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UNIVERSITY OF CALIFORNIA
SANTA CRUZ

PRIORITIZING CONSERVATION EFFORTS ON ISLANDS TO CONSERVE GLOBALLY THREATENED BIODIVERSITY

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Erin E. McCreless

March 2015

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Abstract

Prioritizing conservation efforts on islands to conserve globally threatened biodiversity

By
Erin McCreless

Species and ecosystems worldwide are threatened by human activities, and intensive conservation efforts are needed to slow the ongoing biodiversity crisis (Tittensor et al. 2014). Islands are crucial to the conservation of global biodiversity: in just 5.5% of the earth's land area, they contain a disproportionate amount of terrestrial species, including an estimated 19% of birds and 17% of rodents. Islands are also highly vulnerable to human impact; 77% of known terrestrial vertebrate extinctions have taken place on islands and 40% of critically endangered species currently inhabit them (Tershy et al. In press). The leading cause of extinction and endangerment on islands is introduced species (Tershy et al. In press). In particular, animals associated with humans, such as such as rats, mice, pigs, goats, rabbits, and cats, have become feral on a large percentage of the world's roughly 400,000 islands (Atkinson 1985). These invaders have a myriad of direct and indirect effects on insular species, such as overgrazing of native plants, predation of native animals, competition with natives for food and other resources, and alteration of important physical and chemical ecosystem processes (Croll et al. 2005, Towns et al. 2006,

Fukami et al. 2006, Kurle et al. 2008, Spear and Chown 2009, Simberloff 2011, Medina et al. 2011).

The eradication of invasive mammals from islands is an increasingly utilized conservation tool with a strong record of mitigating or reversing much of the damage caused by invasions (Barun et al. 2011a). Nearly 1,100 successful eradications to date have removed invasive mammals from 750 islands globally (DIISE 2014). Ongoing developments in eradication technologies are creating opportunities to eradicate invasive vertebrates from increasingly large and complex islands (Howald et al. 2007, Burbidge 2011, Campbell et al. 2011). Consequently, national and regional government agencies and conservation organizations are increasingly investing in vigorous eradication programs on islands. However, the global scale of island invasions greatly outweighs the resources available to undertake eradication projects. To ensure that biodiversity conservation resources are allocated as effectively and efficiently as possible, islands must be prioritized for eradications.

In my dissertation I address the island prioritization problem comprehensively. First, I develop a statistical model that explains global island extinctions as a function of invasive mammal presence, native taxonomy, and island attributes (Chapter 1). I use this model to isolate and quantify the impacts of invasive mammals on globally threatened island vertebrate species, and to predict the benefits to these species from invasive mammal eradication. Then, I combine these predicted benefits with eradication cost estimates, and develop an optimization model that identifies sets of islands where specified conservation goals can be attained via

eradication for the minimum cost (Chapter 2). Finally, I assess the importance of socio-political factors in global conservation planning (Chapter 3). Taken together, the sections of my dissertation synthesize global data on island biodiversity, threats, costs, and governance, and provide results and tools that strengthen global prioritization efforts for invasive mammal eradications on islands.

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Introduction

Species and ecosystems worldwide are threatened by human activities, and intensive conservation efforts are needed to slow the ongoing biodiversity crisis (Tittensor et al. 2014). Islands are crucial to the conservation of global biodiversity: in just 5.5% of the earth's land area, they contain a disproportionate amount of terrestrial species, including an estimated 19% of birds and 17% of rodents. Islands are also highly vulnerable to human impact; 77% of known terrestrial vertebrate extinctions have taken place on islands and 40% of critically endangered species currently inhabit them (Tershy et al. In press). The leading cause of extinction and endangerment on islands is introduced species (Tershy et al. In press). In particular, animals associated with humans, such as such as rats, mice, pigs, goats, rabbits, and cats, have become feral on a large percentage of the world's roughly 400,000 islands (Atkinson 1985). These invaders have a myriad of direct and indirect effects on insular species, such as overgrazing of native plants, predation of native animals, competition with natives for food and other resources, and alteration of important physical and chemical ecosystem processes (Croll et al. 2005, Towns et al. 2006, Fukami et al. 2006, Kurle et al. 2008, Spear and Chown 2009, Simberloff 2011, Medina et al. 2011).

The eradication of invasive mammals from islands is an increasingly utilized conservation tool with a strong record of mitigating or reversing much of the damage caused by invasions (Barun et al. 2011a). Nearly 1,100 successful eradications to date

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In my dissertation I address the island prioritization problem comprehensively. First, I develop a statistical model that explains global island extinctions as a function of invasive mammal presence, native taxonomy, and island attributes (Chapter 1). I use this model to isolate and quantify the impacts of invasive mammals on globally threatened island vertebrate species, and to predict the benefits to these species from invasive mammal eradication. Then, I combine these predicted benefits with eradication cost estimates, and develop an optimization model that identifies sets of islands where specified conservation goals can be attained via eradication for the minimum cost (Chapter 2). Finally, I assess the importance of socio-political factors in global conservation planning (Chapter 3). Together, the three chapters synthesize global data on island biodiversity, threats, costs, and governance, and provide results and tools that strengthen global island prioritization for eradication efforts.

My goals in Chapter 1 were to: 1) understand the relative impacts of different invasive mammals on native island species; and 2) use this knowledge to quantify the biodiversity benefits of mammal eradication on islands globally. The degree to which introduced mammals affect native island species depends on a number of interacting factors including the life history traits of the native species and the introduced mammal, the nature of the introduced mammal's ecological interaction with each native species, and geophysical island characteristics. I used a global dataset of threatened island vertebrates and invasive mammals to build a logistic regression model of global island vertebrate extirpations. Most of the variation in extirpations was explained by a model containing island area and annual precipitation, the presence of human populations, and the presence of introduced cats, rats, pigs, mustelids, and mongooses. Different native vertebrate groups (categorized by taxonomy and the ability or inability to fly) responded differently to island characteristics and introduced mammals, with substantial variation in both the strength and magnitude of each factor's impact on different groups. The model's predictions suggest that under current conditions, 45% of globally threatened island vertebrate populations will eventually be extirpated from their breeding islands. However, the control or eradication of introduced mammals on these islands could prevent 40-75% of these extirpations. The results from this chapter strengthen our understanding of the factors that influence extinctions on islands, and quantify the threats posed by different invasive mammals to a wide range of native vertebrate species as well as the threat that can be removed via eradication.

In Chapter 2, I used the model developed in Chapter 1 to generate predictions of extirpation probability for each extant native species on each of its breeding islands. I also determined the portion of the total extirpation probability that was directly attributable to invasive mammals. Finally, I estimated the cost of implementing eradication projects on each island based on the invasive mammals present, the eradication technique required, and island area. I then combined these benefit and cost estimates in a return-on-investment model designed to identify sets of islands that would achieve specified conservation benefits for the minimum cost. I defined conservation targets as the desired number of persisting island populations of each native threatened species. For any given persistence target, the model-predicted persistence for some species was below the target under current conditions (i.e. with invasive mammals present), meaning these species needed a reduction in extinction risk and associated increase in expected persistence. The model identified the portfolio of islands on which eradications would remove sufficient extinction risk to attain the persistence target, and would do so at the lowest possible cost. I ran the ROI model across a range of targets for single-island endemic species and multi-island species. Single-island endemics rarely co-occurred on islands with multi-island species in the dataset, indicating that the selection of islands to protect endemics is largely decoupled from the selection of islands for species that occur on many islands. With increasing targets for multi-island species, island portfolios were nested such that the islands chosen at lower targets remained in all larger portfolios. The addition of islands with increasing targets, and the cumulative cost of eradication for the

growing island portfolios, were not linear; rather, they progressed in a stepwise fashion. The model results suggested that eradicating invasive mammals from 111 islands globally could remove a majority of the threat from invasive mammals to 91 multi-island species, and eradications on an additional 26 islands would remove the threats to single-island endemics. Thus, my optimization approach reduced an initial dataset of >1,500 islands and <1,100 species to less than 150 islands where the world's most threatened vertebrate species can most efficiently be protected by eradicating invasive mammals.

In Chapter 3 I investigated socio-political factors that influence the feasibility, likelihood of success, and broader outcomes of conservation projects. The questions in this chapter extended beyond islands and eradications to address more general topics relating to global-scale conservation planning. Specifically, previous global prioritizations have been based on global models for protected area management costs, but successful project implementation depends on a range of variables in addition to direct (implementation) costs. I analyzed relationships between national-level conservation management costs and country indices for civil society involvement in conservation, political stability, corruption, government effectiveness, and protection of human rights. Countries with low conservation management costs had low levels of civil society involvement in conservation and scored poorly on measures of governance and human rights. Therefore, using only the simple, direct costs to prioritize conservation is problematic, because projects in apparently low-cost countries may be less likely to succeed and more likely to have negative impacts

on people. The results from this chapter highlight the need for improved approaches to developing global conservation cost metrics, and demonstrate that the true cost of avoiding or overcoming potential problems should be included in global conservation planning efforts.

I investigated each of the individual components involved in strategic global island prioritization, and then integrated them into an optimization model to identify islands where global eradication resources should be directed. This work advances island conservation efforts in several ways. My results strengthen our understanding of global island extinction patterns and the roles invasive mammals play in causing those extinctions. It is rare to be able to isolate and quantify the expected benefits of a conservation action, and the model predictions of extinction risk from invasive mammals enable robust, quantitative prioritization analyses. By incorporating these precise estimates of conservation benefit, and then accounting for the threat (or lack of threat) to each species on each island in its range, I was able to identify the species most in need of urgent action and those most likely to benefit from eradication. The optimization approach I used overcomes many of the weaknesses inherent in simpler island prioritization methods, such as ranking islands by the number of threatened species present, using less tangible indices to represent biodiversity benefits or simply dividing biodiversity values by cost to represent cost-efficiency. The optimization model is transparent and can be easily modified to incorporate different island data, or more broadly to address any conservation decision where the benefits and costs of actions can be quantified. Finally, my work emphasizes the

importance of considering socio-political context when planning conservation projects. Implementation costs are important but are only one of many factors that influence the feasibility and outcomes of eradications or any conservation project. A failure to account for these additional factors may lead to unforeseen negative consequences for biodiversity and people. Thus, a rigorous, holistic approach is required to prioritize islands globally for eradication efforts, and in turn, to maximize the use of available resources and achieve the greatest possible benefits to threatened island biodiversity.

1. Chapter 1 – Past and potential future impact of invasive alien mammals on island vertebrate populations

1.1 Abstract

Invasive alien mammals threaten island biodiversity worldwide. However, the relative severity of threats from different mammals, and the roles of additional biotic and abiotic factors in driving extinction risk for island species, remain poorly understood at a global scale. We characterized global patterns of island population extirpations for threatened and extinct vertebrates. Most variation in population extirpations was explained by a model with covariates including native species class and volancy, island size, precipitation, and the presence of humans, invasive rats, cats, pigs, mustelids, and mongooses. Our model predicted that controlling or eradicating these invasive mammals on islands could prevent 41-75% of likely population extirpations. Our quantitative estimates of invasive mammal impacts provide a robust rationale for urgently prioritizing invasive mammal control and eradication on islands.

1.2 Introduction, Results & Conclusions

The introduction and spread of invasive alien species (hereafter 'invasive species') is a leading cause of biodiversity loss (McGeoch et al. 2010). Invasive species are particularly destructive to island species and ecosystems: 77% of recorded terrestrial vertebrate extinctions took place on islands (Tershy et al. In press.) and

most were caused fully or in part by invasive species (Clavero and García-Berthou 2005). Currently, 40% of species threatened with global extinction are island residents (Tershy et al. In press.). Most archipelagos worldwide have been colonized by invasive plants, invertebrates, and vertebrates (Towns et al. 2006), with invasive mammals among the most damaging invaders (Medina et al. 2011). At a global scale, the relative impacts of different invasive mammals on island species, and the influence of island geomorphological and climatic attributes in shaping native-invasive interactions, remain poorly understood. This hinders our ability to mitigate the leading drivers of extinction risk on islands, including invasive mammals.

The degree to which invasive mammals affect native species depends on interacting factors including: (i) life history traits of the native species (e.g. body size, diet) (Hanna and Cardillo 2014); (ii) life history traits of the invasive mammal; (iii) the invasive mammal's ecological interaction with each native species (e.g. predation, competition) (Courchamp et al. 2003); and (iv) island geologic origin, size, topography, and climate (Holt 2010). Furthermore, interactions between multiple invasive mammals on a single island can alter the magnitude and even the direction of their impacts on native species, often with unexpected outcomes (Courchamp et al. 2000).

We modeled factors driving island population extirpations across a range of terrestrial island vertebrate, invasive mammal, and island attribute combinations. Our dataset contained 2,656 island populations of 1,257 globally threatened or extinct vertebrate species (IUCN Red List categories of Endangered, Critically Endangered,

Extinct in the Wild, or Extinct), with breeding records on 1,024 islands worldwide (Threatened Island Biodiversity Database Partners 2012) (Tables 1-1 to 1-3). We determined whether each population persisted on (i.e. recorded since 1990) or has been extirpated from each of its breeding islands. 'Extirpation' was defined as the disappearance of a species from a single island. For most single-island endemic species, extirpation equates to global extinction; 31 species (4% of all single-island species in the data) also have extant continental populations. Species with multiple breeding islands may have had populations extirpated from all, some, or none of their islands.

Our goal was to identify island attributes and invasive mammals most strongly associated with native population extirpations to (i) determine the degree of threat from different invasive mammals in different island conditions, and (ii) inform invasive mammal control and eradication priorities for conserving extant threatened populations. We constructed generalized estimating equations (GEEs) (Hardin and Hilbe 2012) to build logistic regression models in which the response variable was population extirpation or persistence. We tested a range of covariates including native species traits, invasive mammal presence (Table 1-4), and island attributes (all covariates and hypotheses shown in Table 1-5). We classified native vertebrates into six groups based on taxonomic class and flight ability: volant birds, non-volant birds, bats, non-volant mammals, amphibians, and reptiles (this variable is henceforth termed "class/volancy"). We used QIC (quasi-AIC, the GEE equivalent of Akaike's information criterion [AIC]) and model error estimates to select a final model (Fig. 1-

1). The model contained eight main effects (class/volancy, island area, annual precipitation, human presence, and invasive cats, rats, pigs, and mustelids/mongooses [grouped together]) and five interaction terms (class/volancy*area, class/volancy*precipitation, class/volancy*cat, class/volancy*pig, and rat*area) (Tables 1-6 and 1-7). We assessed each variable's effect on model outcomes by calculating odds ratios, which provided quantitative assessments of variable importance by comparing the odds of extirpation on islands with different abiotic conditions and invasive mammal combinations.

Estimated extirpation risk for native vertebrates varied relative to island area and precipitation (Fig. 1-2). Non-volant mammals and volant birds had higher extirpation rates on small islands. This is consistent with the large number of bird and mammal extinctions historically documented on small oceanic islands (Alcover et al. 1998, Blackburn et al. 2004). Contrary to predictions from island biogeography theory (MacArthur and Wilson 1967), non-volant birds, bats, amphibians and reptiles had higher extirpation risk on large islands. Some assumptions of island biogeography theory may not apply here for at least two reasons: first, we focused on a nonrandom subset of species (extinct and threatened vertebrates), and second, anthropogenic impacts leading to extirpations may be greater on large islands due to larger human populations. Extirpation rates for reptiles, non-volant mammals, and bats were lower on wet islands. The species in our study represent a range of life-history traits, and our results were likely influenced by the specific resource needs of

individual species and different vulnerabilities to threats associated with wet or dry environments.

To understand the impacts of each invasive mammal group, we determined the characteristics of islands on which they occurred. Islands in our dataset were either uninhabited by humans (54%) or inhabited (46%). Most uninhabited islands lacked invasive mammals (46%) or contained only rats and/or cats (45%); these were also the most ubiquitous invasive mammals in our data and occurred on 67% and 46% of all islands, respectively. On uninhabited islands, rats increased the modeled extirpation risk particularly for amphibians, reptiles, volant birds, and non-volant mammals (Towns et al. 2006), while cats strongly increased risk for non-volant birds (Medina et al. 2011). Rats and cats had synergistic effects when they co-occurred on the same islands (Fig. 1-3).

We identified six combinations of invasive mammals that occurred on 80% of inhabited islands (Table 1-8). The presence of humans, rats, and mustelids/mongooses increased modeled extirpation risk consistently across all native vertebrate groups, while cats and pigs affected native vertebrate groups differently (Fig. 1-4). Mustelids/mongooses were present primarily on inhabited islands, and the strength of their impacts in our analysis is remarkable given that they occurred on only 11% of the islands in our data (King et al. 2007, Barun et al. 2011a). These results may be partly explained by mustelid/mongoose introductions being relatively recent compared to those of other groups, and more recent extirpations being better documented.

We examined the combined effects of island attributes and invasive mammals by comparing model-fitted values across the range of each covariate. Rats increased extirpation probabilities for non-volant mammals and volant birds most strongly on small islands (Figs. 1-5a and 1-6a). Modeled extirpation probabilities for non-volant mammals, non-volant birds, amphibians, and reptiles varied dramatically across the precipitation gradient (Figs. 1-5b and 1-6b), particularly in the presence of invasive mammals. The strength of invasive mammal impacts varied widely across native groups, with smaller effects on amphibians and reptiles and greater effects on mammals and birds (Figs. 1-5 to 1-8). For all island species, co-occurrence with more types of invasive mammals led to greater extirpation risk (Figs. 1-5 to 1-8). The relative threat from different combinations was context-specific, as it is a function of life-history traits, island characteristics, and the suite of invasive mammals present (Hanna and Cardillo 2014).

Rats were the only invasive mammals whose impacts on native taxa depended on island size, with stronger impacts to some native species groups on small islands (Figs. 1-5a and 1-6a). Large islands are more likely to contain native rodents or other native predators, making native species on these islands better adapted to rodent impacts. In contrast, the effects of invasive cats were constant across island sizes but differed between native vertebrate groups. The striking impact of cats on non-volant birds is likely explained by non-volant birds' weak defenses against such fast, agile predators (Blackburn et al. 2004). Cats had relatively similar effects on amphibians, reptiles, non-volant mammals, and volant birds; our findings are broadly consistent

with previous studies of cat impacts on island vertebrate taxa (Medina et al. 2011). Finally, the effects of pigs varied across native vertebrate groups, with the strongest effects on amphibians, followed by non-volant mammals, bats, and non-volant birds. Pigs may have both direct and indirect impacts on native vertebrates; although our study did not address specific mechanisms, pigs are known to greatly alter habitats through their foraging behavior (Barrios-Garcia and Ballari 2012).

We determined logistic thresholds for translating model-predicted continuous probabilities into binary predictions of population extirpation or persistence (Hosmer et al. 2013). Given the importance of accurately predicting likely future extinctions, we viewed false-negatives (missing a true extinction) as more costly than false-positives (misidentifying a rare population as extinct). Therefore, we selected a threshold associated with an 80% true-positive rate, despite the relatively high corresponding false-positive rate (47%); we tested two additional threshold values to determine the sensitivity of the results to threshold choice (Table 1-9). Model predictions of extirpation probability in the absence of invasive mammals generally lie below the selected threshold, but rise above it when one or more invasive mammals are added (Figs. 1-5 to 1-8). We used the model to estimate extirpation probability for the 1,998 extant threatened vertebrate populations in our data, based on the conditions and invasive mammals present on islands where they occur. The analysis predicts that 896 populations (45%) will potentially be extirpated; at the maximum false-positive rate, the model predicts 475 extirpations (24%). We were unable to predict the timing of these extirpations because about half of the extirpation

records lacked temporal data, and those for which we could estimate an extirpation date took place over a timescale too large to be informative (<10 to ~500 years [Fig. 1-9]). Thus, we conclude that without conservation interventions, the predicted extirpations would take place faster than the background extinction rate and likely in <<500 years. Nearly half the predicted extirpations (n=401) are populations of species whose total global range is restricted to a single island; for these species, island extirpation equates to global extinction.

Seventy-nine percent of threatened vertebrate populations co-occur on islands with rats, cats, pigs, and/or mustelids/mongooses. Conservation interventions to remove the threat of invasive mammals include eradication of invasive populations on small islands (Keitt et al. 2011, Oppel et al. 2011), and the creation of invasive mammal-free reserves in fenced enclosures, peninsulas, or small offshore islands to which threatened species could be translocated (Parker 2008, Burns et al. 2012). To quantify the potential of such conservation interventions on the islands in our data, we recalculated model predictions assuming these invasive mammals were eradicated from islands where they currently threaten native populations. Assuming no false-positive extirpations, complete eradication of invasive mammals could prevent 75% of extirpations (n=669) according to our model. Under the maximum false-positive rate in which 475 extirpations are predicted (the worst-case for model performance), eradication could prevent 41% of extirpations (n=194). Lastly, our results highlight the value of ensuring adequate biosecurity for invasive mammal-free islands, to

prevent invasive mammal incursion and potential additional extirpations (Russell et al. 2005).

Controlling and eradicating invasive cats, rats, pigs, mustelids, and mongooses are urgently needed to prevent vertebrate extinctions. Rat, cat, and pig eradication methods are well developed for islands up to 130 km^2, 300 km^2, and 600 km^2 in size, respectively, while removal of mustelids and mongooses has proven more challenging (Keitt et al. 2011). Conservation efforts on islands should include continued efforts to remove invasive mammals from smaller uninhabited islands, as well as focused research on improving control and eradication methods, particularly on large and inhabited islands that pose unique technical and social challenges (Oppel et al. 2011). Effective conservation of island species depends not only on identifying the most severely threatened species and islands, but also on available technologies, preventing further spread of invasive mammals, funding, and social and political support. Our analysis strengthens prioritization analyses by providing robust, quantitative estimates of the relative benefit invasive mammal removal.

