Eradications projects generally declare success once an arbitrary fixed time has elapsed since the last invasive sighting (e.g. Robinson & Copson 2014; Russell et al. 2016). However, occupancy modelling now allows the probability of eradication to be quantified, which allows managers to declare eradication once a threshold probability of eradication is exceeded (Samaniego-Herrera et al. 2013; Russell et al. 2016; Kim et al. 2020). For example, during the eradication of pigs from Santa Cruz Island (California, USA), managers declared eradication once the probability of island-wide eradication exceeded a threshold of 95% certain (Ramsey et al. 2009). However, this approach still requires an arbitrary threshold to be set (e.g., why not 99%?).

An alternative to declaring eradication based on a probability threshold is the net expected cost (NEC; (Regan et al. 2006). An NEC approach declares a species eradicated (at least, it stops the eradication project) once the cost of additional searches exceeds the cost of premature declaration (i.e., a false-positive declaration), weighted by the probability of the species still persisting. An NEC approach avoids the arbitrary choices involved in fixed-time or fixed-threshold declarations, but with two complications. First, the “costs” of premature declaration include hard-to-quantify factors such as reputational impact – it’s harder to convince people to give you resources if your last eradication failed. Second, even when the two costs have equal expected values, they will have different amounts of variation. The cost of ongoing searches can be accurately predicted, while the cost of declaring eradication is highly variable – either the invasive species is eradicated and the cost of declaration is zero, or it has not been eradicated and the costs are very high. This means that the optimal decision depends on a decision-makers tolerance for risk, with risk-averse decision-makers likely to delay eradication declarations until much later. However, both of these complications are present whenever eradiation is declared successful – the NEC approach simply makes these issues explicit.

Allocating resources between detection and removal

Actions can deplete the population (for example wide-scale poison baiting), detect individuals (for example camera traps) or do both (for example cage traps). Balancing the different types of actions is crucial to designing a cost-effective eradication plan. In an eradication, we want to remove the population and be confident that we have succeeded, meaning we typically want a mix of actions, and models have been used to find ways to do this optimally (Rout et al. 2011). However, there are further layers of complexity to this, as species detection can guide removal efforts, making removal more effective (Baxter & Possingham 2011; Spring et al. 2017). Similarly, spending more on species removal increases the confidence in eradication, meaning that surveillance effort can be reduced (Baker et al. 2017b). Further, allocating resources between different actions goes beyond removal and detection, to include issues around preventing, quarantining, detecting and eradicating (Moore et al. 2010; Rout et al. 2011), early detection of species (Jarrad et al. 2011) and detecting multiple species (Jarrad et al. 2010).

Optimising control through time

Conservation science is familiar with identifying the best places to invest conservation resources – between-island prioritisation, for example, chooses the best locations for eradication projects. Just as there are efficient and inefficient locations in space to invest resources, there are also efficient and inefficient times to invest those resources (Iacona et al. 2017). With a good understanding of population dynamics and the effect of control methods, it is possible to identify the best time to apply intense eradication efforts.

A critical question in temporal optimisation is whether to spend most of the budget early to quickly reduce a large initial population (a "front-loaded" spending schedule), or to start slowly and save the budget for the final eradication (a "back-loaded" schedule)? The decision about when to invest eradication resources affects three important factors: it impacts the total duration of the eradication project, it affects the total eradication costs, and it influences the impacts on the threatened native species (Buckley et al. 2001; Epanchin-Niell & Hastings 2010; Krug et al. 2010; Buhle et al. 2012; Baker et al. 2018a). Devoting significant resources to removal, particularly early on, can result in rapid eradication. However, typically there are diminishing marginal returns in increasing removal effort, meaning that doubling the removal effort won't double the removal rate; this is an incentive to use longer term strategies. However, there are factors that incentivise shorter projects, including project-related costs and native species impacts. There are often overhead costs associated with projects, such as ensuring access to an island, and the longer a project takes, the more these costs impact the total project cost. Further, if the invasive species is directly threatening native species, then it may be to important eradicate quickly. When choosing project length and allocating resources though time, we must balance all of these competing factors.