1.2 Methods

1.2.1 Data: Native and non-native island species

The core dataset in our analysis was the Threatened Island Biodiversity (TIB) Database Version 2012.1 (Threatened Island Biodiversity Database Partners 2012), which contains island distributions for all terrestrial vertebrates classified as Endangered, Critically Endangered, Extinct in the Wild, or Extinct on the IUCN Red List (IUCN 2011). Associated with each threatened species is: a) records of its

breeding islands in the last 200 years (i.e. "historic status"); and b) its presence or absence on those islands from 1990 to 2010 ("current status"). We linked each species record to a geographic island location using the Global Islands Database (GID) (UNEP-WCMC 2013), a spatial dataset of more than 180,000 islands larger than 1 km^2. When an island's identity and/or location were unclear, we used Google Earth (Google 2011), geographic and political information found in the literature, and expert communication to obtain and validate island information. For islands smaller than 1 km^2, we used this information to manually add additional breeding islands to the dataset.

We populated the database using information from peer-reviewed literature, reports, and expert communications to determine whether a species currently persists on or has been extirpated from each of its historic breeding islands. Data collection methods are described in detail in Spatz et al. (2014). In our analysis, extirpation refers to the disappearance of a threatened species from a single island (local extinction). For most species that are single-island endemics, extirpation equates to global extinction. A small number (35) of the single-island species in the dataset also have extant populations on continents. We defined extirpation to include documented extirpations and cases in which: a) a species has not been found during surveys on one of its historic breeding islands in the last 20 years, or b) species experts or the IUCN Red List account define a species as being "potentially extirpated" from an island. We classified these "likely" extirpations as extirpation rather than persistence for two reasons. First, there is reasonable evidence that these species have been

extirpated from an island; second, if they do persist there, the populations are presumably at such low densities that the probability of long-term persistence is low (Millenium Ecosystem Assessment 2005). We excluded cases where a species' historic or current breeding status on an island was unknown or where records were deemed unreliable.

We compiled data on two biological traits of native species that might influence their probability of extinction in general and their vulnerability to introduced mammals in particular: body mass and ability to fly. Body mass data were gathered from scientific literature and online resources. For birds and mammals, where minimum and maximum mass was given or male and female values were listed separately, we used the arithmetic mean of the two values. For amphibians and reptiles, the standard metric for body size is snout-vent length (SVL), and body mass data were not available for most species. Therefore, we used SVL as well as total animal length (TL) when this was provided. We used allometric equations developed for each taxon to convert the minimum and maximum SVL or TL to body mass estimates (Pough 1980), and then took the arithmetic mean of the minimum and maximum mass estimates to obtain a single body mass estimate for each species. For flight ability, we classified birds as volant or non-volant using BirdLife International's species factsheets (BirdLife International 2013). All bats were classified as volant, and all other mammals as non-volant.

For each island in the TIB Database, we recorded the presence or absence of all non-native mammals for which we could find information, using published and

gray literature and expert communications (Threatened Island Biodiversity Database Partners 2012). We identified each non-native mammal to the species level when possible, or to the most specific taxonomic group possible. If a source described a non-native mammal as likely but not confirmed to exist on an island, we classified the animal as present on that island. If there was no information available about the presence or absence of a given invasive mammal on an island, we assumed it was absent. This assumption likely led us to misclassify some invasive mammals as being absent when they are actually present; this is particularly true for rodents, which can be more difficult to detect than larger invasive mammal species (e.g. ungulates). Thus, our model estimates may underestimate the impacts of some invasive mammal groups. We classified as "present" any non-native mammal species that has been eradicated from islands (DIISE 2014), based on the assumption that these species existed on the islands long enough to impact the native vertebrate populations. We accounted for eradications that took place as long ago as 1630, but most eradications in our dataset took place after 1970.

We identified ~160 invasive alien mammal species that had become established on islands and classified them into 12 groups based on a combination of feeding guild, taxonomy, body size, and other traits (Tables 1-4 and 1-5). Our goal was to achieve a balance between creating as few groups as possible to maximize the representation of each group across islands (i.e. sample size within strata) and as many groups as needed to distinguish differing impacts between mammal types. For example, we grouped primates separately from other omnivores such as rodents,

raccoons, and possums due to their primarily arboreal nature and unique behavior. We divided carnivores into three groups—felids, canids, and mustelids/mongooses—because we predicted they would have different impacts on native species based on life history, behavior (e.g. solitary or pack hunters), and home range size. Although mongooses are most closely related to civets and genets (family Herpestidae), which are grouped with other medium-sized omnivores based on diet, we grouped mongooses with mustelids because the common island invasive species in both these groups are largely or entirely carnivorous. We separated rodents from the other omnivore groups due to their generally smaller body sizes, their high densities and population growth rates on islands, and their broad omnivorous diets. In addition, rodents are the most common target of invasive mammal eradication efforts (Keitt et al. 2011), so their unique impacts are particularly important to understand from a conservation perspective. We classified rats and mice separately in order to tease apart potentially different impacts of these groups due to differences in body size and behavior, and because rats are targeted for eradication more frequently than mice. The two most ubiquitous rat species on islands, *Rattus rattus* and *R. norvegicus*, differ in climbing ability (strong and weak climbers, respectively), and may therefore affect arboreal and terrestrial island species differently. However, the particular species of rat present on many of the islands in our dataset is unknown, making it impossible to distinguish their individual impacts.

1.2.2 Data: Island attributes

We obtained island areas from the GID and Google Earth (Google 2011), and elevation and climate data from the publically available BioClim dataset (resolution 30 seconds) (Hijmans et al. 2005). We created GIS overlays of our island dataset and each of the following variables: maximum island elevation, mean annual temperature, temperature seasonality (calculated as the standard deviation of monthly temperatures), and total annual precipitation. We developed a single estimate for each climatic variable per island by calculating the arithmetic mean of the center points of all raster grid cells located within the boundary of an island polygon. A disadvantage of this approach is that more climatic information is lost for larger islands than for small ones, particularly for islands that span large latitudinal gradients, are topographically complex, or have distinct wet and dry regions. However, our distribution data for native and introduced species were at the scale of whole islands, thus the island was the geographic unit of our analysis and we used island-level values for each geographic and climatic variable.

Some islands in the TIB Database had no overlapping raster grid cells in the climate or elevation datasets. For islands located less than 100 km from the nearest continent or island, we used climate values from the nearest grid cell. There were no islands with climate data within 100 km of the Bounty Islands (New Zealand), Pitcairn and Henderson Islands (UK Overseas Territories), or the islands of French Polynesia, so we obtained climate data for these groups from outside data sources

(Brooke et al. 2004, "Vacations to Go: Bounty Islands, New Zealand" 2013, The World Bank 2013). For most islands lacking GIS elevation data, we obtained maximum elevation values from the literature (Schlatter 1993, Arata et al. 2004, Melnick et al. 2006, Kirkwood et al. 2007, Morrison and Woodroffe 2009, Kagiampaki et al. 2011, Office of Te Beretitenti 2012) and from Google Earth (Google 2011). We were unable to find elevation data for some small islands using any of these sources, so we estimated their maximum elevations using linear interpolation. Specifically, we identified all the islands in our dataset that are located in the same archipelago and share the same geologic history (and therefore likely have similar topographic characteristics) with that island. We used the area-elevation relationship of the other islands in the archipelago to interpolate the island's maximum elevation based on its area.

The TIB Database includes information on human habitation for most islands. Precise population data are not available for many islands, so each island is classified into one of six human population categories using whatever information is available. Islands are classified as uninhabited or as having permanent human populations numbering 1-10, 11-100, 101-1,000, 1001-10,000, or >10,000. For many islands, we were unable to find data specific enough to classify them into any of these categories. However, in all cases we were able to asses whether humans likely maintain permanent settlements on islands by conducting Web searches (e.g. many islands are tourist destinations with hotels and other infrastructure) and searching Google Earth images for buildings, roads, agriculture, or other signs of human habitation. Based on

this information, we supplemented the information obtained from the TIB Database and classified all islands in the dataset as either inhabited or uninhabited.

Island isolation is a primary determinant of species immigration rates and equilibrium species richness (MacArthur and Wilson 1967). However, we did not include isolation as a covariate in our model for several reasons. First, island biogeography theory makes no predictions about the effect of isolation on short-term extinction risk, but rather focuses on long-term equilibrium species richness due to intrinsic extinction and immigration rates. Second, the only other global study that measured correlates of extinction risk specifically for threatened island species found no relationship between isolation and either endemism rates or the severity of impacts from invasive mammals (Walsh et al. 2012). Finally, island isolation is unlikely to be related to invasion pressure because most mammal introductions resulted from intentional or unintentional human actions. Rats and mice, for example, are common stowaways on ships, and were introduced to extremely remote islands via landings and shipwrecks throughout the exploration and whaling periods of the last 500 years and earlier (Atkinson 1985, Long 2003). Therefore, we did not consider isolation as a driver of short-term population extinction risk for the species and islands in our dataset.

1.2.3 Extinction probability analysis

We constructed logistic models to investigate global patterns of population extirpation and persistence for threatened island vertebrates. We included each of the covariates described above as main effects, and also considered interactions when we

had specific hypotheses for how an interaction might influence extirpation rates (Table 1-5). The binary response variable was the extirpation or persistence of a native species on one island. Each native threatened species on an island constituted a single data point, in which the species is either extinct on the island (1 = an extirpation event) or it persists there (0 = no extirpation event). Many islands contain multiple native threatened species, each with its own record of persistence or extirpation, while others have only one threatened species. Similarly, some native species occur (or occurred historically) on many islands, while others are (or were) single-island endemics.

We were unable to document the timing of extirpation events with enough precision to include time as a factor in our analysis, or to use our model to predict the timing of future extirpations. About half the extirpation records in our data had associated timing information, which typically consisted of the last year a population was documented on an island and the year the population was declared or presumed extirpated. For populations with sufficient data, we calculated the timespan over which extirpations occurred (i.e. the number of years between these two events), which ranged from <5 years to ~500 years (all species included in the IUCN Red List persisted until after 1500 AD, thus the maximum time to extirpation was 510 years) (Fig. 1-9). This wide range of values, along with the lack of temporal data for half of the extirpations and the geographic and taxonomic bias inherent in historic survey data, prevented us from incorporating time in the analysis.

We used island-level presence-absence data for both native and invasive taxa because most species' within-island population size, density, and geographic distribution are not known. Our analysis was based on island-level co-occurrences between each threatened species and invasive mammal type. For example, a threatened reptile species that currently lives on an island containing introduced rats and mice is assumed to co-occur with, and potentially be impacted by, both rats and mice. If the reptile is extinct on the island, rats and mice are implicated in its extirpation because they are present on the island. The geographic and temporal scale of our study was too large to allow for a more detailed analysis of the direct and indirect impacts of invasive mammals, including but not limited to: predation, competition, habitat modification, disease introduction or transmission, and changes in the abundance of other interacting species.

We used generalized estimating equations (GEEs) to build logistic models of island population extirpations. GEEs are similar to generalized linear models (GLMs), but they include an additional variance component that accommodates clustered data (Hardin and Hilbe 2012). GEEs are well suited for this analysis because our data were clustered by island: extirpation rates may exhibit autocorrelation at the island level—due to stochastic storm events, disease outbreaks, or human impacts such as habitat destruction or pollution—that is not accounted for by any of the variables we measured. We fit models to the data using the R package *geepack* (Hojsgaard and Halekoh 2006). We specified a binomial distribution with a complementary log-log link function (Crawley 2012) because the response dataset

was asymmetric, made up of mostly zeros (persistences; ~75% of the records) and relatively few extirpations. The grouping structure was the island and we used an exchangeable working correlation matrix (Zuur et al. 2009). Four continuous variables—island area, maximum elevation, temperature seasonality, and threatened species body mass—had strongly right-skewed distributions so we used log transformations of these variables.

We first tested for correlations between the covariates. We calculated pairwise Pearson correlation coefficients for all continuous variables: island area, elevation, mean annual temperature, temperature seasonality, and annual precipitation, as well as the ordinal variable human population index. We found strong positive relationships (Pearson's $r > 0.7$) (Dormann et al. 2012) between area and elevation and between area and human population index. The area-elevation relationship of an island is important because it is associated with ecosystem diversity, which in turn can influence native population dynamics and the outcomes of species invasions (Holt 1992). To account for differences in island elevation independent of area—for example, to distinguish continental vs. oceanic islands of similar sizes that differ dramatically in steepness (and likely habitat diversity)—we obtained the residuals from the area-elevation relationship. These residuals represent the independent portion of the variation in elevation, and we used them as a covariate in the GEE instead of elevation. We used the human presence-absence variable instead of the population index because we lacked population index estimates for many islands. The GEE model selection process can only analyze complete rows of data (i.e. rows with

no missing values), and rather than exclude many islands from the analysis, we used the simpler human presence-absence variable to account for human impacts.

We examined the associations between occurrences of different introduced mammal groups on islands using non-metric multidimensional scaling (MDS). In this analysis, clusters represent the grouping of explanatory variables (introduced mammal groups) in relation to themselves and not the grouping of these variables in their relation to the response (native species extirpation rates) (Harrell 2001). We constructed an MDS ordination based on a Euclidian distance matrix generated from the presence and absence of invasive taxa (columns) among all of the islands (samples). We identified no strong relationships among introduced taxa and therefore kept all the mammal groups in the analysis.

We began the model selection procedure with 20 covariates (Table 1-5): two native species traits (class and ability to fly [henceforth "class/volancy"]) and body mass); six island attributes (island area, mean annual temperature, temperature seasonality, annual precipitation, area-elevation residuals, and human presence/absence), and twelve introduced mammal groups (canids, felids, mustelids/mongooses, medium-sized omnivores, small omnivores, primates, pigs, rats, mice, large herbivores, medium-sized herbivores, and lagomorphs). To reduce the initial set of covariates to a more manageable number, we excluded the four introduced mammal groups that occurred on <10% of the islands in the dataset: primates, medium-sized omnivores, small omnivores, and medium-sized herbivores. We also excluded the body mass of threatened species, because the large number of

missing values (particularly for extinct species, for which body mass is unknown and is difficult to estimate) would have removed a substantial number of populations and islands from the analysis, potentially biasing the results. However, we ran the model selection procedure on the subset of data for which we did have species body mass data, and this variable was not selected in any of the top-weighted models.

We built a preliminary model from the 15 remaining covariates using an information criterion-based model selection procedure. We first identified the top weighted model(s) at each level of model complexity, from the minimum (1) to the maximum (15) number of covariates. Specifically, for each model order, we ran all possible models in the R package *MuMIn* (Barton 2013), and identified the highest weighted model or models based on QICu. QICu is similar to Akaike's information criterion (AIC) but is specific to GEEs and is used to rank models that have the same pre-specified correlation structure (Hardin and Hilbe 2012). We considered models with ΔQICu<2 to have equal weight; the number of equally weighted top models at each step ranged from one to four. We then used the highest weighted model, or the model-averaged coefficients from all the top models, to generate fitted values and calculate mean square error (MSE) (Ma et al. 2013) for each model order. We used MSE rather than model and residual deviance to assess model fit because GEEs are not likelihood-based and do not have associated deviance measures. Comparing each one-unit increase in model complexity to the associated MSE estimates allowed us to assess the relative improvement in model sensitivity as covariates were added. Our analysis revealed a trend of diminishing returns, such that model sensitivity improved

substantially with each addition of a covariate up to seven terms, but only minimally with more than seven terms (Fig. 1-1). Therefore, we chose the top-weighted seventh-order model as the preliminary main effects model, which contained the following terms: class/fly, island area, annual precipitation, human presence/absence, and introduced cats, pigs, and mustelids/mongooses.

Next, we tested interactions between these seven covariates that we had hypothesized a priori to be potentially important in explaining island extirpation patterns (Table 1-5). We retained interaction terms that produced a decrease in QICu of >10 – a conservative limit for determining model improvement (Anderson 2008). In this way, four interaction terms were added to the model: class/volancy*area, class/volancy*precipitation, class/volancy*cat, and class/volancy*pig. Finally, while rats did not appear in the preliminary main effects model, we tested their addition to the model for two reasons. First, rats are widely recognized as one of the most destructive mammalian invaders on islands globally (Towns et al. 2006); second, they are the focus of most island mammal eradication efforts (Towns and Broome 2003, Howald et al. 2007). We tried adding rats and each associated interaction term to the model, and found that the addition of rats and a rat*area interaction term decreased QICu by >20. Thus, the final model included eight main effects and five interaction terms (model terms and coefficients are provided in Table 1-6).

We generated observation-level and cluster-level measures of influence using SAS statistical software (SAS Institute 2009), and used deletion diagnostics to assess the contribution of each outlier observation or cluster to overall model fit and

coefficient estimates. We used K-fold cross-validation to calculate four model evaluation statistics for the final model: mean prediction error, mean absolute prediction error, standard deviation of the prediction error, and mean square error (Ma et al. 2013) (Table 1-7). For GEE K-fold cross validation, the clusters (i.e. islands) in the dataset were randomly divided into K groups (K=10). Each of the 10 groups was iteratively removed from the dataset; the nine remaining groups were used to calibrate a new model, and the K^{th} group was used to generate evaluation statistics, construct a receiver operating characteristic (ROC) curve, and calculate the area under the curve (AUC; see below). We repeated the K-fold validation process 1,000 times, resulting in 10,000 validation runs that we used to calculate model errors and AUC.

We assessed the predictive performance of the final model by calculating the AUC for each K-fold validation run. The AUC is a commonly used statistic for evaluating a logistic model's ability to correctly predict binary outcomes in the response variable based on the continuous probabilities in the model's fitted values (Hosmer et al. 2013). An AUC of 0.5 indicates that a model is no better than random at predicting outcomes, while an AUC of 1 means it predicts outcomes perfectly. We assessed the robustness of model prediction performance by calculating the mean, standard deviation, and standard error of model AUC values across the 10,000 validation runs (mean=0.693, SD=0.091).

ROC curves represent the tradeoff between a model's sensitivity (the true-positive rate [TPR]; the ability to correctly identify extirpations) and its specificity (the true negative rate [TNR]; the ability to correctly identify persistences). Unless

the AUC for a model is 1, an increase in the TPR entails a cost of a higher false positive rate (Type II errors). Threshold values for binary prediction are chosen based on the cost of making Type I vs. Type II errors. Given the conservation context of our study and the need to accurately identify extinction risk for island populations, we viewed false-negatives (missing a true extinction) as being more costly than false-positives (misidentifying a rare species as extinct). Thus, for the primary analysis we chose a threshold with an associated TPR of 80% (TNR=53%); we also examined two additional threshold values to assess the sensitivity of the results to threshold choice (Table 1-9).

1.3 Tables

Table 1-1. Summary data for island characteristics for all islands in the dataset (n=1,024).

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.	NAs
Area	0.0	0.6	9.3	4694.0	187.2	783400	0
Elevation	0.3	16.8	83.7	382.5	454.2	4613.0	0
Mean annual temperature (C)	-0.9	15.9	23.8	20.4	26.0	29.1	6
Temperature seasonality	1.1	9.6	17.3	21.3	28.7	114	9
Total annual precipitation	0	702.1	1326	1459	2062	5441	9
Number of threatened species present	1	1	1	2.6	2	97	0
Number of introduced mammal types present	0	1	2.0	2.9	5	10	-

Table 1-2. Human population index by island for all islands in the dataset (n=1,024).

Index	Population size	# Islands
0	0	458
1	1-10	41
2	11-100	70
3	101-1,000	89
4	1001-10,000	121
5	> 10,000	205
NA	Unknown	40

Table 1-3. Summary data for threatened vertebrate species on islands.

				Body mass (grams)						
Native Group	# species	# island records	# extir-pations	Min.	1st Qu.	Med-ian	Mean	3rd Qu.	Max.	NAs
Bat	45	144	29	3.8	11.5	40.5	233.8	377.5	1150.0	0
Non-volant mammal	288	443	103	4	121	1300	41,580	6,000	$4x10^6$	17
Volant bird	364	1046	369	3	30.0	102.8	533.4	434.8	25,000	26
Non-volant bird	28	100	22	60	450	830	4,586	2,726	40,000	6
Amphibian	317	387	55	0.11	1.07	2.35	10.54	5.85	287.5	2
Reptile	215	536	73	0.2	5.1	106.2	11,480	1233	$6x10^6$	2

Table 1-4. Classification of invasive mammal taxa on islands.

Invasive group classification	Family & genus names	Common names
Dogs	Canis Otocyon Vulpes	Domestic dog Fox Wolf
Cats	Felis Caracal	Domestic & feral cat Caracal
Mustelids & Mongoose	Martes Mustela Neovison Atilax, Cynictis, Galerella, Herpestes	Marten Weasel Mink Mongoose
Pigs	Sus Pecari	Pig/boar Peccary
Medium-sized omnivores	Atelerix Erinaceus Viverra, Civettictis, Paradoxurus, Viverricula Genetta Dasyurus Thylamys Nasua Procyon Didelphis Tenrec (family) Trichosurus	African hedgehogs European hedgehog Civet Genet Quoll Opossum Coati Raccoon American opossum Tenrecs Brushtail possum
Small omnivore	Ammospermophilus, Atlantoxerus, Spermophilus Tamias Callosciurus, Funambulus, Heliosciurus, Sciurus	Ground squirrel Chipmunk Squirrel
Primate	Callithrix	Marmoset

	Cercopithecus, Chlorocebus Macaca	Monkey Macaque
Large herbivore	Antidorcas Antilope Raphicerus Damaliscus Rangifer Boselaphus Taurotragus Bison Bos Bubalus Camelus Capra, Oreamnos Hemitragus Ammotragus, Ovis Elaphas Equus Lama Rusa, Axis, Cervus, Dama, Odocoileus Tayassu Wallabia, Pegrogale, Macropus	Springbok Blackbuck Steenbok Antelope Reindeer Nilgai Eland Bison Cattle Buffalo Camel Goat Tahr Sheep Elephant Horse Llama Deer Peccary Wallaby
Medium-sized herbivore	Cavia Cuniculus Dasyprocta Hydrochaeris Phalanger	Guinea pig Paca Agouti Capybara Cuscus
Lagomorph	Lepus Oryctolagus, Sylvilagus	Hare Rabbit
Rat	Rattus Cricetomys	Rat
Mouse	Mus, Peromyscus, Abrothrix, Apodemus Eliomys	Mouse Dormouse

Table 1-5. Covariates and interactions hypothesized to affect extirpation probabilities for threatened island species. For each covariate and interaction, the hypothesized mechanism and direction of impact on extinction probability (+/-) is shown, with references listed where applicable.

	Covariate	**Data type**	**Hypothesized relationship (+/–) and mechanism driving native species extinction risk**
Island charac-	Island area	Continuous (log-transformed)	Higher extirpation rates expected on smaller islands [-] (MacArthur and Wilson 1967)
	Max elevation	Continuous	Habitat heterogeneity could create refuges

teristics		(log-transformed)	from anthropogenic impacts [-] (Holt 2010)
	Annual mean temperature	Continuous	Temperature affects resource availability [+/-]
	Total annual precipitation	Continuous	Higher resource availability on wet islands buffers anthropogenic impacts [-]
Native species traits	Taxonomy (Class) + ability to fly [Class/volancy]	Categorical (Amphibian, Volant bird, Non-volant bird, Bat, Non-volant mammal, reptile)	Taxa differ in intrinsic susceptibility to anthropogenic impacts and effects of invasive mammals [+/-]
	Body mass	Continuous (log-transformed)	Large vs. small species differ in vulnerability to impacts from invasive mammals [+/-] (Hanna and Cardillo 2014)
Intro-duced mammals	Canids	Categorical (presence/absence, P/A)	Predation, competition [+] (Ebbert and Byrd 2000)
	Felids	Categorical (P/A)	Predation, competition [+] (Medina et al. 2011)
	Mustelids & Mongoose	Categorical (P/A)	Predation, competition [+] (King et al. 2007, Barun et al. 2011a)
	Pigs	Categorical (P/A)	Predation, competition, habitat modification [+] (Barrios-Garcia and Ballari 2012)
	Primates	Categorical (P/A)	Predation, competition [+] (Evans 1989)
	Medium-sized omnivores	Categorical (P/A)	Predation, competition [+] (Clout 2006)
	Small omnivores	Categorical (P/A)	Predation, competition [+] (Ebbert and Byrd 2000)
	Rats	Categorical (P/A)	Predation, competition [+] (Towns et al. 2006)
	Mice	Categorical (P/A)	Predation, competition [+] (Angel et al. 2008)
	Large herbivores	Categorical (P/A)	Competition, habitat modification [+] (Spear and Chown 2009)
	Medium-sized herbivores	Categorical (P/A)	Competition, habitat modification [+] (Bovendorp and Galetti 2007)
	Lagomorphs	Categorical (P/A)	Competition, habitat modification [+] (Lees and Bell 2008)
Inter-actions	**Interaction**	**Hypothesis**	
	Area x Invasive mammal type	• Invasive mammals expected to cause more extinctions on small islands due to smaller native populations, fewer alternative resources for invasive mammals, and less habitat available for refuge from invasive impacts • Invasive mammal groups differ in ability to successfully colonize small islands, depending on dietary flexibility and total resource needs	
	Temperature or precipitation x Invasive mammal type	• Invasive mammal impacts may be stronger on resource-poor islands, which correlate with low precipitation and extreme high or low temperatures (Burbidge and Manly 2002) • Invasive mammal groups differ in the ability to successfully invade environments with different climatic characteristics (Prentiss et al.	

		1959)
	Temperature or precipitation x Native class/volancy	• Native vertebrate groups differ in susceptibility to anthropogenic impacts in different climates depending on life history traits (endotherm vs. ectotherm, home range size, ability or inability to fly)
	Native class/ volancy x Invasive mammal type	• Native vertebrate groups differ in their vulnerability to impacts from different invasive mammal groups depending on ecological overlap, body size differences, and predator/prey or competition relationships between natives and invasive mammals
	Native species body mass x Native class/ volancy	• Different-sized species within each native group differ in a variety of life history traits that influence their vulnerability to environmental impacts
	Native species body mass x Invasive mammal type	• Native vertebrates of different sizes vary in susceptibility to invasive predators and to habitat modification by invasive herbivores and omnivores

Table 1-6. GEE model coefficients. C/V = Class/Volancy (categorical variable with six levels; amphibian is the intercept). "+" refers to the presence of humans or introduced mammals.

Main Effect	**Coefficient**
Intercept	-5.261659601
C/V: Bat	2.047784668
C/V: Bird	3.385503305
C/V: Non-volant bird	0.785890569
C/V: Reptile	2.744908587
C/V: Non-volant mammal	4.218883078
Island area (log)	0.123392376
Annual precipitation	0.000289714
Humans +	0.548611701
Rats +	0.741243374
Cats +	0.530254103
Pigs +	0.779079964
Mustelids/mongooses +	0.449417439

Interaction	**Coefficient**
C/V Bat x log Area	-0.018639339
C/V Volant bird x log Area	-0.14571061
C/V Non-volant bird x log Area	-0.059337471
C/V Non-volant mammal x log Area	-0.180046972
C/V Reptile x log Area	-0.047188852
C/V Bat x Precipitation	-0.000441254

C/V Volant bird x Precipitation	-0.000272581
C/V Non-volant bird x Precipitation	0.0000283
C/V Terr. Mammal x Precipitation	-0.00086097
C/V Reptile x Precipitation	-0.000953778
C/V Bat x Cat+	-0.512557599
C/V Volant bird x Cat+	-0.351199304
C/V Non-volant bird x Cat+	1.153571888
C/V Non-volant mammal x Cat+	-0.093296716
C/V Reptile x Cat+	0.11909212
C/V Bat x Pig+	0.285790012
C/V Volant bird x Pig+	-0.509597141
C/V Non-volant bird x Pig+	-0.187092745
C/V Non-volant mammal x Pig+	0.017078176
C/V Reptile x Pig+	-0.970907894
Rat + x log Area	-0.075905496

Table 1-7. Error statistics from K-fold (K=10) cross-validation for the final chosen model. The cross-validation process was repeated 1,000 times to produce 10,000 runs from which to calculate error statistics. The minimum, mean, and maximum values for each statistic across the 10,000 runs is shown.

	Minimum	Mean	Maximum
Mean prediction error	-0.557200	0.005455	0.319500
Mean absolute prediction error	0.2810	0.3311	0.3647
Standard deviation of prediction error	0.3720	0.4299	0.6049
Mean square error	0.1401	0.1903	0.3662

Table 1-8. Numbers and proportions of islands with the most common combinations of introduced mammals. Data include only the introduced mammals included in the final model, and only the islands with complete data that were used to generate the model (n=1,015).

		Invasive mammal types present	**Number of Islands**	**% of Islands**
Uninhabited (humans absent)	466 islands	None (invasive mammal-free)	214	21.0%
		Rats only	144	14.2%
		Cats only	25	2.5%
		Rats & cats	43	4.2%

		Other combinations	40	4%
Inhabited (humans present)	549 islands	Rats only	69	6.8%
		Rats & cats only	168	16.6%
		Rats & pigs only	32	3.2%
		Rats, cats, pigs only	104	10.2%
		Rats, cats, mustelids/ mongooses only	34	3.3%
		Rats, cats, pigs, mustelids/mongooses	34	3.3%
		Other combinations	108	10.6%

Table 1-9. Logistic thresholds for determining population extirpation and persistence according to the chosen model. Shown are the number of predicted population extirpations, and the proportion of the total 1,998 extant populations in the data predicted to be extirpated, under the minimum and maximum false-positive rates (best and worst model performance) associated with each threshold value. Also shown are the proportion of extirpations that could be prevented via invasive mammal eradication under each threshold, under the minimum and maximum false-positive rates. The values in bold (threshold = 0.21) are the values reported in the main text; two additional thresholds were tested to determine the sensitivity of the results to threshold choice.

Threshold value	**True positive rate (TPR)**	**False positive rate (FPR)**	**Max. predicted extirpations (Min FPR)**		**Min. predicted extirpations (Max FPR)**		**% extir-pations prevented (Min FPR)**	**% extir-pations prevented (Max FPR)**
			#	%	#	%		
0.25	0.7	0.34	618	31%	408	20%	97%	47%
0.21	**0.8**	**0.47**	**896**	**45%**	**475**	**24%**	**75%**	**41%**
0.15	0.9	0.59	1111	56%	455	23%	56%	37%

1.4 Figures

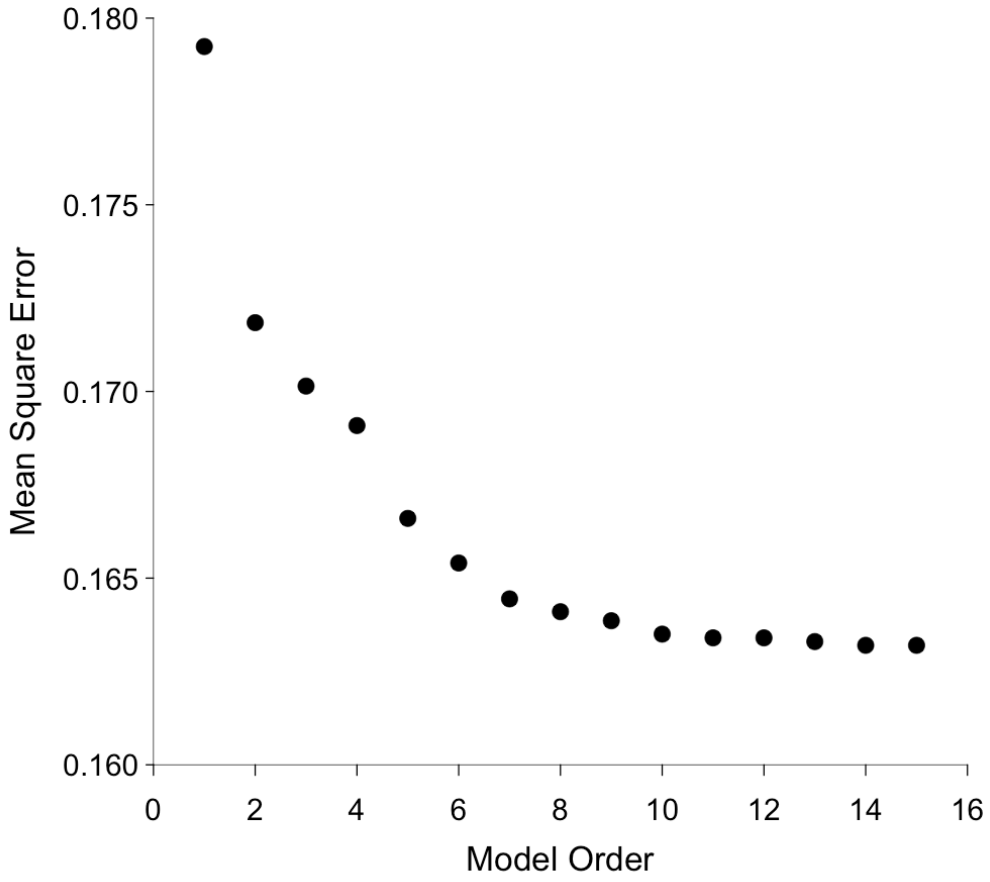


Figure 1-1. Model mean square error (MSE) calculated from the highest weighted model, or model-averaged coefficients from all equally weighted top models (ΔQICu<2), for each model order (one to 15 covariates) used in the model selection process.

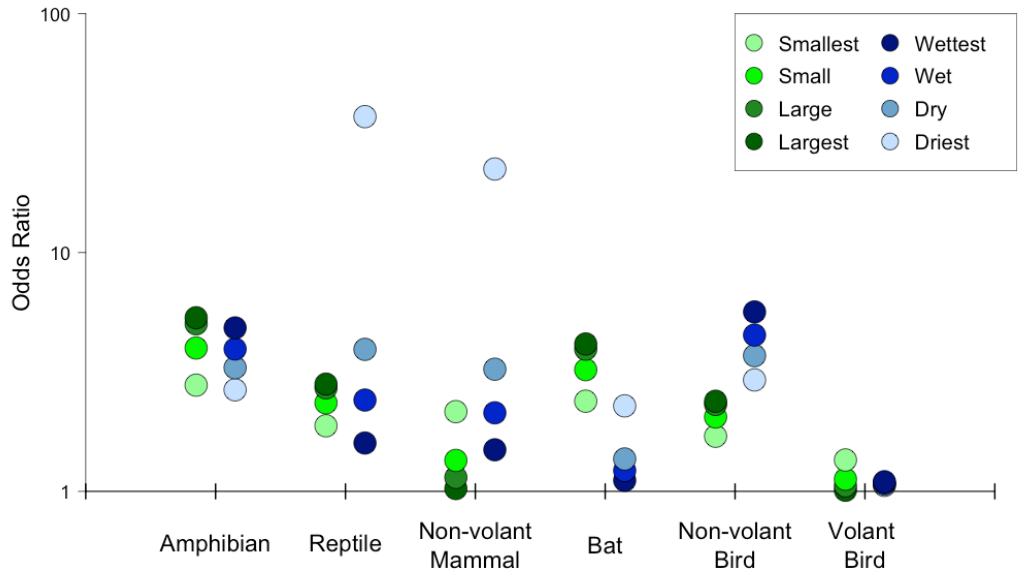


Figure 1-2. Model-predicted odds ratios comparing the odds of extirpation for threatened vertebrate populations on islands with different areas and annual precipitation. Green circles are the ratios of the odds of extirpation on the smallest ($1.0e^{-5}$ km^2) or largest (783,000 km^2) islands in the dataset vs. the odds on small (1^{st} quartile [qu.] area [A]: 1.6 km^2), median A (10.7 km^2), or large (3^{rd} qu. A: 194.4 km^2) islands, calculated with precipitation held at its median value (1,326 mm). Blue circles are the ratios of the odds of extirpation on the wettest (max precipitation [P]: 5,441 mm) or driest (min P: 0 mm) islands vs. the odds on wet (3^{rd} qu. P: 2,062 mm), median P (1,326 mm), or dry (1^{st} qu. P: 702 mm) islands, calculated with area held at its median value (10.7 km^2). All odds ratios were calculated with no invasive mammals present.

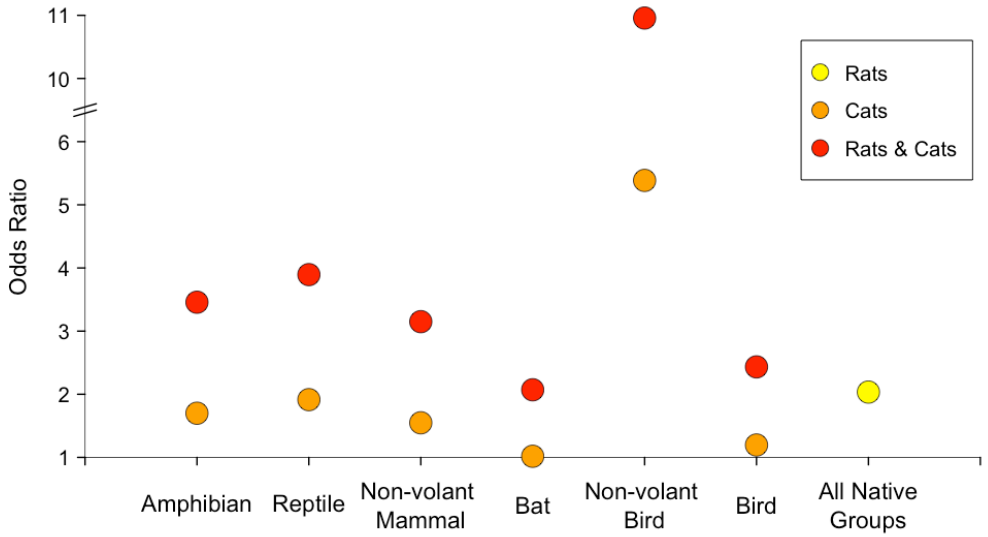


Figure 1-3. Model-predicted odds ratios comparing the odds of extirpation for threatened vertebrate populations on uninhabited islands containing invasive rats, cats, or both to the odds on invasive mammal-free islands. The yellow circle is the ratio of the odds of extirpation on rat-infested vs. invasive mammal-free islands, for all threatened species groups. Orange and red circles are the ratios of the odds of extirpation on islands with cats only (orange) or rats and cats (red) vs. invasive mammal-free islands. The cat*class/volancy interaction term in the model indicates that cats affect native groups differently, while rats affect all native groups equally. Odds ratios were calculated with area and precipitation held at the median values for uninhabited islands (1.5 km^2; 907 mm).

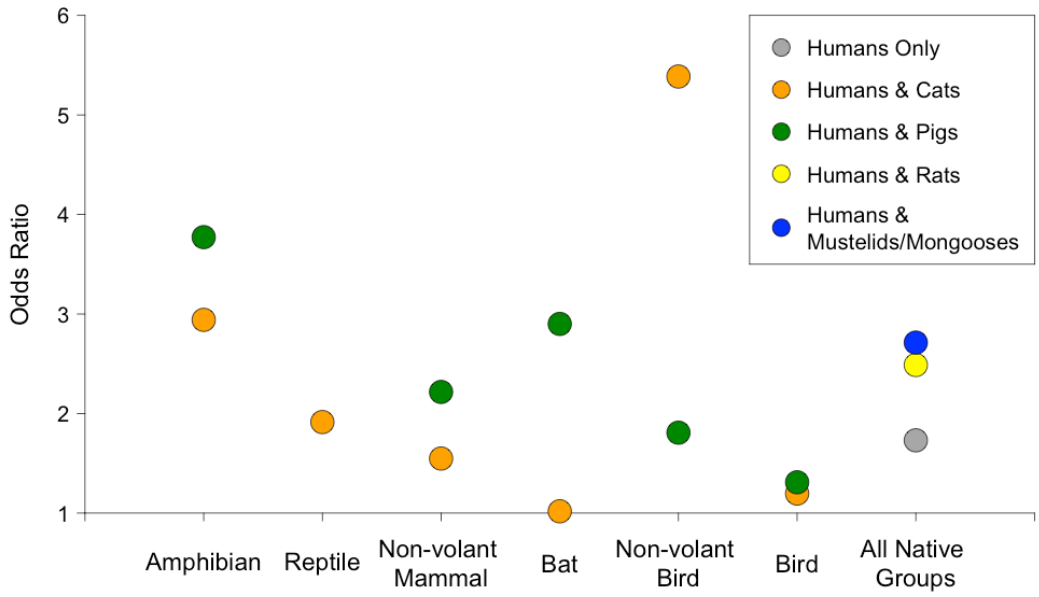


Figure 1-4. Model-predicted odds ratios comparing the odds of extirpation for threatened vertebrate populations on inhabited islands containing invasive cats, pigs, rats, or mustelids/mongooses to the odds on uninhabited, invasive mammal-free islands. The gray circle is the ratio of the odds of extirpation on invasive mammal-free islands with vs. without human populations. The yellow and blue circles are the ratios of the odds of extirpation on inhabited islands containing invasive rats (yellow) or mustelids/mongooses (blue) vs. the odds on uninhabited, invasive mammal-free islands, for all native species groups. The orange and green circles are the ratios of the odds of extirpation on inhabited islands containing invasive cats (orange) or pigs (green) vs. the odds on uninhabited, invasive mammal-free islands. The cat*class/volancy and pig*class/volancy interaction terms in the model indicate that cats and pigs affect native species groups differently, while humans, rats, and mustelids/mongooses affect all native species groups equally. The odds ratio for the effect of pigs on native reptile populations is not shown because it is <1 and thus difficult to interpret (McHugh 2009). Odds ratios were calculated with area and precipitation held constant at the median values for inhabited islands (146.2 km^2; 1,762 mm).