Dealing with environmental variation

One of the great challenges to optimising removal strategies is that environmental conditions are constantly changing. Beyond the impacts of stochasticity on population and ecosystem dynamics, species detection rates are time-varying (Moore & McCarthy 2016), as are the effectiveness of control methods (Baker & Bode 2016). There are a range of mechanisms that lead to time-varying control effectiveness. Feral cats in arid and semi-arid Australia provide an example of this: cats will only consume baits when they are hungry, which generally only occurs during droughts. Bait uptake can therefore be reliably forecast 6 months into the future using rainfall and prey abundance data (Christensen et al. 2013), but beyond this it is difficult to predict the benefits of baiting. There has been progress in incorporating time-varying control and detection for invasive weed management projects (Bonneau et al. 2018) and in mammal control (Holland et al. 2018). However, our ability to forecast there variations varies from system to system, and integrating analysis of optimal management strategies with uncertainty and near-term forecasts is an important research area.

Multispecies modelling and management

It is critical to understand how a target species interacts with its surrounding ecosystem, and to incorporate these relationships into eradication strategies. History has proven that controlling species can have widespread impacts on the ecosystem (Lindenmayer et al. 2017, 2018; McGregor et al. 2019) and to avoid the negative consequences of eradication, we would therefore need to consider eradication as an ecosystem perturbation (Glen et al. 2013). However, gaining a good understanding of species interactions takes dedicated research over decades (Greenville et al. 2014), which is rarely feasible. A way forward is to reframe the problem. Rather than firstly seeking to understand the system and then secondly use that information to inform management, we can instead ask: is our current knowledge sufficient to choose a management strategy, and, if not, what data are required? In simplified ecosystems of two invasive species and one native species, some eradication decisions can be made with very little information (Bode et al. 2015; Baker et al. 2019b). These analyses showed that if the invasive species were a predator and a prey species, it is best to remove the predator first. If, instead, the invasives are an apex predator and a mesopredator, it is generally best to remove them simultaneously. Understanding how these rules of thumb might generalise to different other network structures is an important further question (Norbury 2017).

Assessing novel methods

New methods for dealing with invasive species are constantly being proposed, and models can help understand the current effectiveness and potential future cost-effectiveness of them. While early trials for new methods can be encouraging, it's always important to consider their costs and the fact that they need to be more cost-effective than any existing methods (Campbell et al. 2015). For example in the context of fire ant detection, models show that detector dogs are cost-effective if their probability of detection is above 80% and they are used 8 or more times (Baker et al. 2017b). Importantly, this calculation was possible without having to train dogs and test them in-situ. More broadly modelling has provided important insights into the effectiveness of novel methods, paving a way for strategic implementation of detector dogs (Glen et al. 2018; Bennett et al. 2019; Kim et al. 2020) and eDNA (Smart et al. 2015, 2016). One of the most recent technologies is drones. They have proven to be useful in conservation management (Hodgson et al. 2018), and drones are a candidate for invasive species detection (Juanes 2018) and control (Marris 2019).

KNOWN-UNKNOWNS: ISLAND ERADICATION DECISIONS UNDER UNCERTAINTY

Types of uncertainty

As a general rule, islands are remote and hard to visit, and this makes it difficult to estimate key processes and parameters – ecological or economic. As we stated previously, this uncertainty is no reason to avoid quantitative modelling, but it does make it essential to consider uncertainty when managing these systems (Milner-Gulland & Shea 2017). In this section we review quantitative methods for managing uncertainty, we discuss aspects where further methodological development is required, and we show simulation results to demonstrate why the treatment of uncertainty is such an important and challenging area.