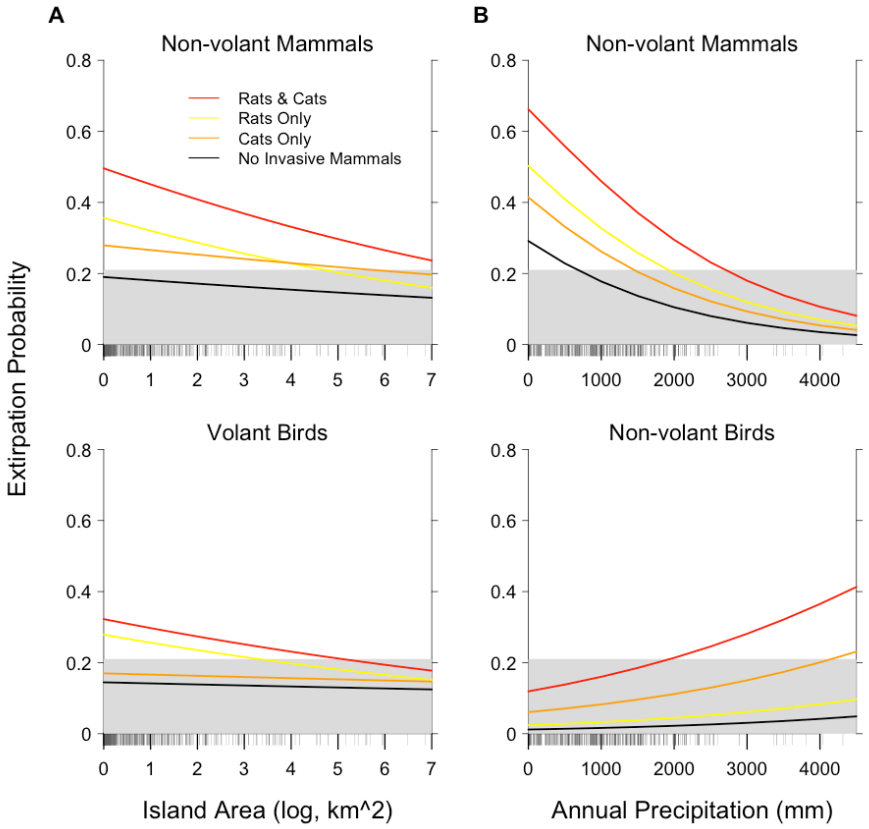


Figure 1-5. Modeled extirpation probabilities across (A) island areas and (B) precipitation levels on uninhabited islands containing no invasive mammals, rats, cats, or both. Model fitted values in (A) were calculated with precipitation held at the median value for uninhabited islands (907 mm), and in (B) with area held at the median value for uninhabited islands (1.5 km^2). Rug plots on the x-axes correspond to the area (A) and precipitation (B) values for island-species records on uninhabited islands in the dataset. The gray shaded areas represent likely population persistence based on a logistic extirpation threshold of 0.21 (80% true-positive rate); the white area represents likely population extinction. Standard errors for the predictions were calculated from K-fold cross-validation (K=10) repeated 10 times, and are not shown because they are too small to appear in the graphs (min SE=0.0002, max SE=0.0158).

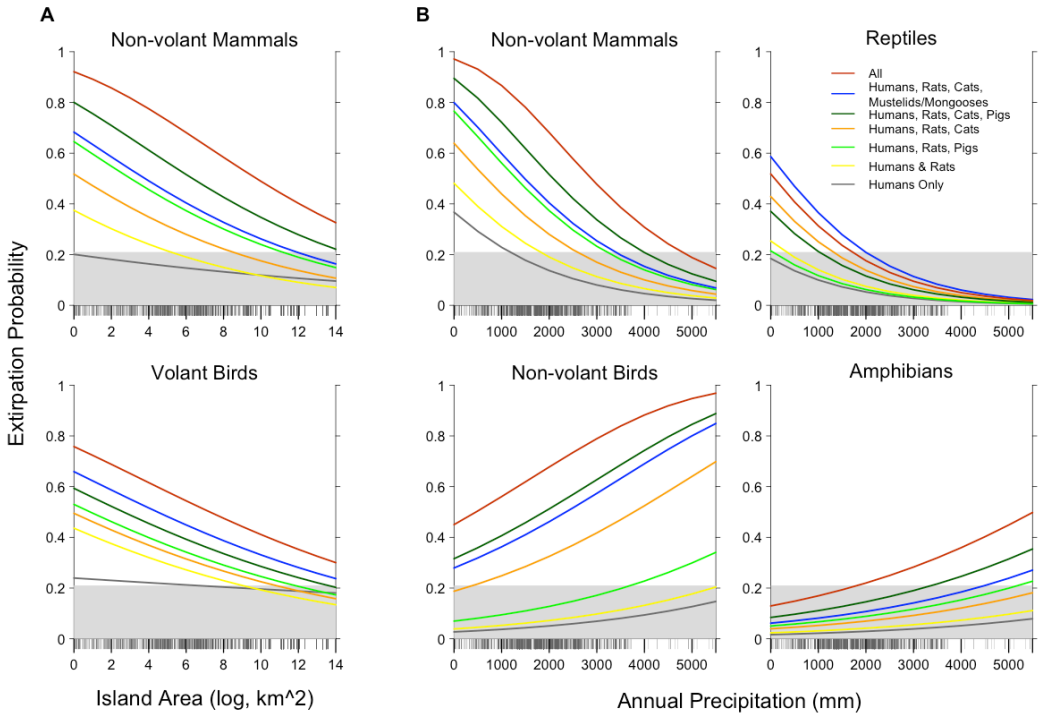


Figure 1-6. Modeled extirpation probabilities across (A) island areas and (B) precipitation values on inhabited islands with only humans and with common combinations of invasive mammals. Model fitted values in (A) were calculated with precipitation held at the median value for inhabited islands (1,762 mm), and in (B) with area held at the median value for inhabited islands (146.2 km^2). Rug plots on the x-axes correspond to the area (A) or precipitation (B) values for all island-species records in the dataset. The gray shaded areas represent likely population persistence based on a logistic extirpation threshold of 0.21 (80% true-positive rate); the white area represents likely population extinction. Standard errors for the predictions were calculated from K-fold cross-validation (K=10) repeated 10 times, and are not shown because they are too small to be seen in the graphs (min SE=0.0002, max SE=0.0202).

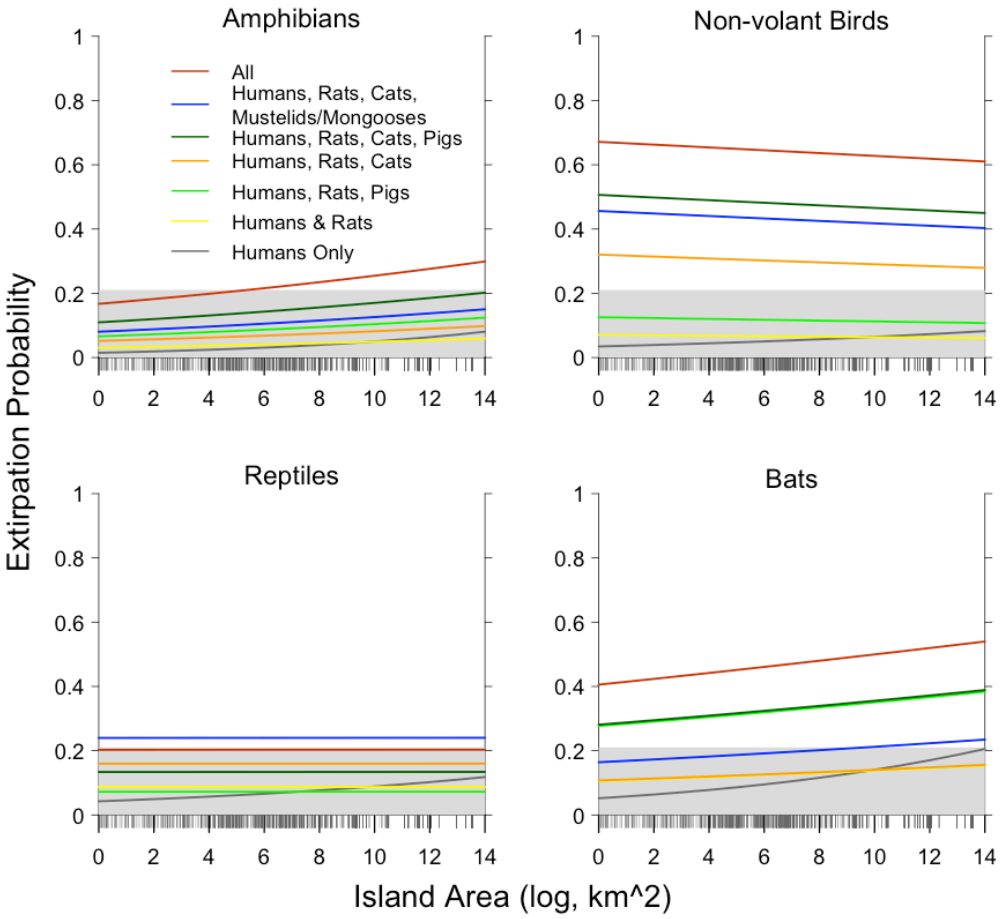


Figure 1-7. Modeled extirpation probabilities across island areas on inhabited islands with only humans and with common combinations of invasive mammals. Model fitted values were calculated with precipitation held at the median value for inhabited islands (1,762 mm). Rug plots on the x-axes correspond to the area values for all island-species records in the dataset. The gray shaded areas represent likely population persistence based on a logistic extirpation threshold of 0.21 (80% true-positive rate); the white area represents likely population extinction. Standard errors for the predictions were calculated from K-fold cross-validation (K=10) repeated 10 times, and are not shown because they are too small to be seen in the graphs (min SE=0.0005, max SE=0.0154).

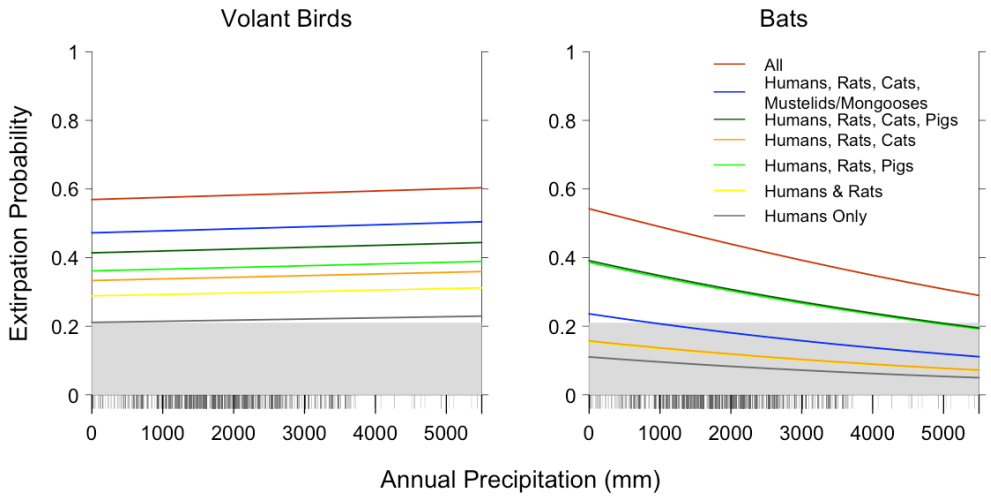


Figure 1-8. Modeled extirpation probabilities across island precipitation values on inhabited islands with only humans and with common combinations of invasive mammals. Model fitted values were calculated with area held at the median value for inhabited islands (146.2 km^2). Rug plots on the x-axes correspond to the precipitation values for all island-species records in the dataset. The gray shaded areas represent likely population persistence based on a logistic extirpation threshold of 0.21 (80% true-positive rate); the white area represents likely population extinction. Standard errors for the predictions were calculated from K-fold cross-validation (K=10) repeated 10 times, and are not shown because they are too small to be seen in the graphs (min SE=0.0015, max SE=0.0103).

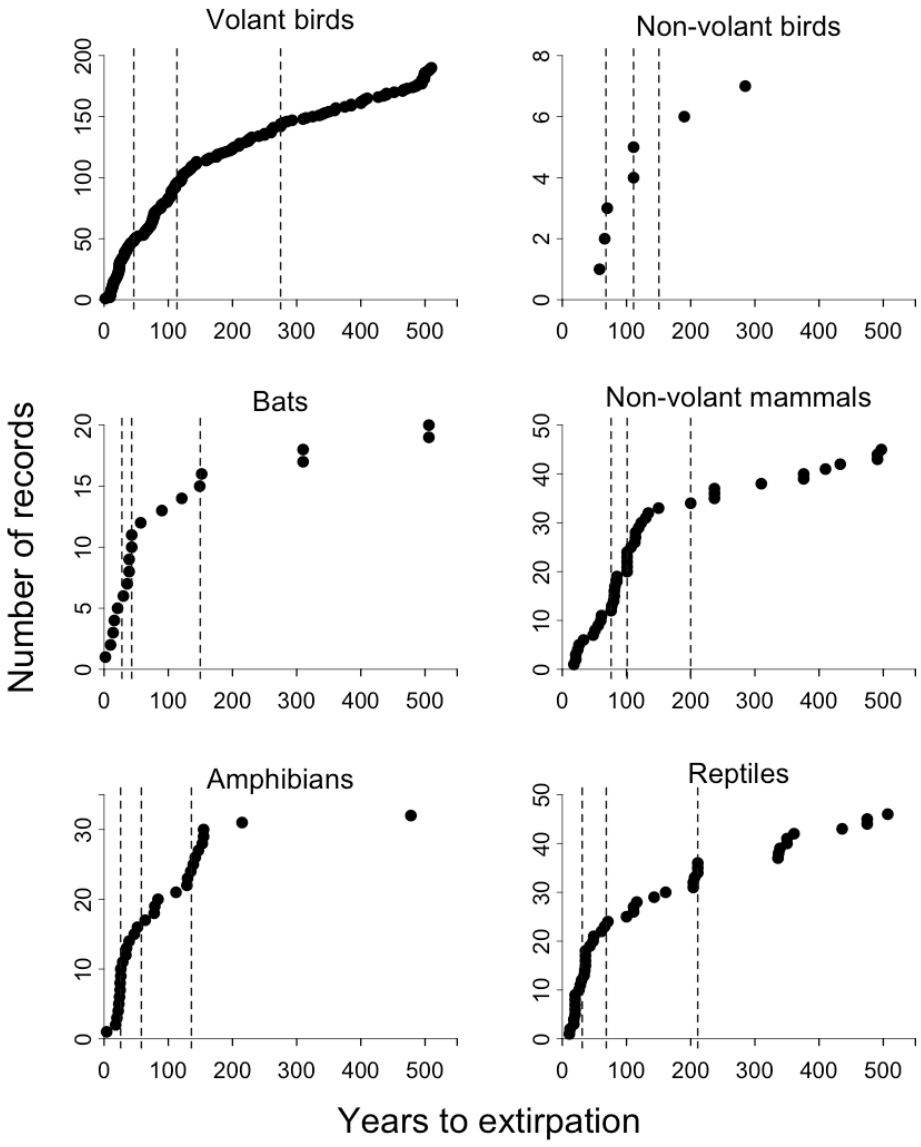


Figure 1-9. Cumulative distribution plots showing the timespan over which native vertebrate population extirpations took place, for all populations that had associated information about the known or estimated year of extirpation (volant birds, n=190; non-volant birds, n=7; bats, n=20; non-volant mammals, n=45; amphibians, n=32; reptiles, n=46). A single point is shown in cases where multiple populations of a native species group were declared extirpated in the same year; this is consistent with the GEE model formulation, which grouped the data by island. Dotted lines show the 25th, 50th, and 75th percentiles for the number of years to extirpation for each native species group.

2. Chapter 2 – Optimizing conservation benefits and cost-efficiency of invasive mammal eradications to conserve globally threatened island species

2.1 Abstract

Island biodiversity is disproportionately threatened, particularly by invasive mammals. The eradication of invasive mammals from islands is a powerful conservation tool. However, the magnitude of the threat from invasive mammals to native island species greatly outweighs the resources available for eradications. Thus, priorities must be set to maximize conservation benefits and cost efficiency. Optimization models are useful tools for setting priorities because they quantify the return on investment for portfolios of alternative actions to achieve specified goals. We quantified the benefits and costs of invasive mammal eradications on islands worldwide, and integrated these benefit and cost estimates in an optimization model. We estimated the extinction risk caused by invasive mammals to each insular terrestrial vertebrate species listed as Critically Endangered or Endangered on the IUCN Red List, and identified portfolios of islands where specified portions of the extinction risk from invasive mammals could be removed via eradication for the minimum cost. We identified four global portfolios of islands (135 islands in total) from which eradication of invasive mammals would cost-efficiently reduce extinction risk to 126 of the most threatened island vertebrate species. This approach builds on previous island prioritization efforts by quantitatively evaluating biodiversity benefits in terms of extinction risk reduction, and by identifying complementary portfolios of islands rather than treating islands as individual, entirely independent entities. In

addition to identifying a global portfolio of high conservation value islands for invasive mammal eradications, our analysis illustrates a robust, transparent, and repeatable approach to conservation prioritization that can be easily adapted to other conservation decision-making situations. This type of strategic return-on-investment approach is necessary for maximizing conservation gains in a world of limited resources.

2.2 Introduction

Species and ecosystems worldwide are threatened by human activities, and conservation interventions are needed to slow biodiversity loss (Tittensor et al. 2014). Islands comprise 5.5% of the earth's land area, but they support a disproportionate amount of terrestrial biodiversity, including an estimated 19% of known bird species and 17% of known rodent species (Tershy *et al.* In press). Island biodiversity is also disproportionately impacted by human activities: 77% of terrestrial vertebrate extinctions have taken place on islands and 37% of species listed as Critically Endangered on the IUCN Red List are insular (Tershy *et al.* In press). A leading cause of extinction and endangerment on islands is invasive alien species (Tershy *et al.* In press.). In particular, mammals associated with humans, such as rats, mice, pigs, goats, rabbits, and cats, have been introduced to a large percentage of the world's ~400,000 islands (Atkinson 1985, UNEP-WCMC 2013). These invaders have a myriad of direct and indirect effects on native insular species, such as overgrazing of native plants, modification of plant succession dynamics, predation of native animals, competition with native species for food and other resources, and alteration

of important physical and chemical ecosystem processes (Croll et al. 2005, Towns et al. 2006, Fukami et al. 2006, Kurle et al. 2008, Spear and Chown 2009, Simberloff 2011, Medina et al. 2011).

The eradication of invasive alien mammals (hereafter 'invasive mammals') from islands is an increasingly utilized conservation tool with a strong record of mitigating or reversing damage caused by invasions (Veitch et al. 2011). To date, nearly 1,100 successful eradications have removed invasive mammals from 750 islands globally (DIISE 2014). Ongoing developments in eradication technologies are creating opportunities to eradicate invasive vertebrates from increasingly large and complex islands (Howald et al. 2007, Burbidge 2011, Campbell et al. 2011). Consequently, national and regional government agencies and conservation organizations are increasingly investing in eradication programs on islands. However, the global scale of island invasions greatly outweighs the resources available for eradications, and only about 20 eradications per year have taken place since 1980 (Keitt et al. 2011). Thus, it is necessary to prioritize islands on which to undertake eradications, to ensure that eradication resources are allocated as effectively and efficiently as possible.

Optimization and return on investment (ROI) approaches are increasingly used for setting conservation priorities (Sarkar et al. 2006). These approaches typically involve: 1) definition of a measurable objective, 2) evaluation of conservation opportunities, 3) estimation of benefits, 4) estimation of costs, and 5) allocation of a portfolio of actions (Murdoch et al. 2007, Joseph et al. 2009).

Researchers have developed sophisticated prioritization algorithms, which have been applied to reserve design and a variety of other conservation contexts (e.g. Pressey *et al.*, 1993; Regan *et al.*, 2006; Strange *et al.*, 2006; Wilson *et al.*, 2006).

Invasive mammal eradications from islands offer unique opportunities to utilize optimization models, and to identify optimal portfolios of islands to achieve particular objectives, e.g. attaining at least one island free of invasive mammals for each insular threatened species (Donlan et al. 2014). Islands are geographically and ecologically discrete systems, with a known primary threat (invasive mammals) that can be completely removed by a specific action (eradication). Furthermore, they involve logistical, social, and economical challenges that can generally be well quantified. The recent creation of a comprehensive dataset of threatened native species and invasive mammals on islands (Threatened Island Biodiversity Database Partners 2012) facilitates evaluation of island threats and opportunities at a global scale. A recent global analysis of threats from invasive mammals to threatened taxa (Chapter 1) improved our knowledge of the impacts of different invasive mammals to different native taxa, and enables the explicit calculation of potential benefits resulting from eradication. Similarly, knowledge of the costs of eradication is improving, with proposed frameworks for categorizing major cost components strengthening our ability to predict eradication project costs (N. Holmes *et al.*, Unpublished data).

Previous attempts to prioritize islands for the eradication of invasive species have typically used methods that assess ROI for each island independently (Brooke et

al. 2007, Dawson et al. 2015). However, the resulting lists of islands may not be cost-effective when considered as a set, because islands have overlapping benefits that make it challenging to identify complementary sets that offer maximum benefits for minimum costs. Furthermore, the use of ranks to determine relative (versus explicit) cost and/or benefit (Brooke et al. 2007, Capizzi et al. 2010) may limit the real-world application of results. Finally, island prioritization efforts to date have been focused only at smaller regional scales (Capizzi et al. 2010, Harris et al. 2011, Donlan et al. 2014, Dawson et al. 2015) or on particular taxa at larger spatial scales (Brooke et al. 2007). We used recent estimates of eradication benefits and costs in a ROI model to identify portfolios of islands that maximize conservation gains, in terms of quantified reductions in extinction risk to globally threatened island vertebrates, for a minimum cost. Our approach builds on previous island prioritization efforts by: a) explicitly and quantitatively evaluating predicted biodiversity benefits; b) integrating robust benefit and cost estimates across islands to identify cost-efficient island portfolios for achieving specified conservation goals; and c) treating the island prioritization problem systematically by considering islands as sets rather than as individual, entirely independent entities. Our model illustrates a flexible approach to conservation prioritization that can be easily adapted to other conservation decision-making situations.