Managing under uncertainty

Model predictions can help managers prepare for the costs, benefits, and potential negative outcomes of an eradication program. Forecasting is still valuable when we acknowledge our uncertainty, except we must now produce a distribution of outcomes for each action, often through Monte Carlo simulations. If the system is stochastic, then each simulation will produce a different result, while if there is uncertainty of model parameters, then each simulation should also draw the model parameters from a distribution that represents our uncertainty surrounding that parameter. Figure 2 shows the impact of uncertainty on a between-island prioritisation decision, where both model (parameter) uncertainty and inherent randomness are present. As a consequence of our uncertainty, we may not be able to confidently state that one action will always be better than another. The simplest way forward is to choose the action that has the best expected value. However, this is not always preferable, as sometimes it is most important to ensure a very bad outcome doesn't occur, and choosing options that minimise that risk is called robust decision-making (Regan et al. 2005; Rout et al. 2009).

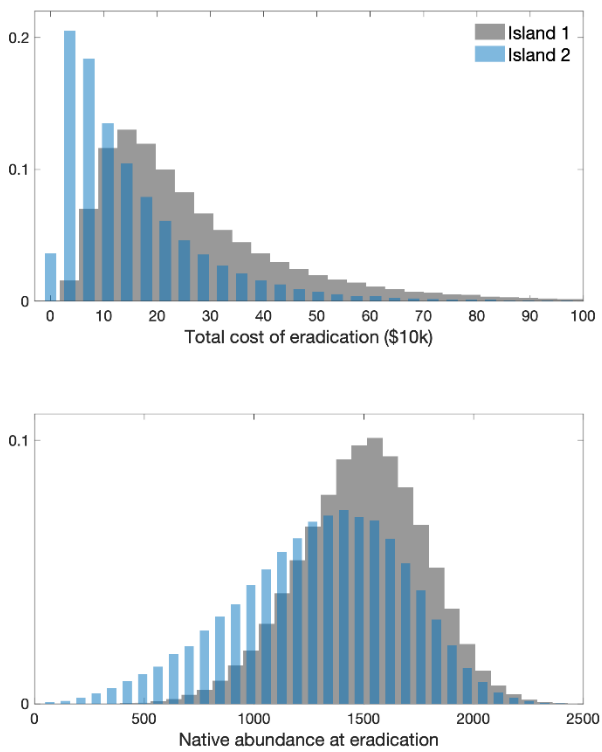

Figure 2: Forecasts of the costs (panel A) and benefits (panel B) of two island eradication decisions. Colour-coded bars show the probability distributions for eradicating the same invasive species from two different islands. Model results are produced by Monte Carlo simulations that contain both model (parameter) uncertainty and inherent randomness. On average, the eradication on island 1 delivers superior benefits for a higher cost. However, the variation is sufficiently large that either island could be better on either metric. The model assumes a constant probability of eradication success on each island $p_1 = 0.8$; $p_2 = 0.5$, *where each eradication*

attempt costs an uncertain amount $c_1 \sim LogNormal(3,0.5)$; $c_2 \sim LogNormal(2,0.5)$. The native species has an uncertain initial population $n_0 \sim Normal(2000,300)$; each native individual has a constant, known probability of mortality following each unsuccessful eradication attempt $n_{t+1} \sim Binomial(n_t, 0.8)$. Each simulation runs until eradication is successful.

Uncertainty must be represented in the outputs of different forecasts; it must also be shown for prioritisation outputs. If our uncertainty affects our ability to predict the costs and benefits of different actions, it follows that it will also affect our calculation and ranking of the return on investment (ROI) for each island. This ambiguity becomes marked in larger prioritisation analyses. Figure 3 shows a very simple treatment of uncertainty for a prioritisation exercise, based on a return-on-investment (ROI) framework. The priority of each island is defined by four factors: (1) the benefit that will accrue to threatened species if the project is successful, measured by the reduction b in extinction probability for a threatened insular species. (2) The relative importance of threatened species w, on a scale from 0-1, which could be measured culturally, or phylogenetically. (3) The probability p that a key invasive species eradication will be successful if attempted. (4) The cost c of undertaking that eradication in dollars. We take values for these parameters for 32 different conservation projects, described by Joseph and colleagues (Joseph et al. 2009). These values are for a range of threatened species management projects in New Zealand. Most are not island eradications, but they give some idea of parameter variation and cross-correlation in conservation prioritisations and it is the same method that is applied to island prioritisations. Figure 3 ranks the projects by their mean ROI, shown by the circular markers. As is common in conservation priority lists, the ROI values have an exponential distribution (note the logarithmic scale on the y-axis), with the highest ranking projects exhibiting an ROI that is several orders of magnitude higher than the lowest rankings. However, if we add a modest amount of normally-distributed error to each of the model parameters (with coefficient of variation $C = 0.25$), we can see that many of the rankings become less clear-cut. For example, the dark red-shaded region shows that the “best” project cannot guarantee a better ROI than 5 other projects (at a 95% confidence level). The light red-shaded region shows that more than half of the projects are statistically indistinguishable from the “top 10”.