2.3 Materials & Methods

2.3.1 Model Formulation

The goal of our analysis was to identify sets of islands where invasive mammal eradications would achieve a range of specified conservation targets for each threatened vertebrate species, for the minimum cost. We defined conservation targets *T* as the desired number of surviving island populations of each threatened species (details on the selection of values for *T* are provided in the next section). We structured the prioritization model as **M*D ≥ E**:

$$\begin{array}{cc} & \begin{array}{cccc} \text{Islands} & & & \end{array} \\ \text{Species} & \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31} & m_{32} & m_{33} & m_{34} \\ m_{41} & m_{42} & m_{43} & m_{44} \\ m_{51} & m_{52} & m_{53} & m_{54} \end{bmatrix} \end{array} \bullet \begin{array}{c} \text{Decision} \\ \begin{bmatrix} d_1 \\ d_2 \\ d_3 \\ d_4 \end{bmatrix} \end{array} \geq \begin{array}{c} \text{Constraint} \\ \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix} \end{array}$$

(M) **(D)** **(E)**

In this equation, the left-hand side matrix **M** has dimensions *N* x *I*, where *N* is the total number of species needing conservation action to achieve a specified target *T* and *I* is the total number of islands on which those species face threats from invasive mammals. Each cell in the matrix contains either: a) the extirpation probability *m* that would be removed via eradication for species *n* on island *i*; or b) 0, if species *n* does not occur on island *i*. Thus, m_{ni} is the extinction risk to a single species on a single island that could be removed by eradicating invasive mammals. The dimensions of **M** change with different values of *T*, because lower target values require conservation actions for fewer species, on fewer islands (i.e. some species already meet the targets

under current conditions). Similarly, at higher *T*, more threatened species on more islands require conservation action to achieve the target. Thus, **M** is generally larger at higher values of *T*.

The binary decision vector **D** has length *I* and represents potential conservation actions, with the *i*th entry corresponding to eradication (1) or not (0) of all globally harmful invasive mammals (rats, cats, pigs, and mustelids/mongooses [see below section and Chapter 1]) on island *i*. We solve the equation by choosing an eradication strategy **D** that will yield species-level benefits equal to or greater than **E**. In other words, we choose islands for eradications such that each threatened species will attain the specified conservation target, or will come as close to the target as possible if the amount of removable extinction risk is less than the amount required to reach *T*.

The vector **E** has length *N* and contains the constraints in the system: the total amount of extinction risk to each threatened species that must be removed to attain a specified conservation target. The goal of the analysis is to select islands for eradications such that each threatened species experiences a cumulative reduction in extinction risk ($\sum_i m_n$) sufficient to attain the target. For instance, for Species 3 in the above matrix, this equates to

$$\begin{bmatrix} m_{31} & m_{32} & m_{33} & m_{34} \end{bmatrix} \bullet \begin{bmatrix} d_1 \\ d_2 \\ d_3 \\ d_4 \end{bmatrix} = m_{31} * d_1 + m_{32} * d_2 + m_{33} * d_3 + m_{34} * d_4 \geq e_3 \ ,$$

noting that matrix multiplication is the sum(row x column). Thus, for each species *n*, $\sum_i m_{ni} * d_i \geq e_i$ must be true.

In some cases, the amount of extinction risk that can be removed via eradication may be less than the amount required to reach a given target. This is the case when either: 1) invasive mammals pose only minor threats to a native species, meaning that eradication would only produce small reductions in extinction risk; or 2) a threatened species is naturally restricted to one or a few islands, and thus cannot achieve higher population targets. In these cases, the *n*th entry in the vector **E** is the maximum possible amount of removable extinction risk for species *n*, rather than the amount required to reach *T*.

The cost of eradication on each island is represented in a vector **C** of length *I*, with the *i*th element representing the cost of eradicating all invasive mammals included in our analysis (rats, cats, pigs, mustelids/mongooses) on island *i.* Using vector multiplication, we calculate the total cost $\mathbf{C_T}$ of any particular eradication strategy. The objective of the analysis is to choose an eradication strategy **D**, which meets the constraint **E** for the minimum total cost.

$$\begin{bmatrix} d_1 \\ d_2 \\ d_3 \\ d_4 \end{bmatrix} \bullet \begin{bmatrix} c_1 & c_2 & c_3 & c_4 \end{bmatrix} = C_T$$

We conducted the optimization analysis using integer programming implemented in the lpSolve package, in the R statistical language (R Development Core Team 2011). The following sections address the methods used to calculate each parameter in the model.

2.3.2 Calculation of conservation targets (Constraints)

We used the Threatened Island Biodiversity Database (Threatened Island Biodiversity Database Partners 2012) to identify: (1) all known breeding islands for terrestrial vertebrates listed as Extinct, Critically Endangered, or Endangered on the IUCN Red List; and (2) all invasive mammals present on those islands. In a previous analysis (Chapter 1), we tested the importance of a variety of biotic and abiotic factors in predicting island vertebrate population extirpations on islands globally. We built a logistic model that contained the factors we found to be most important. In that analysis we classified native vertebrates into six categories based on taxonomy and the ability or inability to fly ("class/volancy"): amphibians, reptiles, bats, non-volant mammals, volant birds, and non-volant birds; we maintained these groupings in this analysis. We selected a final model that contained the eight most important covariates in determining likelihood of population extirpation—class/volancy, island area and precipitation, the presence of human populations, and introduced rats, cats, pigs, and mustelids/mongooses—and five interaction terms (class/volancy*area, class/volancy*precipitation, class/volancy*cat, class/volancy*pig, and rat*area) (Fig. 2-1). The area under the receiver operating characteristic curve for the full calibration

dataset was 0.75, indicating that the model had an acceptable ability to discriminate extirpations from non-extirpations (Hosmer et al. 2013).

Here, we use this model to calculate the island-level extirpation probability for each population of extant insular vertebrate species classified as Critically Endangered or Endangered (hereafter referred to as 'threatened', noting that we excluded Vulnerable species because these are not comprehensively documented in the Threatened Island Biodiversity Database), based on the island characteristics and introduced mammals present on each population's breeding islands. We used the model fitted values as the extirpation probability, P_e, for each threatened species on each of its breeding islands under current conditions. From this, we calculated the island-level persistence probability ($P_p = 1 - P_e$) for each species on each breeding island. Then, the sum of the persistence probabilities for a single species across all the islands in its range, $\sum_i P_p$, is the total number of populations of the species that are expected to persist under current conditions. For example, in the simplest case, a species that occurs on three islands and has no risk of extirpation on any of them has $\sum_i P_p = 3$; i.e. we expect three island populations of the species to persist. More realistically, island populations have persistence probabilities <1 due to background extinction rate, threats from invasive mammals, and other factors. In this case, $0 < \sum_i P_p < 3$ and $\sum_i P_p$ is the number of island populations expected to persist under current conditions.

We defined conservation targets T as the desired number of persisting populations of each species. For any value of T, the expected persistence $\sum_i P_p$ for a given species might be greater or less than T. A species with $\sum_i P_p > T$ already has more than the desired number of persisting populations, meaning no reduction in extinction risk is needed for the species at the specified T. Conversely, a species with $\sum_i P_p < T$ requires that the extinction probability be reduced on one or more islands such that the total expected persistence after conservation interventions (eradications) will equal or exceed T. Specifically, the amount of extinction probability that must be removed is $T - \sum_i P_p = e$, where e is the required reduction in extinction probability for a given species at a given target (or the maximum possible reduction in extinction probability, if e cannot be attained due to range restrictions or small amounts of threat from invasive mammals).

2.3.3 Calculation of eradication benefits (M)

We estimated the portion of the extirpation risk caused by invasive mammals to each threatened species on each island. Using the logistic model described above, we calculated the difference between each native population's extirpation probability under current conditions (i.e. invasive mammals present) vs. the probability under a hypothetical scenario in which rats, cats, pigs, and mustelids/mongooses were eradicated (i.e. invasive mammals absent). The difference between these values is the amount of the total extirpation probability that is directly attributable to invasive

mammals and that would be removed via eradication. We used this value as the measure of conservation benefit from invasive mammal eradication in our prioritization analysis. We examined these four invasive mammal groups because they were the ones previously found to be most important in driving extirpation risk at a global scale (Chapter 1). We did not address the presence and potential eradication of other widespread introduced mammals on islands (e.g. rabbits, mice, goats) in our analysis, although we note that on some islands, these pose major threats to native species (e.g. Angel *et al.*, 2008).

Our measure of conservation benefit from invasive mammal eradications was calculated at the entire island level for two reasons. First, the original dataset contained only island presence-absence records for both native and invasive taxa; indeed, the intra-island population size, density, and geographic distribution of both native and invasive species are rarely known. The modeled estimates of threats were therefore based on island-level co-occurrences between each threatened species and invasive mammal type. Second, eradications occur at the scale of whole islands: invasive mammals are eradicated from an entire island, or they are not. Although in practice eradication of a subset of the suite of invasive mammals on an island is often undertaken, this can be economically inefficient (Griffiths 2011) and can lead to unanticipated ecological consequences (Zavaleta et al. 2001, Bergstrom et al. 2009, Morrison 2011). We therefore made the additional assumption that all the invasive mammals present on an island would be eradicated simultaneously. Thus, our estimates of eradication benefits reflected the reduction in extirpation risk from the

removal of all invasive mammals, which may be comprised of partial threats from several different mammal groups.

2.3.4 Calculation of eradication costs (C)

The total cost of a mammal eradication project can be divided into several components: planning and management, permitting and compliance with environmental regulations, building local capacity and support, project implementation, non-target species mitigation, and monitoring and evaluation of outcomes (Holmes et al. Unpublished manuscript). The total and proportional costs among these components varies widely between projects, and with the exception of implementation costs, most components are rarely documented or reported. Furthermore, the islands in our global dataset span a wide range of bureaucratic conditions, permitting requirements, and local capacity, making it difficult to generalize many of the cost components across the islands in our dataset. Because of this, we limited our cost estimates to project implementation, as this is the only cost component with sufficient historic data to use for future estimates. In addition, implementation costs are comparable across islands globally because the same techniques are generally used regardless of island geography, ecology, bureaucracy, or social environment. Rat eradications are conducted using aerial or ground-based application of rodenticide bait (Howald et al. 2007), and cats, pigs, mustelids, and mongooses are eradicated using a combination of trapping and hunting methods (Elliott et al. 2010, Parkes et al. 2010, Barun et al. 2011b, Campbell et al. 2011). Previous estimates of eradication costs found that implementation costs scale with

island area (Martins *et al.*, 2006; Holmes *et al*. Unpublished manuscript), although we note this may not be the case for ground-based rodent baiting (Holmes *et al.* Unpublished manuscript).

We used cost estimates of \$50,000 km^{-2} for rat eradications and \$20,000 km^{-2} for cat, pig, and mustelid/mongoose eradications, based on recent surveys of eradication costs (Holmes *et al.* Unpublished manuscript). For rat eradications, we assumed that: (1) all rat eradications would employ aerial methods; (2) all rat species (primarily *Rattus rattus, R. norvegicus,* and *R. exulans* in our data) would require the same eradication methods; and (3) multiple rat species on the same island would be eradicated in the same campaign (i.e. there is no need for two separate eradications). For each island in our dataset, we generated an island-level eradication cost by summing the individual costs of eradicating each mammal group that was present. Efficiencies in the timing and cost of eradication efforts can be gained by targeting multiple species on the same island simultaneously or sequentially (Griffiths 2011). However, we did not account for such efficiencies in our cost estimates because the extent to which such savings can be generalized across islands, and the actual total cost reduction, is highly unpredictable at the scale of our analysis.

We estimated eradication costs only on islands where eradication would be considered feasible using current methods. The primary limiting factors in eradication ability are large island size and human population sizes (Glen et al. 2013). We followed Dawson et al. (2015) in considering eradication feasible on islands containing fewer than 1,000 human inhabitants. The maximum feasible island size for

the four target mammal groups in our study varies by group. For islands containing invasive rats, cats, and pigs, we used size cutoffs based on the largest island from which each group has been successfully eradicated to date [rats: Macquarie Island, sub-Antarctic Pacific Ocean, 128 km^2 (Australian Minister for the Environment 2014); cats: Marion Island, sub-Antarctic Indian Ocean, 293 km^2 (Bester et al. 2002, Campbell et al. 2011); pigs: Santiago Island, Galapagos, 585 km^2 (Cruz et al. 2005)]. Techniques for eradicating mustelids and mongooses lag behind those for the other mammal species, and it is difficult to predict feasible island sizes and eradication costs due to the small number of successful attempts to date (Elliott et al. 2010, Barun et al. 2011b). However, mustelids and mongooses are targeted with the same hunting and trapping techniques used for cats, so we used the same size cutoff for these taxa as for cats. In our data, rats were present on most of the islands that contained one of the other mammal groups; therefore, the maximum size of most of the islands included in our analysis was less than 130 km^2. We identified only four islands larger than 128 km^2 that lacked rats but contained one of the other species (all cats) and fell within the feasible size and human population ranges, so we included these islands as well.

The cost estimates used here should not be mistaken for total cost but rather should be considered a baseline for comparing island mammal eradication costs at a global scale. Total project costs are generally significantly greater than implementation costs, depending on island-specific social, economic, and political characteristics, plus factors associated with planning and mitigating the direct impacts

of eradications to native fauna (e.g. mitigating the effects of toxin application to non-target species).

2.4 Results

2.4.1 Data Summary

We identified 524 islands that contained threatened vertebrate populations and fell within the size and human population thresholds (<128 km^2 for rats; <293 km^2 for cats and mustelids/mongooses; <585 km^2 for pigs; <1,000 human inhabitants) to be considered feasible for invasive mammal eradication. Of these, 243 islands contained one or more of the invasive mammal groups included in our analysis (rats, cats, pigs, and/or mustelids/mongooses). These 243 islands had 317 breeding populations of 137 threatened vertebrate species (Table 2-1). Thirty-five of these species occurred on only one island globally; most of these species are either single-island endemics (i.e. the entire historic breeding range is one island) or only remain on one island out of a larger historic breeding range. One single-island species (*Atelopus elegans*) also has an extant continental population, but we retained it in the prioritization analysis because (1) islands are often the best conservation opportunity for removing extinction risk from invasive mammals, and (2) for this species, there is only a single island where invasive mammal removal could result in conservation benefits. Hereafter, all species that currently occur on only one island are termed "endemic." The remaining 102 native species have populations on two or more islands globally, although some occur on only one island where eradication is feasible. All species that

have populations on multiple islands are hereafter termed “non-endemic.” The number of islands inhabited by each native species ranged from 1 to 54, but only 22 species occurred on more than 10 islands, and 40 species occurred on more than 5 islands.

The most common invasive mammal combinations on the 243 islands with invasive mammals were rats alone (119 islands), rats and cats (53 islands), and rats, cats, and pigs (27 islands). Small human populations (<1,000 people) were present on 106 of these islands. The estimated cost of project implementation (excluding planning, permitting, non-target mitigation, and monitoring) on these islands ranged from US $85, for a small islet (0.2 ha) containing only invasive rats, to US $8.7 million, for a large island (125 km^2) containing both rats and cats. The mean eradication cost was US $1 million and the median was $124,000.

We identified 281 islands with threatened vertebrate populations that fell within the eradication feasibility thresholds but were already free from invasive rats, cats, pigs, mustelids, and mongooses. Many of these islands were never occupied by these invasive species, although 72 (26%) were previously invaded but had successful eradication projects. These invasive mammal-free islands contained 381 populations of 70 threatened species; 34 of these species were single-island endemics (one of these “endemic” species, *Sterna lorata*, also has an extant continental population).

Many native species occur both on islands where eradication is feasible and invasive mammals are present, and on islands that fall within the feasibility thresholds but where invasive mammals are absent. To assess eradication benefits and

determine conservation needs and targets for threatened species, we evaluated all native species that occurred on feasible islands containing invasive mammals (243 islands) and lacking them (281 islands). Thus, our full dataset contained 524 islands, with 698 populations of 207 threatened species (69 single-island endemics; 138 non-endemics).

2.4.2 Eradication benefits

Our earlier logistic model (Chapter 1) indicated that population extirpation risk for the six native vertebrate groups varied across island areas and annual precipitation levels. For the range of island characteristics on the 524 islands included in this analysis, model predictions showed that extirpation probability for most native groups responded strongly to changes in precipitation and weakly to differences in island area (Fig. 2-1a). The presence of humans and invasive mammals on islands increased extirpation risk for all native groups (Fig. 2-1b). Humans, rats, and mustelids/mongooses had a consistent impact across all native groups, while cats and pigs affected each group differently.

The species-level expected persistence (i.e. the sum of persistence probabilities) across all of each species' breeding islands—including both single-island endemic and non-endemic species—ranged from 0.5 to 44.7 (Fig. 2-2a). Fifty-four species occur only on islands lacking invasive rats, cats, pigs, and mustelids/mongooses, and thus had no estimated extirpation risk caused by invasive mammals. Our data contained 153 species that co-occur with invasive mammals on

one or more islands; the proportion of total extinction risk caused by invasive mammals to these species ranged from <1% to 89% (mean 47%) (Fig. 2-2b).

The number of populations expected to persist (i.e. the sum of the persistence probabilities) for non-endemic species ranged from 0.84 to 44.7 (mean 5.3, median 3.5). This wide range largely reflects the number of islands on which each species occurs. Many non-endemic species face threats from invasive mammals on both large islands, where eradication is not practical, and on smaller islands where eradication is a viable option. In these cases, the threat from invasive mammals to a particular species can be subdivided into a portion that cannot currently be addressed via eradication, and another portion that is potentially removable (Fig. 2-2b). In our optimization analysis, we used this second portion as the measure of conservation benefit from eradications.

Thirty-five endemic species in our data are threatened by invasive mammals on 30 islands. The remaining 34 endemic species occupy islands lacking invasive rats, cats, pigs, and mustelids/mongooses. The total expected persistence under current conditions for the full set of endemic species was 55.8, or about 81% of the total 69 endemic species populations.

2.4.3 Optimization analysis

Only four islands in our data contained both endemic and non-endemic species (Tables S1, S2). The selection of individual islands for eradications to benefit endemic species was therefore largely decoupled from the selection of islands for

non-endemic species, so we ran the prioritization analysis separately for endemics and non-endemics.

The minimum possible endemic conservation target, defined as the desired proportion of endemic populations that will persist, was 81%. This value derives from the model prediction stated above, that the current expected persistence for all endemic species is 55.8 (81% of all endemic populations). It follows that endemic conservation targets must be greater than this value to select islands for eradications to further reduce extinction risk (and thus increase persistence probability) for endemics. Our model estimates of the extinction risk caused by invasive mammals on islands where eradication is feasible suggested that eradications could increase the endemic persistence probability to a maximum of 87%. The remaining threats to these species are due to other causes and therefore would not be removed via eradications.

Based on these initial results, we ran the optimization analysis for endemic species across a range of conservation targets from 81% to 87%. At each endemic persistence target value *T*, the optimization model selected portfolios of islands where eradication would achieve *T* for the minimum cost. With each increasing increment in *T*, up to four islands were added to the growing portfolios (Fig. 2-3). In addition, with increasing *T*, island portfolios were largely nested such that islands chosen at lower targets usually remained in larger portfolios. In three cases, one to three islands that were included in a given set did not appear in the subsequent set (i.e. the island portfolio chosen at the next highest target). However, these islands were usually

added again to island portfolios in the subsequent stepwise increase in *T*, and thus did not substantially change the overall makeup of island portfolios across increasing conservation targets. These cases of non-nestedness occurred because some islands contained more than one endemic species and therefore offered relatively higher or more cost-effective conservation gains than other islands (or island portfolios) for a given target. There was a generally linear increase in the cumulative cost of eradications to meet increasing endemic conservation targets. Eradicating invasive mammals on all islands with threatened endemic species would require eradications on 30 islands covering a total of 1,710 km^2, at a total base cost of ~$90 million (Fig. 2-3, Table S1).

For non-endemic species, we ran the prioritization analysis across a range of conservation targets from 0 to 5 desired populations. The minimum conservation target for non-endemic species was less than 1 because the expected persistence for some species was as low as 0.84 (e.g. a species may occur on two islands and have a low persistence probability on each of them, such that the sum of the two persistence probabilities is <1). We chose a maximum conservation target of 5 because the majority of species in our dataset occur on (or have a total expected persistence of) <5 islands, and these are the species most in need of conservation action. Furthermore, we show below that eradications on the islands selected for the maximum target of 5 would remove or substantially reduce extinction risk for 89% of the species threatened by invasive mammals on islands where eradication is currently possible. Most of the remaining 11% of threatened species currently occur on >10 islands.

With each stepwise increase in conservation target for non-endemic species, up to 12 islands were added to the growing portfolios (Fig. 2-4). The portfolios were completely nested. In contrast to the results for endemic species, the addition of islands and the cumulative cost of eradication to benefit non-endemic species were not linear; rather, they progressed in a stepwise fashion, with the largest increases in island portfolio size and cost at lower targets. The full portfolio at T=5 contained 109 islands (Table S2) on which invasive mammal eradication would remove some or all of the extinction risk from invasive mammals to 91 non-endemic species (36 volant birds, 4 non-volant birds, 27 reptiles, 9 amphibians, 9 non-volant mammals, and 6 bats). Invasive mammal eradications on these 109 islands would cover a land area of 2,295 km^2 and would have a base cost of US $140.2 million.

We divided the complete island portfolio for non-endemic species into four priority sets for eradications, based on relative increases in island portfolios size and cost. We determined the portfolios based on asymptotes in the cumulative cost for achieving specified conservation targets (Fig. 2-4). These asymptotes represent strategies in which eradications would achieve substantial conservation gains for relatively little additional cost, provided all the islands necessary to achieve lower targets have been completed.

We considered the islands chosen for endemic species to be a complete portfolio, independent of the non-endemic species portfolios. We quantified the conservation benefits of eradicating invasive mammals on all the islands in each portfolio, in terms of the extinction risk to native species that would be removed.

Specifically, we isolated the proportion of the total extinction probability that is potentially removable via eradication (Fig. 2-2b), and calculated the portion of that risk that would be removed if eradications were completed for each island portfolio (Fig. 2-5). Some threatened species gained the maximum possible benefits from eradication in a single portfolio of islands, while others gained partial, sequential benefits via eradication on islands in sequential portfolios.

2.5 Discussion

Strategically selecting islands for invasive mammal eradication requires an understanding of the type, severity, and geographic distribution of threats to island species. Recent advances that facilitate island prioritization efforts include (1) the Threatened Island Biodiversity Database, which identifies just over 1,500 islands (out of c. 400,000 worldwide) that support highly threatened vertebrates (>1,100 Critically Endangered and Endangered species), (2) quantification of the relative threats posed by different invasive mammals to each native species on each of these islands (Chapter 1), and (3) development of more refined eradication costing frameworks (Holmes *et al*. Unpublished manuscript). Optimization approaches allow selection of island portfolios that achieve conservation goals cost-efficiently across all species' island distributions (Donlan et al. 2014), as opposed to selecting islands independently (Brooke et al. 2007). We highlight the value of optimization approaches for prioritizing islands by identifying a global portfolio of 135 islands, on which invasive mammal eradications could remove a substantial portion of the extinction risk from invasive mammals to 126 globally threatened vertebrate species.

Our model estimates indicated that both the total extinction risk to each threatened species and the portion of the risk caused by invasive mammals varied widely across species. For example, some island species had a high overall risk of extinction, with only a small portion caused by invasive mammals. In contrast, some species had a small total extinction risk but most of this was caused by invasive mammals. Understanding such patterns is critical for identifying eradication priorities. Without explicit knowledge of the drivers of extinction risk, eradication resources might be directed toward species with higher total risk of extinction, even though the actual benefits from eradication may not be substantial. Furthermore, many native species occurred on both small islands, where eradication is feasible, and on large islands where it is currently not. For these species, we subdivided the total extinction risk from invasive mammals into the risk that could or could not be averted via eradication. The ability to isolate and quantify threats from a specific source, independent from the background extinction rate or other anthropogenic causes, is rare in conservation and is most feasible in discrete systems such as islands. Yet, this ability is important for prioritizing eradications because it allows a more precise estimate of the benefits, in terms of reduced extinction risk, that are expected to result from a particular conservation action. Integrating the distribution of threats and benefits across many islands with eradication costs is a transparent way to identify cost-effective island portfolios for removing extinction risk to native species.

Half of the 69 single-island endemic species (including one species that also breeds on a continent) in our dataset currently face threats from invasive mammals,

and our model predicted that about 56 of these species will persist given current conditions. Nevertheless, up to 75% of the total extinction risk for some endemic species is due to invasive mammals and thus could be removed via invasive mammal eradication. Few islands where eradication is feasible support both endemic and non-endemic threatened species. The optimization model identified portfolios of islands where the extinction risk to endemic species could be removed most cost-efficiently. However, we view all islands with threatened endemics as high priorities for eradications, as these species require targeted conservation actions on the single islands where they persist.

For each non-endemic species persistence target we tested, the optimization model identified a portfolio of islands to achieve that target for the lowest cost. As targets increased, the island portfolios grew, but included all islands in the smaller portfolios identified for lower target thresholds (i.e. portfolios were nested). This result was not necessarily expected, as the complex distribution of biodiversity values across islands could have led to the removal of some islands and the addition of others to more efficiently attain a specified target. However, a similar nested pattern was found in a smaller-scale island prioritization analysis that used the same optimization technique (Donlan et al. 2014). This nested pattern in our results may occur because species occurring on multiple islands may only occur on one island where eradication is feasible, or because some islands present opportunities to reduce extinction risk for multiple threatened species through a single eradication project. If the eradication cost on such an island is low, or if the native species occur on few

other islands, this type of island should offer disproportionately high conservation benefits. This type of nestedness is beneficial from the perspective of long-term conservation planning because it implies consistency: the smallest, top-priority island portfolios can be tacked first, with islands in the larger portfolios added incrementally under the same optimal allocation strategy.

Eradicating invasive mammals on the islands in each portfolio may lead to benefits beyond those required to meet a given target. First, eradication on an island to reach a target may result in more benefit to a species than was needed just to reach the target. In addition, when an island is chosen to help a species meet a particular target, other species on the island may have already met that target but will receive additional, ancillary benefits from eradication. The extent to which these benefits will accrue depends on the target, the set of chosen islands, and the suite of threatened species present on each island. Our analysis focused on the most threatened vertebrate species globally (Critically Endangered and Endangered), and extending this analysis to include Vulnerable and Near Threatened species is an important next step. In addition, most of these islands contain threatened taxa such as plants and invertebrates that are less well studied but that would likely benefit from invasive mammal eradications (Aslan et al. 2015). When IUCN Red List assessments of these groups become available, our methods can be used to perform similar analyses to identify high-priority islands for these taxa, as well as overlaps between priorities for the different native taxa.

Improved estimates of conservation benefits and eradication costs will improve optimization models for eradication of invasive mammals on islands. The benefit values we used here were generated by a global model with its own set of assumptions and simplifications, and address the benefit to individual threatened species (Chapter 1). Outcomes of invasive mammal eradication for the broader island ecosystem are island-specific (Zavaleta et al. 2001, Rayner et al. 2007) and were not considered in our analysis. Further, island isolation, topography, and climate affect an eradication project's logistical complexity, the ability to employ each method, and the time needed to undertake projects. In addition, the presence of sensitive non-target native species often adds additional complexity (Howald et al. 2009). Every island is part of a broader social and political environment, with many stakeholders including island residents or users (e.g. seasonal fishers or farmers), and local, regional, and national governments (Oppel et al. 2011, Glen et al. 2013). Island-specific combinations of all these factors will determine the feasibility and likelihood of success of any eradication project. As benefits, costs, and socio-political variables that influence eradications become better understood and, ideally, quantified, these improved estimates can be incorporated into models to more clearly understand relative benefits and costs across islands (Donlan et al. 2014).

Our study advances the use of transparent, return-on-investment models for planning conservation actions. To our knowledge, the optimization method we used here has been used only one other time in designing eradication portfolios, to address a much simpler context within one archipelago (Donlan et al. 2014). Our study builds

on that and other island prioritization analyses by incorporating explicit quantitative estimates of the threat caused to individual species by different invasive mammals. By incorporating more precise estimates of conservation benefits, and then accounting for the threat (or lack of threat) to each species on each island in its range, we were able to identify the species most in need of urgent action and those most likely to benefit from eradication. Our optimization strategy also overcomes many of the weaknesses inherent in simpler island prioritization methods, such as ranking islands by the number of threatened species present, using indices to represent biodiversity benefits (Brooke et al. 2007, Dawson et al. 2015), or simply dividing biodiversity values by cost to represent cost-efficiency (Brooke et al. 2007). The approach we used is transparent and can be easily modified to incorporate different island data or take account of inter-dependencies among islands. Application of this approach may be particularly useful at the national scale, where decisions about funding are typically made (Carrion et al. 2011). More broadly, our approach can be extended to address any conservation decision-making situation in which the benefits and costs of potential actions can be quantified. This type of return-on-investment approach is critical for achieving the greatest possible conservation gains in a world of limited resources.

2.6 Tables

Table 2-1. The number of Critically Endangered or Endangered species on islands where invasive mammals are present and eradication is feasible (n=243). Shown are the number of single-island endemic species and populations for each species group 'Invasive mammals' refers only to those included in this analysis (all species of invasive rats, cats, pigs, mustelids, and mongooses).

	# Species	# Endemic Species	# Populations on islands containing invasive mammals
Volant birds	81	15	123
Non-volant birds	10	1	14
Non-volant mammals	28	7	20
Bats	9	2	26
Amphibians	18	2	21
Reptiles	61	8	113
Total	**137**	**35**	**317**

2.7 Figures

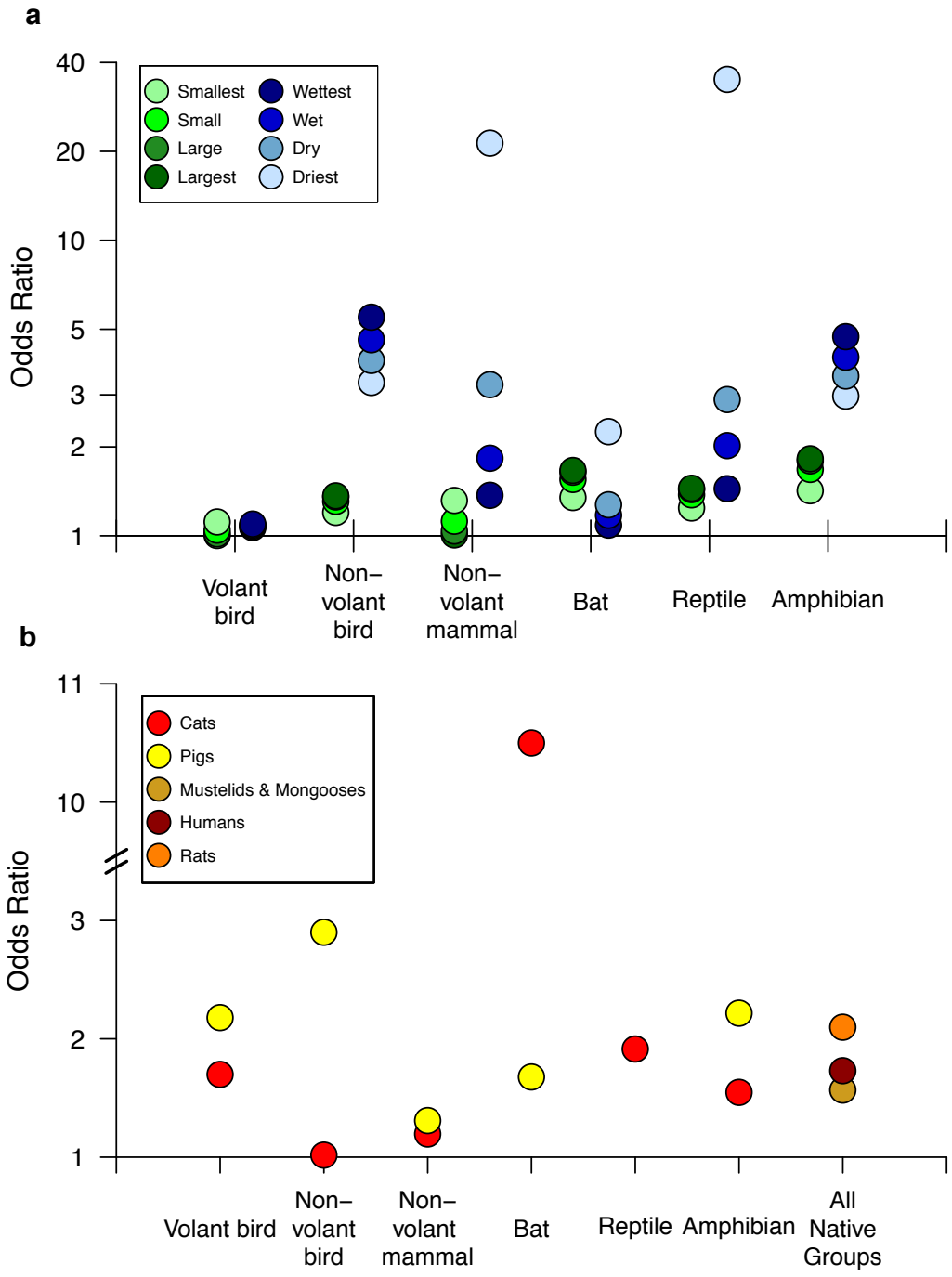

a
Odds Ratio
40
20
10
5
3
2
1
Smallest
Small
Large
Largest
Wettest
Wet
Dry
Driest
Volant bird
Non–volant bird
Non–volant mammal
Bat
Reptile
Amphibian
b
Odds Ratio
11
10
3
2
1
Cats
Pigs
Mustelids & Mongooses
Humans
Rats
Volant bird
Non–volant bird
Non–volant mammal
Bat
Reptile
Amphibian
All Native Groups

Figure 2-1.

The effect size, shown as model-predicted odds ratios, of island physical characteristics and invasive mammals on native species extirpation probability. (a) Odds ratios comparing the odds of extirpation for threatened vertebrate populations on islands with different areas and annual precipitation. Green circles are the ratios of the odds of extirpation on the smallest ($1.0e^{-5}$ km^2) or largest (273.2 km^2) islands in the data vs. the odds on small (1^{st} quartile [qu.] area [A]: 0.14 km^2), median A (0.97 km^2), or large (3^{rd} qu. A: 6.69 km^2) islands, calculated with precipitation held at its median value (1,1059 mm). Blue circles are the ratios of the odds of extirpation on the wettest (max precipitation [P]: 5,357 mm) or driest (min P: 0 mm) islands vs. the odds on wet (3^{rd} qu. P: 1,599 mm), median P (1059 mm), or dry (1^{st} qu. P: 553 mm) islands, calculated with area held at its median value (0.97 km^2). All odds ratios were calculated with no invasive mammals present. (b) Circles compare the odds of extirpation on islands containing cats, pigs, mustelids/mongooses, rats, or humans, to the odds on uninhabited, invasive mammal-free islands. The effects of cats and pigs on differ across native vertebrate groups, while the effects of rats, mustelids/mongooses, and humans are the same across all groups. The effect of pigs on reptiles is not shown, as the odds ratio was less than one and therefore difficult to interpret. Odds ratios were calculated with area and precipitation held constant at the median values for inhabited islands (0.97 km^2; 1,059 mm).

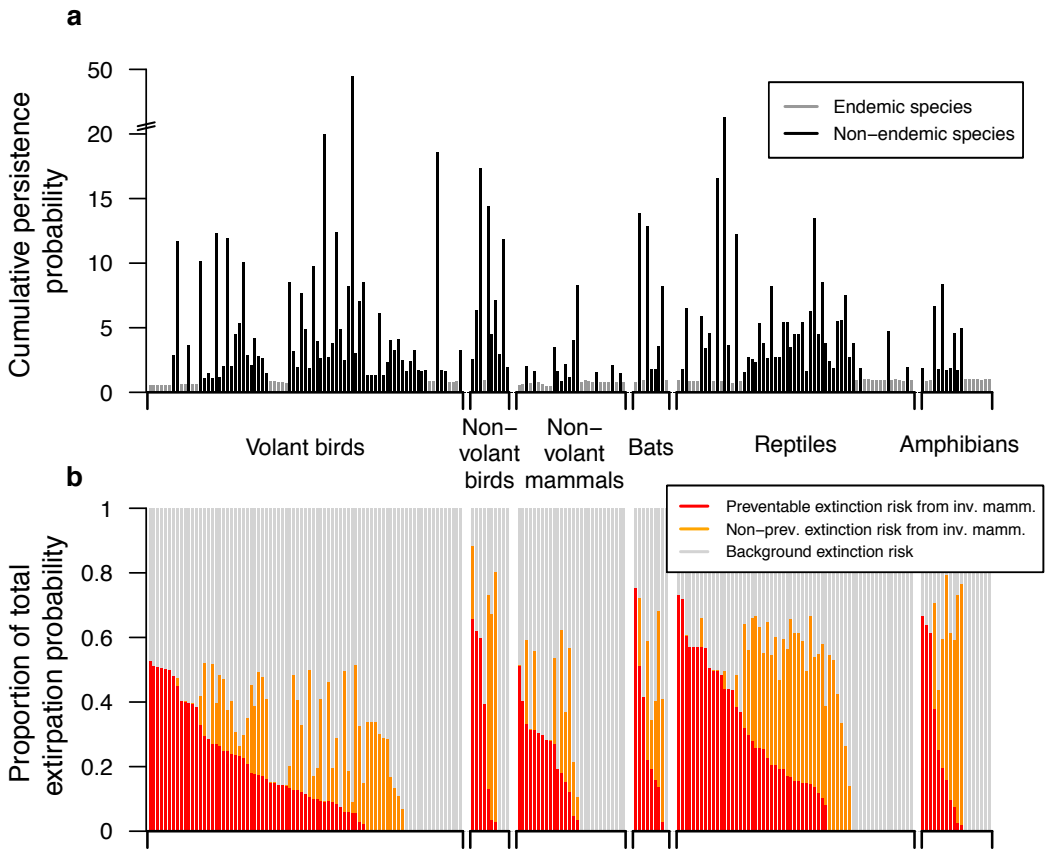


Figure 2-2.

Modeled expected persistence (a) and extirpation probability due to invasive mammals (b) (rats, cats, pigs, mustelids, and mongooses) by native species. (a) Expected number of persisting populations for each species in the analysis (n=207), across all the islands on which each species occurs (1 to 48 islands per species). Each bar represents a species. (b) Proportion of total extinction risk due to invasive mammals by native species. Each bar represents the total amount (100%) of the extirpation risk for each native species, across all islands on which each species occurs, with species shown in the same order as in (a). Each bar (i.e. the total extinction risk) is divided into: the proportion of risk due to invasive mammals on islands where eradication is feasible (red); the proportion due to invasive mammals on islands where eradication is not currently feasible (orange); and the proportion due to background extinction risk or other anthropogenic threats (gray). The red portions of the bars thus represent the proportion of extirpation risk that can be removed via eradication.

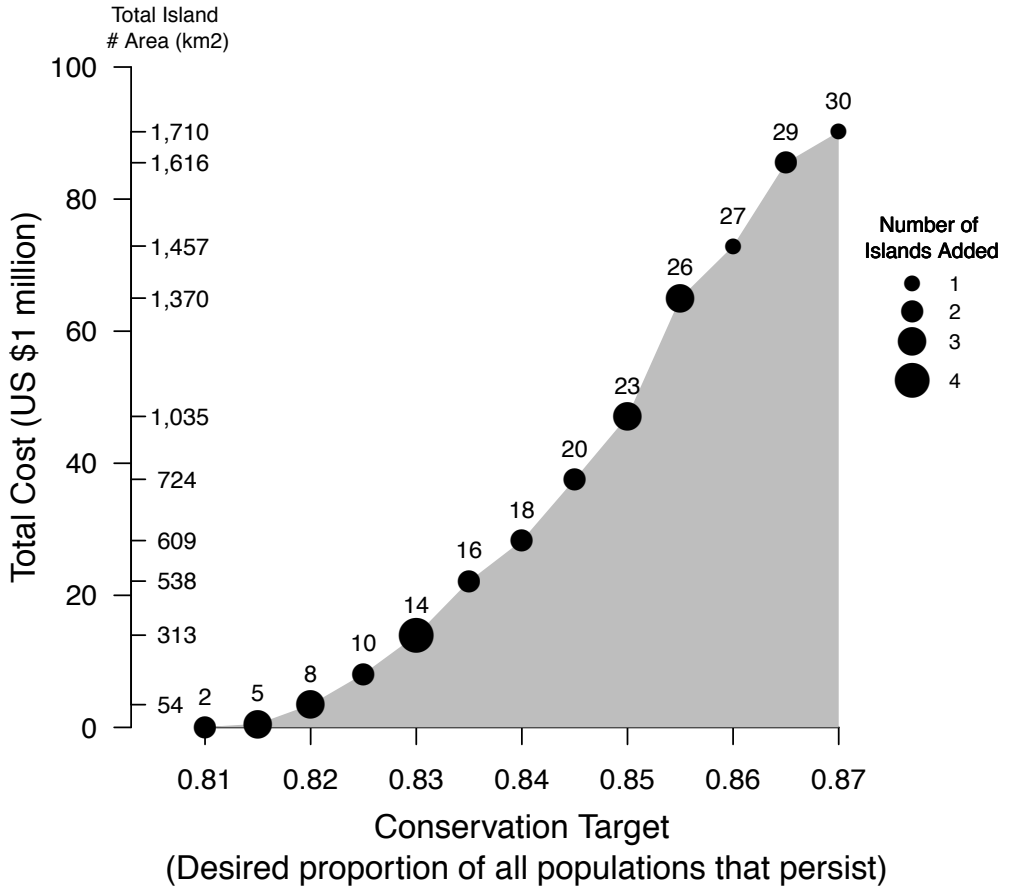


Figure 2-3.

Cumulative cost (and island area covered) for invasive mammal eradications on portfolios of islands to achieve specified conservation targets for single-island endemic species. Targets for endemic species are defined as the desired proportion of all endemic species that will persist, measured as the sum of the persistence probability for all endemic species. The numbers above the plot are the total number of islands on which eradication would take place to achieve each target.