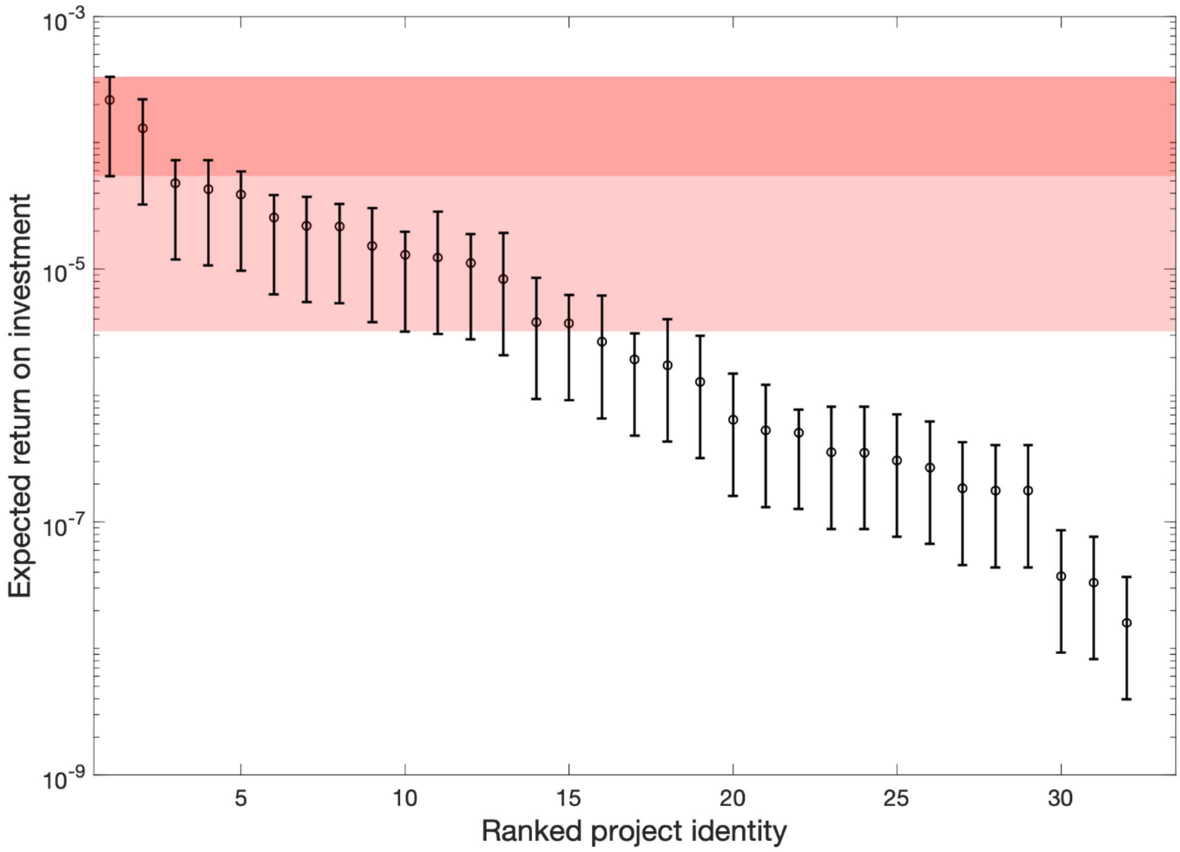

Figure 3: Expected return on investment (ROI) for 32 New Zealand conservation actions, assessed by Joseph et al. (2009). The circle indicates the Return on Investment of each project, based on the best-estimates of its parameters. The error bars enclose 95% of the variation in ROI that results from uncertainty in each of those parameters (specifically, when each parameter value has relative multiplicative variation of $\epsilon_i \sim Normal(1,0.25)$. The dark red shading indicates the error bars of the best project, and the light red shading indicates the lower error bar of the 10th ranked project. The output can still distinguish between high ROI projects and low ROI projects, but the fine-scale ordering is more ambiguous.

Reducing uncertainty

Decisions are still possible in the presence of uncertainty, but new data can refine parameter estimates and make decisions more straightforward. As we described earlier, island eradication prioritisation depends on a large number of parameters, and so it is therefore important to decide what information should be pursued first. This question can be formally answered using *value of information theory* (Runge et al. 2011; Shea et al. 2014; Canessa et al. 2015; Davis et al. 2019b). We start by choosing a management action, based only on our current system knowledge. We then consider scenarios where we collect more data and calculate the probability that the new data would change that management action. Finally, to obtain the expected value of information we must quantify how much better the more-informed action would be for the system and multiply it by the probability that the new information would change our decision. This is a quantitative method for deciding whether it is worth collecting more data, and, if so, which data would be most valuable.

Adaptive management is an important approach to conservation decision-making that compliments value of information theory. Rather than considering a decision being a 'one-off', adaptive management explicitly incorporates the potential future learning in the system that will come through management (McCarthy & Possingham 2007; McDonald-Madden et al. 2010; Williams 2012; Chadès et al. 2016). For island eradications, managers could produce a set of models that represent different understandings of the system (e.g., a top-down versus a bottom-up structure). The preliminary predictions of these models would then be compared to early observations, and our relative confidence in the different models would be updated. This "forecasting cycle" approach (Dietze et al. 2018) is an effective way to approach adaptive management. "Active adaptive management" analyses update their beliefs in the same way, but they can also incorporate the expected future learning in each decision, developing a management strategy that is robust to uncertainty and aware of how the system and our knowledge of the system can evolve.

Species interactions

An important source of uncertainty in island eradications is the potential implications of species interactions; we are currently unable to reliably predict how removing a species will affect others. Removing a predator that is consuming a threatened species, for example, will likely result in an increase in the abundance of that threatened species. However, it is also possible that species interactions could undermine or reverse the benefits of an eradication program for the target species, or have negative consequences for other native species. Our inability to foresee some indirect effects of eradication reduces our ability to choose between alternative eradication tactics. Theoretically, the effects of species interactions can be predicted by quantitative ecosystem models, which generally describe ecosystem dynamics using large coupled systems of differential equations (Fulton et al. 2011). However, despite their application to island eradication planning, parameterising these models with enough accuracy to separate beneficial actions from detrimental actions is likely impossible (Raymond et al. 2011; Bode et al. 2015, 2016). Qualitative modelling (also known as loop analysis) offers an alternative prediction tool that does not require any parameter estimates (Levins 1974), since it is based solely on the structure of interactions. However, the method is only applicable to relatively small networks of species (i.e., fewer than 5 species).

Recent work has taken a computational approach to qualitative modelling (Raymond et al. 2011) – a philosophy shared by ecosystem ensemble modelling and fuzzy cognitive maps – and this has allowed predictions for much larger systems. This computational qualitative modelling has allowed the parameter-free approach to analyse large ecosystem models (e.g., dozens of key species, or species groups), but the resulting predictions are generally ambiguous. In other words, if we used computational qualitative modelling to predict how the removal of cats would impact the abundance of seabirds on a given island, the answer would almost certainly be: "Under some conditions (i.e., model parameter values) the seabird abundance would increase, under other conditions the abundance would decrease." The approach can be used to generate distributions of outcomes, for example "In 80% of simulations the seabird abundance increased, in 20% of simulations the abundance decreased." But it is arguable whether this should be considered probability distributions (Kristensen et al. 2019), even though they are sometimes treated as such. The argument may seem semantic, but unfortunately probability distributions are the only description that can be coherently included in standard risk analysis and utility theory.