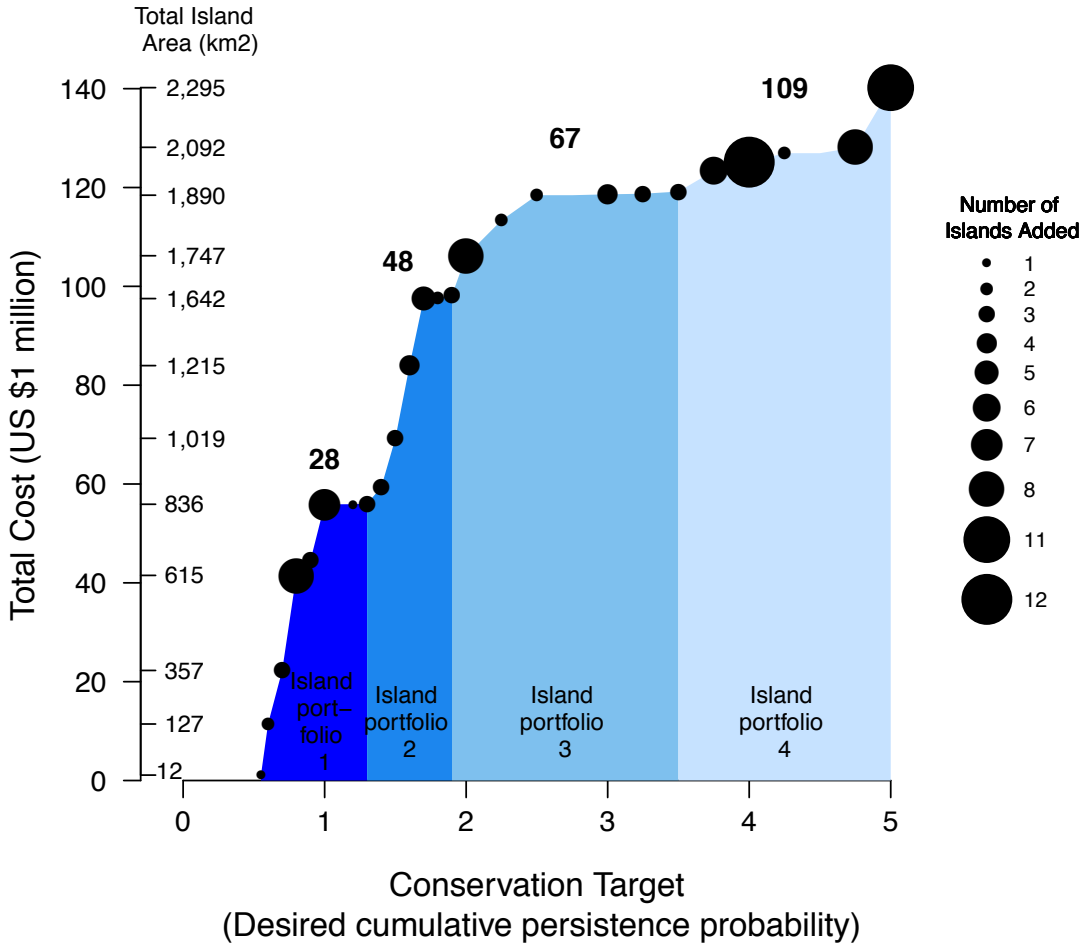


Figure 2-4.

Cumulative cost (and island area covered) for invasive mammal eradications on portfolios of islands to achieve specified conservation targets for multi-island species. Targets for multi-island species are defined as the desired cumulative persistence probability for each species, or the highest persistence probability possible within the natural limits of a species' native range. The full island portfolio (n=109) is divided into four smaller, nested portfolios based on cost-efficiencies for achieving given targets. The numbers in bold above the plots are the total numbers of islands on which eradications would take place as portfolios are completed.

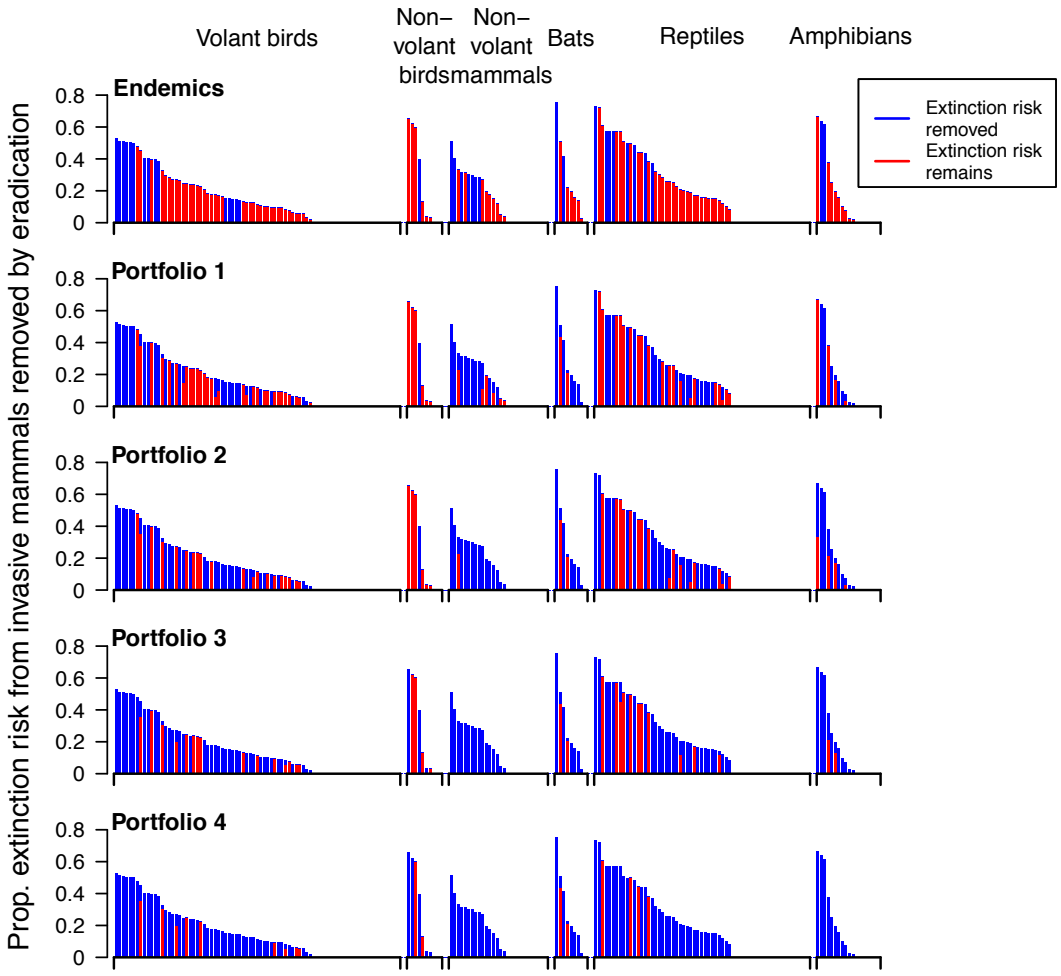


Figure 2-5.

Estimated reduction in extinction risk to threatened island species as eradications are completed in each island portfolio. Each bar represents a species and species are shown in the same order as in Fig. 2-2. Bars represent the proportion of each species' total extinction risk that can potentially be removed by eradicating invasive mammals on one or more islands (bars shown here are the same as the red portions of the bars in Fig. 2-2b). Blue sections of each bar represent the proportion of extinction risk that would be removed as eradications are completed on islands with endemic species (top panel) and on islands in the 1st, 2nd, 3rd, and 4th prioritized portfolios (lower panels).

3. Chapter 3 – Cheap and nasty? The negative impacts of using management costs to identify global conservation priorities

3.1 Abstract

The financial cost of biodiversity conservation varies widely around the world, so such costs must be considered when identifying countries where conservation investments are best focused. Previous global prioritizations have been based on global models for protected area management costs, but this metric may be related to other factors that negatively influence the effectiveness and social impacts of conservation. Here we investigate such relationships and first show that countries with low predicted costs are less politically stable. Local support and capacity can mitigate the impacts of political instability, but we also found that these countries have less civil society involvement in conservation. Therefore, externally funded projects in these countries must rely on government agencies for implementation. This can be problematic, as our analyses show that governments in countries with low predicted costs score poorly on indices of corruption, bureaucratic quality and human rights. Taken together, our results demonstrate that using national-level estimates for protected area management costs to set global conservation priorities is simplistic, as projects in apparently low-cost countries are less likely to succeed and more likely to have negative impacts on people. Therefore, we urgently need a new approach to develop global conservation cost metrics that better capture the true costs of avoiding or overcoming such problems. Critically, conservation scientists must engage with practitioners to better understand and implement context-specific solutions. This

approach assumes that measures of conservation costs, like measures of conservation value, are organization specific, and would bring a much-needed focus on reducing the negative impacts of conservation to develop projects that benefit people and biodiversity.

3.2 Introduction

Biodiversity is declining at a rapid rate (Butchart et al. 2010) but there is little spatial overlap at a global level between conservation need and local funding availability. Many countries therefore rely on funds from international donors (Balmford and Whitten 2003) and a number of studies have developed prioritization schemes to identify the most cost-effective places for conserving biodiversity (Halpern et al. 2006). The first and best known of these schemes were developed by international conservation non-governmental organizations (NGOs) and based on patterns of biodiversity distribution and threat (Myers et al. 2000, Olson and Dinerstein 2002, Brooks et al. 2006) to identify and fundraise for priority regions (Smith et al. 2009). However, these systems attracted criticism for their theoretical weaknesses and the coarse spatial resolution of the underlying biodiversity data (Brummitt and Lughadha 2003, Murdoch et al. 2010) and subsequent schemes used more robust methods and fine resolution biodiversity data to identify finer-scale priority areas (Orme et al. 2005, Grenyer et al. 2006, Ceballos and Ehrlich 2006). Finally, global conservation prioritization became more systematic with the emergence of target- and complementarity-based approaches (Rodrigues et al. 2004, Ceballos et al. 2005, Loyola et al. 2009, Terribile et al. 2009).

These early analyses were instrumental in shifting the focus from single species to more holistic biodiversity conservation schemes (Adams 2004), but fell short of identifying cost-efficient priorities because they did not account for spatial variation in conservation costs (Murdoch et al. 2010). Similar analyses at the sub-national scale moved to overcome this issue by including acquisition, management or opportunity cost data (Pence et al. 2003, Naidoo et al. 2006). These costs could then be combined with biodiversity values to calculate and compare the expected return on investment for a range of potential conservation actions (Ando et al. 1998, Murdoch et al. 2007). Return-on-investment approaches were subsequently applied at a global scale, using models that predicted protected area management costs by country based on each country's purchasing power parity (PPP) and gross national income (GNI) (Balmford et al. 2003, Moore et al. 2004). This work revealed that variation in protected area management costs overwhelmed the effects of biodiversity and threat in determining global conservation priorities, largely because country-level costs ranged by seven orders of magnitude (Underwood et al. 2008, Bode et al. 2008).

The strong influence of cost on global prioritizations makes it vital to select a cost metric that accurately reflects the true, realized costs of achieving conservation goals (O'Connor et al. 2003, Knight et al. 2010). However, the most widely used global cost estimates for managing protected areas may inaccurately predict the realized costs of project implementation. Ideally, global conservation cost metrics should reflect the probability of long-term project success because: a) obstacles to implementation decrease the likelihood of attaining conservation objectives, and b)

overcoming these obstacles will increase project costs. Many countries with low predicted costs are developing countries (Balmford et al. 2000) where less stable socio-political environments might make conservation investments risky. Foreign investors often avoid these countries due to their unreliable business environments (Wei 2000, Biswas 2002, Busse and Hefeker 2005), and the same factors that deter economic investments likely present challenges to conservation as well.

Successful project implementation depends on a range of factors beyond the direct costs of staff wages, equipment and time (O'Connor et al. 2003, McBride et al. 2007). For example, civil society involvement and support are critical to conservation success (Rodríguez et al. 2007, Smith et al. 2009). When international agencies work in foreign countries but fail to engage local communities, they must rely on national governments to manage funds and implement projects. This reliance on governments can be problematic in countries where political institutions are weak, unstable, or corrupt, as projects will be vulnerable to changes or failures of national governments or economies (Barrett et al. 2001, Smith et al. 2003). Without strong local capacity and support, outside organizations may not be able to carry projects forward in times of instability, or may face ongoing resistance from local communities whose interests are not well represented. Thus, failure to engage civil society may reduce the long-term success of conservation initiatives. These issues can be mitigated or avoided by working closely with local stakeholders through all stages of planning and implementation (Smith et al. 2009), but the extent to which these efforts increase project costs is difficult to predict and has not been well studied.

Conservation planning efforts must also consider implications for local people, as any negative impacts can reduce human wellbeing and erode support for conservation. This is particularly important because many nations with low predicted management costs are developing countries with large populations of rural, disenfranchised poor (Sanderson 2005, Convention on Biological Diversity 2010). It is these people who bear the brunt of conservation opportunity costs (Brockington 1999, Ghate 2003, Adams et al. 2010) through the loss of agricultural land, limitations on infrastructure development and restrictions on harvesting wild species (Ferraro 2002). Indeed, strict enforcement of protected area policies often results in the displacement or eviction of these people from their land (Geisler and De Sousa 2001, Cernea and Schmidt-Soltau 2006, Agrawal and Redford 2009), sometimes involving the illegal use of force (Bijoy 2011).

Conservation NGOs are committed to improving project success and minimizing negative impacts on project stakeholders and neighbors, but the costs of achieving these goals are rarely considered in global prioritization exercises. There is, therefore, an urgent need to investigate whether using modeled management costs in global conservation prioritizations highlights countries where implementation is more difficult and negative impacts on people more likely. Here, we investigate the relationships between national-level protected area management costs and a range of factors that broadly relate to conservation effectiveness and impacts on people.

Conservation actions involve a range of costs beyond direct management costs, including acquisition, transaction, damage, and opportunity costs (Naidoo et al.

2006). In this analysis we focus only on management costs for several reasons. Our broad goal here is to investigate issues relating to where international conservation donors should spend money to have the greatest, most cost-effective impact on conservation. Management cost is the metric most often used in global-scale conservation prioritization (Balmford et al. 2003, O'Connor et al. 2003, Moore et al. 2004, Bode et al. 2008, Wilson et al. 2011), and it is the only cost that is ongoing and is directly related to the success or failure of conservation interventions. Using acquisition cost is inappropriate in many places where land cannot be bought or sold (Knight et al. 2011), and to our knowledge transaction and damage costs have not been studied or modeled at a global scale. Global data on opportunity costs do exist (Naidoo and Iwamura 2007), and like management costs these costs are ongoing, but estimates of opportunity costs are generally based on agricultural value and are only weakly related to conservation effectiveness. In addition, many international donors are interested in funding existing protected areas, where measures of agricultural opportunity costs are not relevant. Moreover, because acquisition, transaction, and damage costs are one-off costs, they will be outweighed in the long term by the ongoing costs of management. Therefore, management costs are the most important cost type for international donors to consider in the initial stages of global prioritization.

In this paper we compare modeled country-level conservation management costs to widely used global indicators for civil society involvement in conservation, governance, and human rights. We hypothesize that countries with low predicted

management costs also tend to have lower levels of civil society involvement in conservation, less effective and stable governments, and less protection of human rights. Support of these hypotheses would suggest that the management cost estimates most often used in global conservation prioritization are simplistic and neglect important factors that impact project implementation and outcomes. Therefore, achieving long-term conservation success in countries with low predicted costs, and avoiding unintended negative impacts on people, may be more difficult or more expensive than current cost models predict.

3.3 Methods

3.3.1 Data: Conservation management cost

Our analysis adopted the most widely used approach for calculating the protected area management costs for each country, the Balmford-Moore equation (Balmford et al. 2003, Moore et al. 2004). This model has been criticized for inflating the predicted management costs of conservation in the more expensive countries, as the original data for developed countries included habitat restoration and other more intensive management actions (Arponen et al. 2010). However, it remains the primary approach for estimating national-level management costs and is the basis of most global cost-based conservation prioritization schemes published in the literature (Balmford et al. 2003, Moore et al. 2004, Bode et al. 2008, Wilson et al. 2011).

The Balmford-Moore equation states that the cost of managing land as protected areas is a non-linear function of the nation's gross national income (GNI)

scaled by its total area, its purchasing power parity (PPP), and the size of a protected area (PA):

$$\log_{10}(\text{annual cost, US\$ km}^{-1}) = 1.765 - 0.299*\log_{10}(\text{PA, km}^2) + 1.014*\log_{10}(\text{PPP}) + 0.531*\log_{10}(\text{GNI, US\$ km}^{-2}) - 0.771*\log_{10}(\text{PA, km}^2)*\log_{10}(\text{PPP})$$

For this analysis we used a standard reserve size of 100 km^2 for all countries to enable comparison of conservation costs for equal-sized protected areas across countries. While data on the extent of protected areas exist for most countries (UNEP and IUCN 2009), we used a standardized area for all countries because this method is better suited to our goal of comparing the standard cost metrics used in global prioritizations against several other national-level socio-political indicators. Data for GNI, PPP, and country land area were obtained from the United Nations Statistics Division (unstats.un.org) and are available in the supplementary material.

3.3.2. Data: Civil society involvement in conservation

The extent to which civil society is involved in conservation efforts is difficult to measure and quantify, particularly at the national level. To our knowledge, there are three datasets that provide unbiased, quantifiable, and comparable information about this issue for many countries globally. We used all of these datasets in an effort to capture as much information as possible regarding civil society involvement in conservation.

i. *Membership in BirdLife International partner organizations*: BirdLife International (BLI) is the world's largest global partnership of conservation

organizations, maintaining partnerships with local, independent, membership-based NGOs in over 100 countries on all inhabited continents. Data on citizen membership for BirdLife partner NGOs is available online for 86 of these countries (www.birdlife.org/worldwide/national/index.html). While BLI is a UK-based NGO, we detected no bias toward the existence of more BLI partnerships in former British colonies, and countries with BLI partners are widely distributed across all continents. To compare membership between countries, we standardized the data by dividing NGO membership by the country's total population (population data obtained from unstats.un.org). The resulting value is the proportion of a country's population that belongs to a leading local conservation NGO.

ii. *IUCN member organizations*: The International Union for the Conservation of Nature (IUCN) is the world's oldest and largest global environmental organization, with more than 1200 member organizations (200+ government and 900+ non-government) in 160 countries (www.iucn.org). The number of IUCN organizations per million people was one of many variables used to create the Environmental Sustainability Index (ESI) (Esty et al. 2005). We obtained values directly from the ESI (www.yale.edu/esi/c_variableprofiles.pdf).

iii. *Local Agenda 21 Initiatives*: Agenda 21 is a voluntary action plan of the UN regarding sustainable development, intended to motivate action at international, national, regional, and local levels

(http://www.un.org/esa/dsd/agenda21/). Local Agenda 21 initiatives are measures undertaken and overseen by local authorities to address problems of environmental sustainability, and represent the involvement of civil society in environmental governance. The number of Local Agenda 21 initiatives per million people was another variable calculated for the 2005 ESI (Esty et al. 2005), and we used these values in our analyses (www.yale.edu/esi/c_variableprofiles.pdf).

3.3.3 Data: Political stability, corruption, and government effectiveness

One of the most widely used systems for measuring quality of governance at the national level is the Worldwide Governance Indicators (WGI), constructed by the World Bank and based on consultations and surveys with citizens, experts, businesses, and international organizations (Kaufmann et al. 2010). We used three of the six "dimensions of governance" assessed by the WGI: Political Stability and Absence of Violence, Control of Corruption, and Government Effectiveness. All data and background information for each index are available online (info.worldbank.org/governance/wgi/sc_country.asp) and in the supplementary material.

3.3.4 Data: Human rights

The most comprehensive, national-level global dataset on protection of human rights is the Cingranelli-Richards Human Rights Dataset (CIRI) (Cingranelli and Richards 2010). The CIRI dataset contains standards-based, quantitative information

on government respect for a wide range of human rights in most countries. In our analyses we used the Empowerment Rights Index, an additive index constructed from seven individual indicators: Foreign Movement, Domestic Movement, Freedom of Speech, Freedom of Assembly and Association, Workers' Rights, Electoral Self-Determination, and Freedom of Religion. The index ranges from 0 (no government respect for these seven rights) to 14 (full government respect for these seven rights). Data are available online (ciri.binghamton.edu) and in the supplementary material.

For all datasets we used the most recent data available. Years of the data range from 2001 (Local Agenda 21 initiatives) to 2012 (membership in BLI partner organizations).

3.3.5 Statistical Analysis

We separately examined the relationships between national-level modeled protected area management costs and each socio-political variable: civil society involvement in conservation (NGO membership, IUCN Organizations, and Agenda 21 Initiatives), quality of governance (bureaucratic effectiveness, control of corruption, and political stability), and human rights (Empowerment Rights Index). We also investigated the relationships between each of the three measures of civil society involvement. Because none of the individual datasets satisfy the normality assumptions for parametric correlation, we used nonparametric Spearman rank correlations for all analyses.

Analyses were performed in the statistical packages JMP (SAS Institute Inc 2012) and R (R Development Core Team 2011).

3.4 Results

The modeled costs of managing a 100km^2 terrestrial protected area in each country varies between US$34 for Mongolia and US$1.7 million for Monaco, with a median value of US$4,260. Political stability is correlated with protected area management costs (N=184, Spearman ρ=0.5071, p<0.0001; Fig. 3-1): estimates for management costs in the ten most stable countries are 82 times higher than in the ten least stable.

We found positive correlations between each of the metrics for civil society involvement in conservation (Table 3-1), and between conservation management cost and each of these metrics (Table 3-2, Fig. 3-2). Together, these analyses suggest that populations are less involved in conservation efforts in countries with low modeled management costs.

We found positive correlations between predicted conservation cost and control of corruption (N=184, Spearman ρ=0.6401, p<0.0001; Fig. 3-3a): protected area management costs in the ten least corrupt countries are 41 times higher than in the 10 most corrupt countries. Governments are also less effective in low-cost countries (N=184, Spearman ρ=0.6729, p<0.0001; Fig. 3-3b): protected area management costs in the ten countries with the most effective governments are 56 times higher than in the ten with the least effective governments.

There is a positive correlation between conservation cost and protection of human rights (N=181, Spearman ρ=0.3720, p<0.0001; Fig. 3-4): countries with low protected area management costs generally have poorer human rights records, so that

the seven countries sharing the highest Empowerment Rights Index score are 6.3 times more expensive than the seven countries sharing the lowest score.

3.5 Discussion

This analysis investigates the broader implications of a commonly proposed approach for identifying 'cost-efficient' globally important areas for conservation investment. As we predicted, our analyses show that national-level estimates for conservation management cost are correlated with socio-economic and governance issues that can affect conservation cost and outcomes. Our results suggest that conservation investments in countries with low predicted costs could be prone to a suite of negative outcomes that increase the realized cost of conservation actions and make some projects less likely to succeed.