STRENGTHS, WEAKNESSES, AND FUTURE DIRECTIONS

This review reveals island invasive species eradication to be a subfield of conservation that is replete with quantitative models. For decisions at both strategic and tactical levels, a host of decision-support tools are available to determine where and when to act, how much to spend, and which species to spend those resources on. These quantitative modelling tools incorporate complex ecological dynamics, but they also grapple with economic and social constraints, and they can draw on extensive datasets about past actions to inform future planning decisions.

It's worth pausing to note how unusual this situation is for conservation science. Ecological models date to the early 19th century (Verhulst 1838), but the uptake of these models in conservation decision-making is slow, and relatively limited. This review shows island eradication to be an outlier among conservation disciplines. More surprising than the plethora of quantitative models is the availability of datasets to parameterise them (with the exception of species interaction models). Despite its long history and extensive activity, conservation has a woeful track-record of collecting and retaining accurate logistical data (Sutherland et al. 2004; Bernhardt et al. 2005; Ferraro & Pattanayak 2006; Pullin & Salafsky 2010). Data on successful projects are rare in conservation, and datasets that include failures, as well as successes, are almost unheard-of (Ferraro & Pattanayak 2006; Mills et al. 2019). In island eradication modelling, multiple such datasets exist, and the fact that some contain information on the costs of the project, the actions undertaken, and their timeline, is almost unique. The quality of these data can be partly attributed to the modular nature of islands, to the fact that an eradication is a conceptually consistent, and to the time-constrained nature of the projects. Nevertheless, there is a culture of careful record-keeping in island conservation that is deeply admirable.

The challenge of predicting the ecosystem-wide impacts of management actions is still a glaring gap. In this review, we have described how it is important for both large scale prioritisation and for project management. But it is a problem that goes beyond island eradications. It arises anywhere that species are being introduced into an ecosystem, whether for assisted colonisation or for species reintroductions (Ricciardi & Simberloff 2009). While there has been substantial progress in modelling in the last ten years, there are still important gaps, and we are still not ready to use ecosystem models as a standard part of prioritisations or risk assessments for islands.

While there has been great progress in modelling for island eradications, actually understanding the impact on policy and on-ground actions is challenging. Scientific papers – even when they are explicitly decision-focussed – typically do not report on the decision itself and what role the modelling played. Speaking from our own experience, papers can be published before any decision was made (Baker et al. 2018a), and policy-makers do not always follow recommendations (Baker et al. 2017b). In the latter case, there are often issues (which can be, but not limited to, political) that go beyond the scope of the modelling and that are challenging to discuss in a scientific publication. However, good decision-support tools should operate in close collaboration with decision-makers, as they have crucial data and experience. Recent prioritisation examples (e.g., Spatz et al. 2017; Holmes et al. 2019) were developed in direct collaboration with conservation actors (specifically, Island Conservation and Birdlife International), and are presumably more likely to influence practice as a result. Finally, close collaborations with end-users during model development and parameterisation can avoid the decision tools coming across as “black boxes”. If managers have a better understanding of the models behind the tools, their trust in their recommendations may increase (Parrott 2017; Samson et al. 2017; Southwell et al. 2017). Despite our optimism, moving from science to policy is clearly still a big challenge (Cook et al. 2013), and assessing the impact of conservation science is an ongoing area of research (Maas et al. 2019).

The availability of quantitative modelling tools for island eradications is a fortunate situation. Eradications are large, expensive projects in remote, difficult environments; planning eradication projects is therefore challenging and uncertain. Our approach needs to be efficient (we act with limited funding), effective (we can’t afford to fail), and defensible (we need to be able to explain our decisions because they’ll often go wrong). We need to incorporate system complexity, and carefully represent our uncertainty. Quantitative modelling is required to achieve all of these needs.

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Authors' Contributions

CB and MB contributed to the review equally.

Data Accessibility Statement

Data to replicate Figure 3 are available in Joseph et al. (2009).

Conflict of Interest

The authors have no conflicts of interest.

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