Our first result (Fig. 3-1) shows that political instability is higher in countries with low modeled conservation management costs. This instability is a recognized problem in conservation, where it is linked with breakdowns in local or national institutional support for projects, threats to project management and enforcement staff, and biodiversity loss through the impacts of militias and refugees (Dudley et al. 2002). It is also a prevalent problem, as 81% of violent conflicts between 1950 and 2000 took place completely or partially within biodiversity hotspots (Hanson et al. 2009).

Case studies have shown the impacts of political instability can be mitigated by support from the local population (Hamilton et al. 2000, Barrett et al. 2001), but our results also showed that civil society involvement is lower in these less stable

countries (Fig. 3-2; Table 3-2). Local capacity and involvement in conservation efforts is a complex social phenomenon that varies widely within countries as well as between them, and the three metrics we used to quantify this variable are only broad-scale approximations of local involvement at the country level. However, to our knowledge these are the only multi-country datasets that provide useful and quantifiable measures for this issue. Each index addresses a slightly different aspect of local involvement, and together they represent the conservation-related activities of local people and governments through both international NGOs (BLI partners) and multilateral agencies (IUCN organizations and UN Agenda 21 Initiatives). The significant correlations we found between the metrics (Table 3-1) indicate that they capture complementary features of local involvement that tend to vary together across countries globally. Our study does not address the reasons that people are less involved in some countries, or the consequences of this lower level of involvement. However, both anecdotal evidence and formal studies demonstrate that conservation efforts are more successful when local people are engaged in the process (Ostrom and Nagendra 2006). Thus, if conservation interventions are to succeed, external donors may need to spend more time and money developing relationships at the local level and gaining project support.

This lower involvement of civil society in countries with low predicted costs highlights another problem with using protected area management cost estimates as a metric for realized conservation costs, as volunteering and local fundraising are likely to be higher in countries with an engaged civil society (Halpern et al. 2006). Even

more importantly, externally funded projects in low-cost countries must rely heavily on local and national government agencies for implementation. This is worrying in light of our results (Fig. 3-3a), which indicate that governments in low-cost nations are more corrupt, and the results of earlier studies showing that conservation success is lower in corrupt countries (Smith et al. 2003, Wright et al. 2007). This issue might not affect estimates of direct working costs, as recent research suggests the relatively weak purchasing power in corrupt countries still makes conservation projects cost effective (Garnett et al. 2011). However, accounting for the quality of governance in addition to biodiversity and direct costs can change cost-effective investment priorities at a global scale (Eklund et al. 2011), and a number of case studies have shown the impacts of corruption often involve more than an increase in direct costs. For example, the misappropriation of conservation benefits or exposure to rent-seeking officials often results in loss of local support and project failure (Peh and Drori 2010, Waylen et al. 2010).

We found that countries with low predicted costs score poorly on bureaucratic effectiveness measures (Fig. 3-3b). This is a critical result, given that a wide range of conservation initiatives rely on effective bureaucratic systems for implementation: most protected areas are state-managed, many donor-funded projects work with and through local or national governments, and community based conservation relies on government support. The impacts of this problem likely extend beyond short-term project effectiveness, as the success of conservation initiatives often depends on changing institutional, economic and socio-ecological frameworks (Barrett et al.

2001). Indeed, many of conservation's negative impacts on people, from poorly implemented compensation or resettlement programs to the capture of ecotourism resources by local elites, are related to this issue (Thompson and Homewood 2002, McLean and Stræde 2003, West et al. 2006, Milgroom and Spierenburg 2008, Barua et al. 2013). Moreover, the literature shows that such negative interactions with the state are not always indirect, as there are a number of documented human rights abuses that arose from heavy-handed enforcement of conservation policy (Duffy 2010). This is why our final result (Fig. 3-4) – that low-cost countries also have the worst human rights records – is particularly troubling. The implications of this finding are obvious: relying on governments with poor human rights records to achieve action on the ground is more likely to negatively impact people.

Taken together, our results suggest that using country-level estimates of protected area management costs in global conservation prioritization, without accounting for other related factors, is problematic. Projects in apparently low-cost countries could be less likely to succeed, more expensive to implement than originally expected, and more likely to have negative impacts on local people. Some donors already implicitly recognize the importance of accounting for implementation factors when directing funds, by avoiding difficult countries or working where they have historically built long-term collaborations and already have local support (Miller et al. 2013). This may partly explain why the published fine-scale global prioritization schemes have had a relatively minor influence on conservation policy (Brockington and Scholfield 2010, Hickey and Pimm 2011). There is a real need, therefore, to

move beyond the simplistic assumption that there can be one globally relevant equation for estimating the long-term costs of successful conservation implementation and management, and to develop more nuanced and context-specific cost metrics.

Efforts to include broader socio-political factors in cost estimates must, however, be undertaken with caution for two major reasons. First, recent studies at sub-national scales that accounted for some cost types and implementation factors, such as opportunity costs and local support, reveal complex and dynamic relationships between costs, biodiversity values and favorable conditions for conservation (Adams et al. 2010, Knight et al. 2011). The non-biological factors that influence conservation opportunities and outcomes, and the relative importance of these factors over different temporal and spatial scales, are highly variable but are known to be essential for achieving both biodiversity conservation and human wellbeing (Polasky 2008, Klein et al. 2008, Perhans et al. 2008). Developing reliable and broadly applicable metrics for realized costs, and understanding the broader factors that influence conservation opportunity and outcomes but are not captured in cost estimates, will require an intensive research effort to better understand the nature of these relationships both within and between countries.

Second, caution must be used when generating global cost metrics that include data on potential negative impacts on people. Traditionally, developing such global metrics has involved converting different factors into a common currency, such as predicting lost revenues to local people by calculating opportunity costs (Adams et al.

2010), or considering these negative impacts independently and then investigating trade-offs or returns on investment (Cameron et al. 2008). This is a reasonable method when accounting for factors such as local fundraising, volunteering and the direct impacts of political instability, corruption and bureaucratic quality (O'Connor et al. 2003, McBride et al. 2007, Eklund et al. 2011). However, measures of human welfare or human rights cannot be considered simply as factors to be traded off against biodiversity benefits. Instead, there is a need to gather data to better understand the economic costs of avoiding negative impacts. Current prioritization approaches fail to capture the strategies used by conservation organizations to reduce the risk of negatively impacting people, such as changing their approach in high-risk countries or building long-term relationships with existing local partners. Many organizations do this in an *ad hoc* manner, and would benefit from adopting a more systematic approach. Producing a relevant cost metric for such systematic analyses will involve capturing types of information that are rarely used in conservation planning. The critical next step is for conservation scientists to engage with practitioners in order to produce more robust prioritization schemes that are based on explicitly defined goals and appropriate measures of conservation costs, opportunities and threats (Joseph et al. 2009, Game et al. 2013).

3.6 Conclusions

We have long recognized there is no one global measure of conservation value, as different organizations favor different aspects of biodiversity (Brooks et al. 2006). However, there is an implicit assumption in the literature that there can be a

single global measure of conservation costs and that estimates of direct conservation cost based on macro-economic differences automatically make working in some countries better value for money. Our work reveals this assumption to be simplistic, because these basic economic indicators are linked with factors that make implementation more difficult and negative impacts on people more likely. Overcoming these challenges will add to the cost of implementation in predicted low-cost countries. Conservation donors and organizations are well aware of the difficulties and tailor their projects accordingly (Game et al. 2013), but this makes any estimate of their projects' costs just as organization-specific as their measures of conservation value. Calculating the total, realized cost of conservation efforts remains vital for decision making, and the need to produce these data adds to the list of compelling reasons for conservation researchers to collaborate closely with practitioners (Smith et al. 2009).

3.7 Tables

Table 3-1.
Results of Spearman rank correlation analyses comparing each metric for civil society involvement in conservation.

Variable comparison	***N***	**Spearman ρ**	**p-value**
NGO Membership & IUCN Organizations	80	0.5524	<0.0001
IUCN Organizations & Agenda 21 Initiatives	106	0.6338	<0.0001
NGO Membership & Agenda 21 Initiatives	62	0.7666	<0.0001

Table 3-2.
Results of Spearman rank correlation analyses comparing predicted conservation cost (US$ 100km^{-2} year^{-1}) with each metric for civil society involvement in conservation.

Civil society involvement metric	***N***	**Spearman ρ**	***p*-value**
NGO Membership	89	0.5728	<0.0001
IUCN Organizations	140	0.3369	<0.0001
Agenda 21 Initiatives	104	0.4474	<0.0001

3.8 Figures

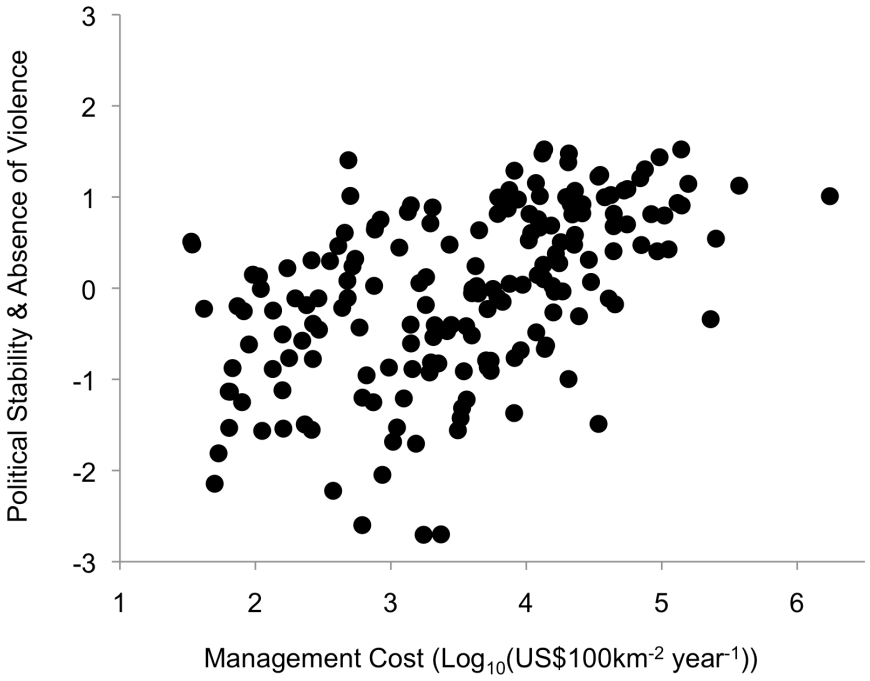


Figure 3-1.

Plot of predicted conservation management cost (log_{10} transformed) vs. index for Political Stability and Absence of Violence (*N*=184).

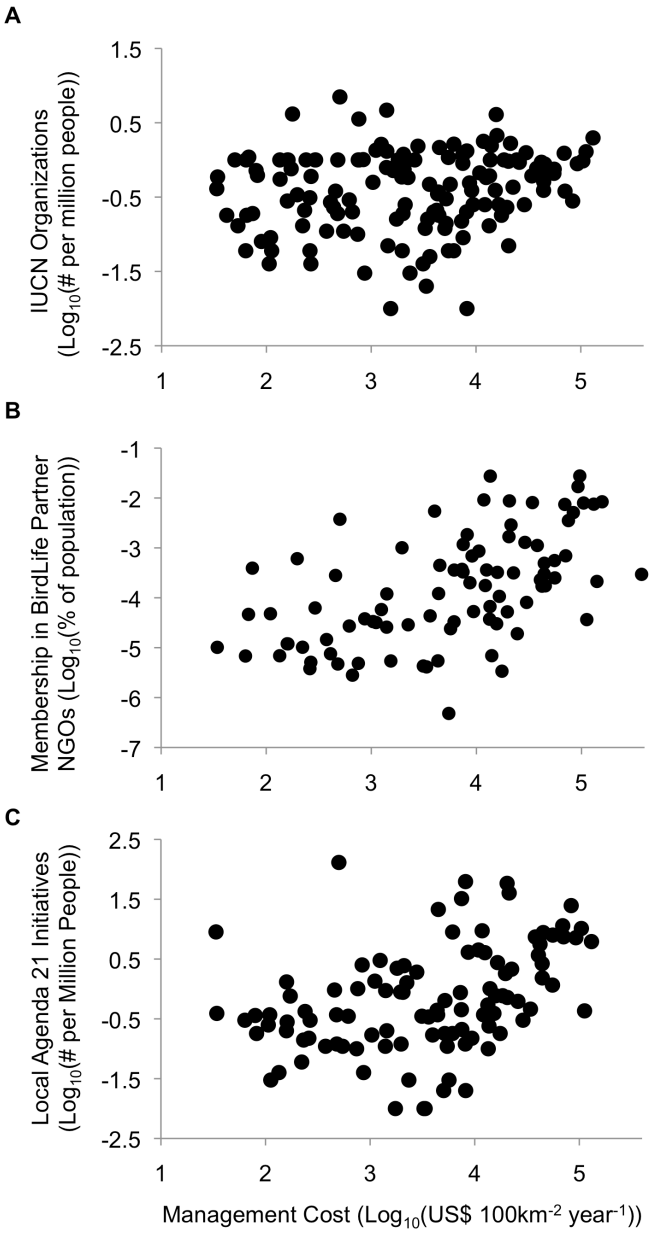


Figure 3-2.

Plots of predicted conservation management cost vs. three metrics of civil society engagement in conservation action (all values $\log_{10}$ transformed): (a) Proportion of a country's population belonging to BirdLife International partner NGO (N=89); (b) IUCN member organizations per million people (N=140); (c) Local Agenda 21 initiatives per million people (N=104).

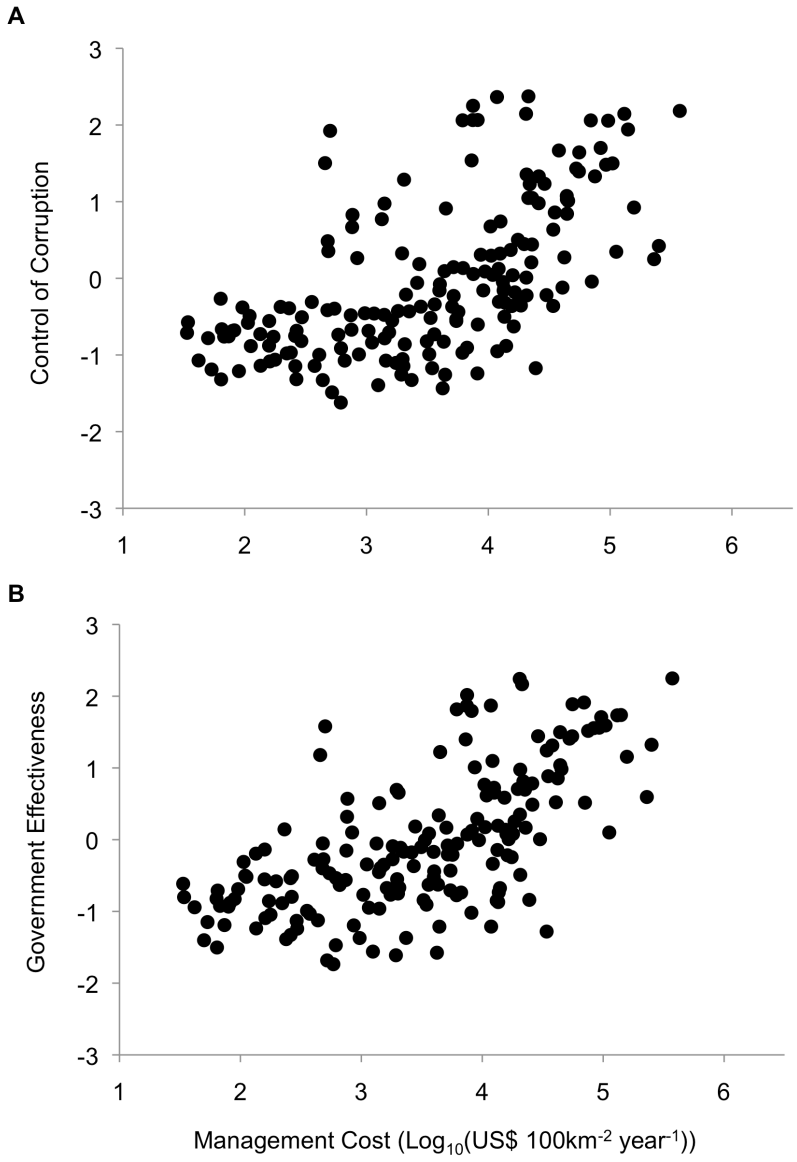


Figure 3-3.

Plots of predicted conservation management cost (log_{10} transformed) and indices for: (*a*) Control of Corruption (*N*=184); (*b*) Government Effectiveness (*N*=184).

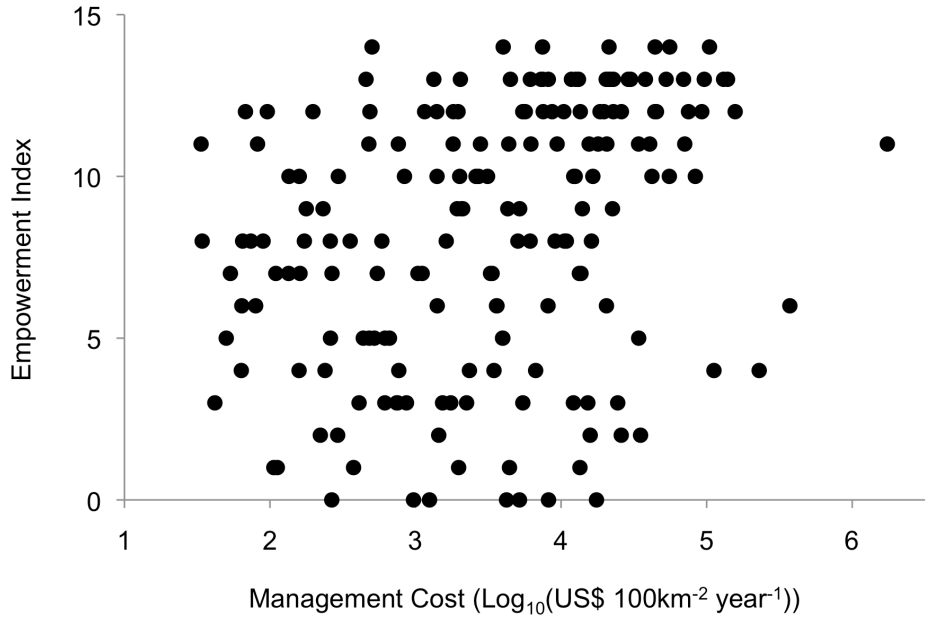


Figure 3-4.

Plot of predicted conservation management cost (log_{10} transformed) and Empowerment Rights Index (*N*=181).

Conclusion

My dissertation advances the fields of island ecology, island conservation, and conservation prioritization by: 1) improving our understanding of the biotic and abiotic drivers of island extinctions globally; 2) integrating quantitative estimates of eradication benefits and costs in a transparent global prioritization model; and 3) demonstrating the importance of considering socio-political factors in conservation planning to avoid unintended negative consequences for biodiversity and people.

Eradicating invasive cats, rats, pigs, mustelids, and mongooses should be a top priority for preventing extinctions on islands worldwide. Rat, cat, and pig eradication techniques have advanced greatly in recent decades (Howald et al. 2007, Parkes et al. 2010, Campbell et al. 2011) while the removal of mustelids and mongooses has proven more challenging (King et al. 2009, Barun et al. 2011b). Global island conservation efforts should include focused research on improving control and eradication methods for all these species, particularly on large and inhabited islands that pose unique technical and social challenges to eradication efforts (Oppel et al. 2011). In addition, other types of invasive mammals did not appear in our model (e.g. mice, rabbits, and goats) and thus may not be strong global drivers of island extinctions; nevertheless, these animals are widespread on islands globally and are known to cause substantial damage to island species and ecosystems in some situations. Regional-scale studies should more thoroughly investigate the threats these additional species pose to particular island taxa or regions, and improved eradication technologies should be developed to mitigate these threats as well.

The estimates of conservation benefits, eradication costs, and overall island priorities I presented should be considered a baseline from which to further investigate the biological, technical, and socio-political outcomes of eradication on high-priority islands. While the ability to precisely quantify the expected benefit from a given conservation action is rare and is highly valuable for prioritizing efforts, the benefit values we used here were generated by a global model with its own set of assumptions and simplifications. In reality, the outcomes of invasive mammal eradication for threatened species and for broader island ecosystems are island-specific and are difficult to predict even for individual, well-studied islands (Zavaleta et al. 2001, Rayner et al. 2007). In addition, we were unable to assess many components of eradication feasibility and cost. From a technical standpoint, the islands in our dataset may be more or less challenging places to conduct eradications depending on the suite of invasive species present (possibly including others that we did not consider in this analysis), island isolation, and other factors.

The socio-political context on an island strongly affects project costs and likelihood of success as well. National and regional governments vary widely in their required permitting processes, bureaucratic efficiency, and capacity for approving or facilitating conservation actions. Furthermore, every island has a unique combination of stakeholders that may include island residents, landowners, local or regional committees or governments, environmental organizations, or animal rights activists, among others. For eradications, and for conservation projects more generally, it is important to develop nuanced and context-specific cost metrics that account for the

socio-political environment. Producing a relevant cost metric for such systematic analyses will involve capturing types of information that are rarely used in conservation planning. The critical next step is for conservation scientists to engage with practitioners in order to produce more robust prioritization schemes that are based on explicitly defined goals and appropriate measures of conservation costs, opportunities and threats (Joseph et al. 2009, Game et al. 2013).

Appendix I

Supplementary Data Table 1. Prioritized island portfolios for invasive mammal eradications to benefit single-island endemic species. Sensitive species-island distribution records have been removed from the table.

Supplementary Data Table 2. Prioritized island portfolios for invasive mammal eradications to benefit non-endemic species. Sensitive species-island distribution records have been removed from the table.

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